ON THE EYE AND THE SO-CALLED PRE-ORBITAL LIGHT ORGAN OF THE ISOSPON-DYLOUS DEEP-SEA FISH *BATHYLACO NIGRICANS* GOODE & BEAN, 1896

By OLE MUNK
The Institute of Comparative Anatomy, University of Copenhagen
and
The Ophthalmic Pathology Laboratory, Rigshospitalet, Copenhagen

INTRODUCTION

This paper is meant as a supplement to the systematic study of the genus *Bathylaco* made by NIELSEN & LARSEN (1968). In the course of this study it proved desirable to check the nature of the so-called preorbital light organ of *Bathylaco*. PARR (1948) described this organ as a comma-shaped preorbital luminous organ (Fig. 1) showing a fairly close resemblance to that of many stomiatoids and myctophids, rather than the similarly located small circular light organs which are said to be present in some alepocephalids (i. e., the alepocephalids and the searsids, cf. PARR 1951).

There has been some uncertainty in the literature concerning the systematic position of Bathylaconidae within the group Isospondyli (cf. PARR 1948 and BIGELOW 1964). The present investigation has revealed certain ocular structures in *B. nigricans* which probably deserve some consideration in a discussion of the systematic position of the family. The known vertical distribution of *B. nigricans* is c. 450-2000 m (cf. NIELSEN & LARSEN 1968).

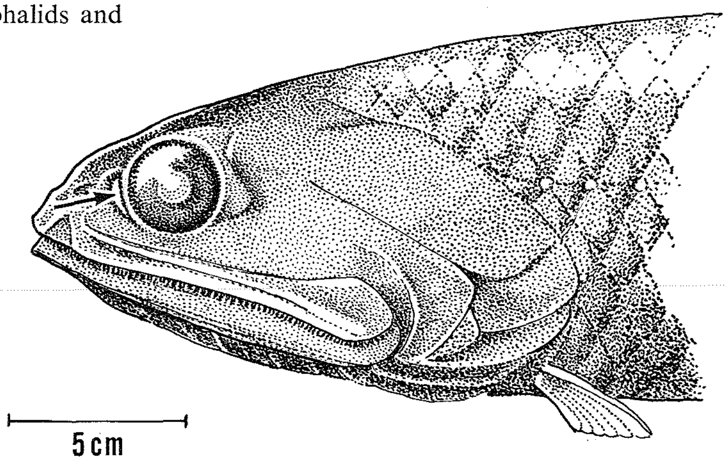

Fig. 1. Lateral view of head of *Dana* specimen of *Bathylaco nigricans*. Arrow points at so-called preorbital light organ. Redrawn from PARR (1948).

MATERIAL AND METHODS

Two formalin-fixed specimens of *B. nigricans* were used for histological examination:

Specimen 1. Standard length: 214 mm. *Dana* St. 1208 (4), 1922. The right eye was enucleated, embedded in celloidin, and cut into 30 μ serial horizontal sections. The right so-called preorbital light organ was removed, embedded in tissuemat, and cut into 8 μ serial transverse sections.

Specimen 2. Standard length: 220 mm. *Galathea* St. 299, 1951. The right eye was removed together with the so-called preorbital light organ, the dorsal part of the eyeball was cut off, and the lens removed; the specimen was decalcified, embedded in tissuemat, and cut into 8 μ serial horizontal sections corresponding to the pupil region of the eye.

The left eye was enucleated, decalcified, and embedded in tissuemat. 8 μ serial horizontal sections were made of the ventral part of the eyeball, 15 μ serial horizontal sections of the pupil region. The left so-called preorbital light organ was embedded separately in tissuemat and cut into 8 μ serial transverse sections.

Fig. 2 was drawn after a 234 mm (standard length) specimen of *B. nigricans* from R/V *A. Bruun* St. 186, 1963 (21°30′ N-64°08′ E).

For comparison, the insertions of the eye muscles were examined on an enucleated eyeball of a formalin-fixed 84 mm (standard length) specimen of the searsid *Platytroctegen mirus* Lloyd, 1909 from *Galathea* St. 299, 1951. Serial horizontal sections of the left eye of a 78 mm (standard length) previously examined specimen of this species were also used (Munk 1966a).

Furthermore, a 235 mm (standard length) formalin-fixed herring (*Clupea harengus* Linnaeus, 1758) was used for examination of the palpebral folds and the secondary skin-fold located rostral to each eye (Fig. 4). The rostral vertical lid and the secondary skin-fold on the right side of the head were removed as a whole, decalcified, embedded in tissuemat, and cut into 8 μ serial horizontal sections; sections through the middle of the folds were mounted and stained. The insertions of the eye muscles were examined on the enucleated left eyeball (Fig. 5).

The celloidin-sections were stained with Ehrlich's hematoxylin and eosin (H-E), the tissuemat-sections with Ehrlich's hematoxylin – eosin – orange G (some of these sections were depigmented before staining), tetrachrome (Alcian blue – Chlorantine fast red – orange G – Weigert's iron hematoxylin), PAS, Alcian blue (1 per cent AB in 1 per cent acetic acid), AB-PAS, and 1 per cent aqueous solution of toluidin blue of pH 5. Some sections were digested 1 hour at 38°C. in 1 per cent malt diastase in distilled water before they were stained with PAS; undigested control sections were left in distilled water at 38°C. for 1 hour and stained together with the digested sections.

RESULTS

A. GROSS ANATOMY

Bathylaco nigricans is specialized in rostral binocular vision, as is apparent from the shallow horizontal sighting grooves in front of the eyes and the marked rostral asymmetry of the eyeball (Fig. 2 and Fig. 3B). The pupil is horizontally oval, with a large rostral aphakic aperture. The rostral part of the palpebral fold is fairly broad and on intact specimens is seen as a peculiar whitish crescent-shaped structure; this broad portion of the palpebral fold is delimited rostrally by a skin-fold which was recognized by means of a probe. This delimiting secondary skin-fold has a very short extension in the rostro-caudal direction. A deeply located dark pigment can be seen through the whitish tissue of the proximal portion of the rostral part of the palpebral fold. The structure interpreted as a preorbital photophore by Parr (1948) is probably the narrow light comma-shaped distal part of this fold (cf. Figs. 1 and 2).

During enucleation of the eyeball the sclera was found to be very rigid, which is not normally the case in teleosts. Some peculiarities were noted on the enucleated eyeball (Fig. 3). Only five muscles are seen to insert into the eyeball. Four of these (the superior and inferior oblique, the superior and inferior rectus) are easily identified because of their typical locations and insertions. The fifth muscle, which may be called the medial eye muscle, inserts approximately into the centre of the medial wall of the eye, apparently into a peculiar scleral protuberance.

In the right eye of the *Galathea* specimen, from which the dorsal part of the eyeball was cut off and the lens removed, a dark line was seen on the retina. The line starts at the temporal equator-region of the retina, slightly dorsal to the horizontal meridian, forms a slightly rostrally convex arch across the ventral fundus, and ends at the ora terminalis retinae, somewhat rostral to the medio-ventral part of the eye. Slightly lateral to the temporal end of the said line a dark point was seen on the retina.

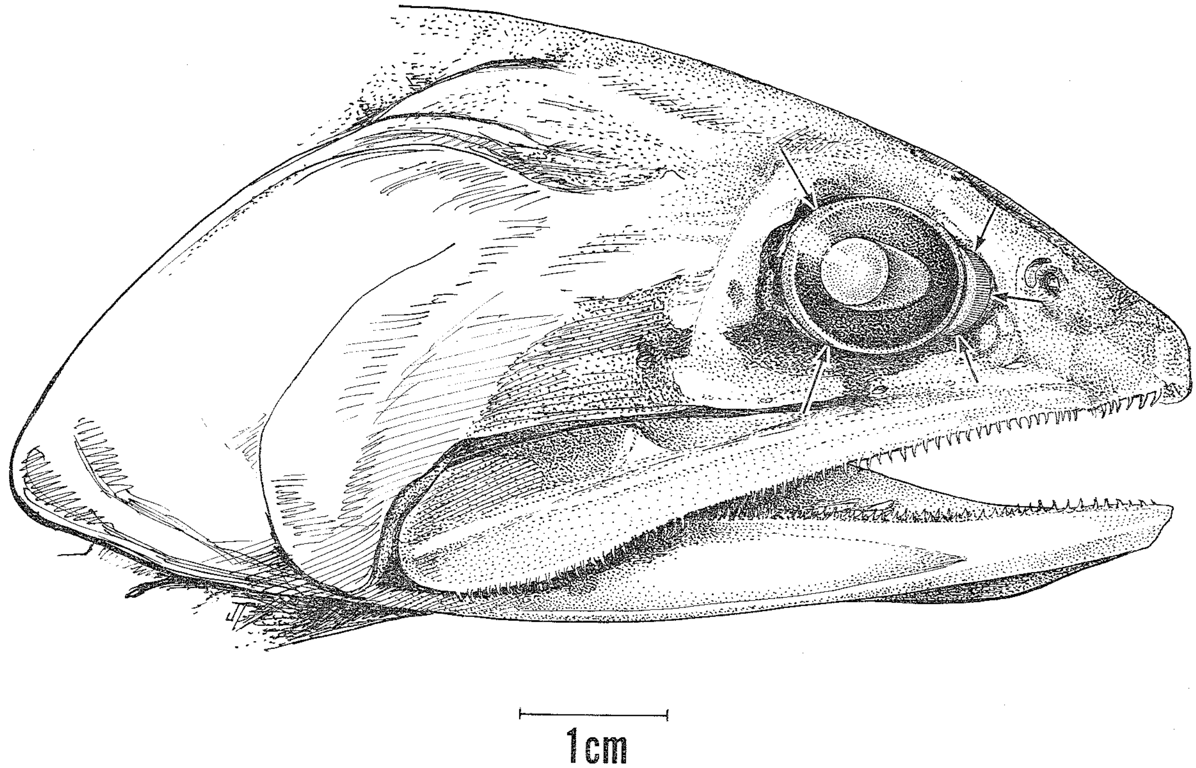

Fig. 2. Lateral view of head of *Bathylaco nigricans,* 234 mm in standard length. Two left arrows point at margin of palpebral fold. Three right arrows point at margin of secondary skin-fold delimiting whitish portion of palpebral fold rostrally; the extension of the secondary skin-fold in dorso-ventral direction indicated by upper and lower arrows.

B. HISTOLOGY

1. So-called Preorbital Light Organ

As mentioned above, the preorbital light organ of *B. nigricans* described by PARR (1948) is probably the distal part of the fairly broad rostral portion of the palpebral fold. There is, however, no histological evidence of luminous tissue in the rostral portion of the palpebral fold (Pl. XI, Fig. 1). It consists of a peculiarly modified connective tissue with very few cells and irregularly distributed holes of varying sizes. The tissue consists of a fine network of connective tissue fibrils which show a rather heavy staining with PAS and Alcian blue; they do not

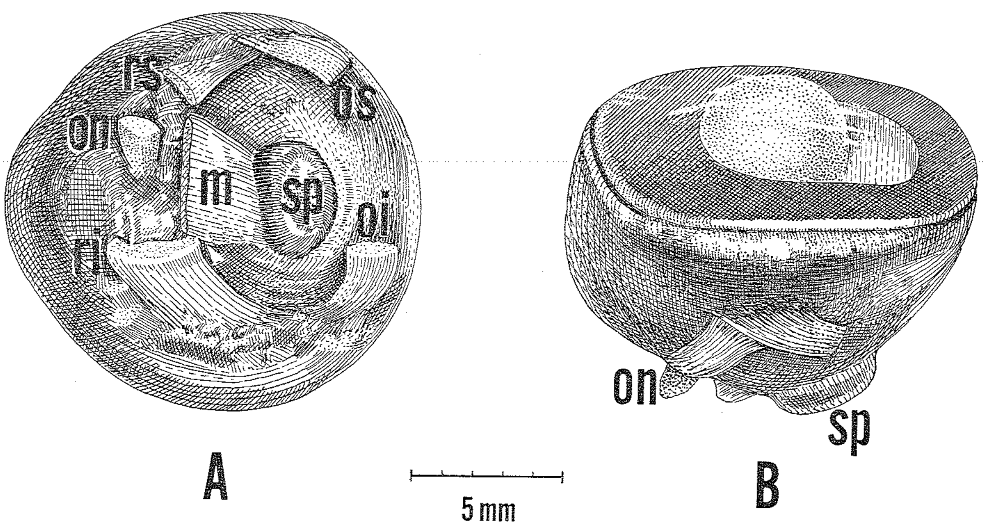

Fig. 3. Medial (A) and dorso-lateral view (B) of enucleated left eyeball of *Galathea* specimen of *Bathylaco nigricans.* Horizontal diameter of eyeball 13.5 mm. Lettering: m: medial eye muscle; oi: inferior oblique muscle; on: optic nerve; os: superior oblique muscle; ri: inferior rectus muscle; rs: superior rectus muscle; sp: scleral protuberance.

stain metachromatically with toluidin blue. Mast cells are not present. In the herring the same type of tissue is found in the rostral vertical lid and in the superficial part of the secondary skin-fold rostral to the eye. In the herring there is apparently a gradual transition from an ordinary connective tissue with typical collagenous fibres to the loose network of fine fibrils, especially in the secondary skin-fold.

In *Bathylaco nigricans* the proximal part of the palpebral fold is pigmented. This is the deeply located pigment which can be seen on intact specimens. The epithelium on the fold has been completely lost, but the PAS-positive basement membrane is present as a continuous covering on the surface. Part of the inside of the simple secondary skin-fold rostral to the palpebral fold is still covered by a pigmented epithelium.

2. The Eye

The sclera shows some peculiarities. The scleral protuberance (Pl. XI, Fig. 3) is a bulge formed by the thickened marginal part of the hyaline scleral cartilage in the medial wall of the eyeball rostral to the fibrous portion of the sclera around the optic nerve. In the *Dana* specimen the scleral cartilage attains its maximum thickness, c. 925 µ, in the scleral protuberance. The medial eye muscle inserts into the caudal part of the protuberance. The medial fibrous part of the sclera continues as a fairly thick connective tissue coat on the outside of the scleral cartilage; it becomes very thin on the lateral part of the cartilage (Pl. XI, Fig. 2). A similar condition has been found in some other teleosts by LANGHANS (1865: 248).

In the *Dana* specimen of *B. nigricans* cellular bone is present laterally in the sclera in the rostral and temporal parts of the eye. The two scleral bones or ossicles of the teleostean eye are usually located on the outside of the scleral cartilage, one rostrally, the other temporally, or they may replace the scleral cartilage in these regions (LANGHANS 1865: 254; ROCHON-DUVIGNEAUD 1943: 257-259). However, in the *Dana* specimen of *B. nigricans* the scleral ossicle is a perichondral bone which forms a continuous coat on the lateral part of the scleral cartilage, i. e., it covers the inside, the margin, and the outside of the cartilage (Pl. XI, Fig. 2). The temporal scleral bone has the larger extension, both in the medio-lateral and the dorso-ventral directions. Laterally, the parts of the cartilage which are in contact with the scleral bone show a fairly heavy staining of the interstitial substance with hematoxylin. This hematoxylin-stained zone is perhaps calcified cartilage. According to LANGHANS (1865: 258), calcification of the scleral cartilage in teleosts is rare.

In the *Galathea* specimen the scleral bone is absent rostrally. Temporally there are only two thin bony plates on the scleral cartilage in the equator-region, one located on the inside of the cartilage, the other on its outside, i.e., the lateral margin of the scleral cup is formed by cartilage. According to BERGER (1883: 128-129), the temporal scleral bone is ontogenetically the first to appear.

A *m. sphincter pupillae* is present in the pupillary region of the iris. No dilatator muscle was seen.

A *choroid gland* is present. The choroid gland is normally horseshoe-shaped, with one limb on either side of the optic nerve and choroid fissure. In *B. nigricans,* however, the two limbs are separated, one located rostral to the optic nerve, the other temporal to the optic nerve. This is also the case in *Platytroctegen mirus.*

The Retina. The black line seen by dissection of the right eye of the *Galathea* specimen of *B. nigricans* was identified with the linear optic papilla (Pl. XII, Fig. 2) and the choroid fissure, the small dark point with a temporal fovea of convexiclivate type (Pl. XII, Fig. 1). The medial end of the linear optic papilla is located near the temporal fovea, slightly dorsal to the horizontal meridian. From here it can be followed across the ventral fundus-retina to the very short choroid fissure located in the peripheral retina somewhat rostral to the medio-ventral part of the eye. A nerve (n. accommodatorius) and one or two blood vessels enter the interior of the eye through the choroid fissure and run in a temporal and slightly dorsal direction along the inside of the iris to the *m. retractor lentis.*

There are some obvious artefacts in the retina of both specimens examined. In the best preserved regions of the retina three superposed layers of equally long rods are clearly seen (Pl. XII, Fig. 2). No cones were observed. Short pigmented processes from the retinal pigment epithelium are present in the temporal part of the retina, especially in the fovea region (Pl. XII, Fig. 1). As far as the evidence goes, there seems to be only a single layer of rather long thread-like rods in the centre of the temporal fovea. Hyaloid vessels are absent.

In the outermost part of the inner nuclear layer a single layer of peculiar cells with a marked PAS-positive cytoplasm is present (Pl. XII). These cells have rather crude processes which form a horizontal network between the other cells located in the outermost part of the inner nuclear layer, and their nuclei are flattened, with the longest diameter parallel to the surface of the retina. These peculiar cells are probably horizontal cells. The PAS-positive content of their cytoplasm is obviously not glycogen, because digestion of the sections with diastase before staining does not diminish or abolish the PAS-reaction. It is not stained with Alcian blue, nor does it stain metachromatically with toluidin blue.

DISCUSSION

1. Palpebral Fold and Medial Eye Muscle

It can be stated with certainty that the rostral part of the palpebral fold in *B. nigricans* does not contain luminous tissue. Comparison with the herring, in which the palpebral fold has been modified into so-called vertical lids covering a considerable part of the cornea (Fig. 4, cf. also HARMAN 1900, pl. 1, fig. 2, and HEIN 1913, fig. 24: 266), has shown that the same peculiar type of connective tissue is present in the palpebral folds of both species. A similar tissue is undoubtedly present in the vertical lids of *Clupea pallasii,* which were seen to be composed of parallel fibres when viewed under polarized light (STEWART 1962). A secondary skin-fold rostral to the eye is found in a number of teleosts (HEIN 1913: 274 et seq.). The specially modified rostral portion of the palpebral fold and the secondary skin-fold in *B. nigricans* show a close resemblance to those of the salmonids (HARMAN 1900: 7; HEIN 1913: 275-276 and fig. 27: 268; WALLS 1942: 384 and fig. 132a: 383). According to HARMAN (l.c.), the modified rostral portion of the palpebral fold, which he calls pseudo-membrana nictitans, in the salmon is constituted by muco-areolar tissue.

The functional significance of the modified connective tissue in the palpebral folds of teleosts is unknown (cf. HARMAN 1900: 8-9, and WALLS 1942: 384). STEWART (1962) has suggested that the vertical lids of *Clupea pallasii* may function as a lens or may make it possible for the fish to detect polarized light, because he found that the tissue of the vertical lids is birefringent and that the amount of light absorbed varies with the plane of polarization. In *B. nigricans* it is hardly possible for the tissue in the rostral portion of the palpebral fold to have any optical function because of the location of the fold (Fig. 2).

It may be mentioned that in systematic literature the whitish structures located within or on the eyes

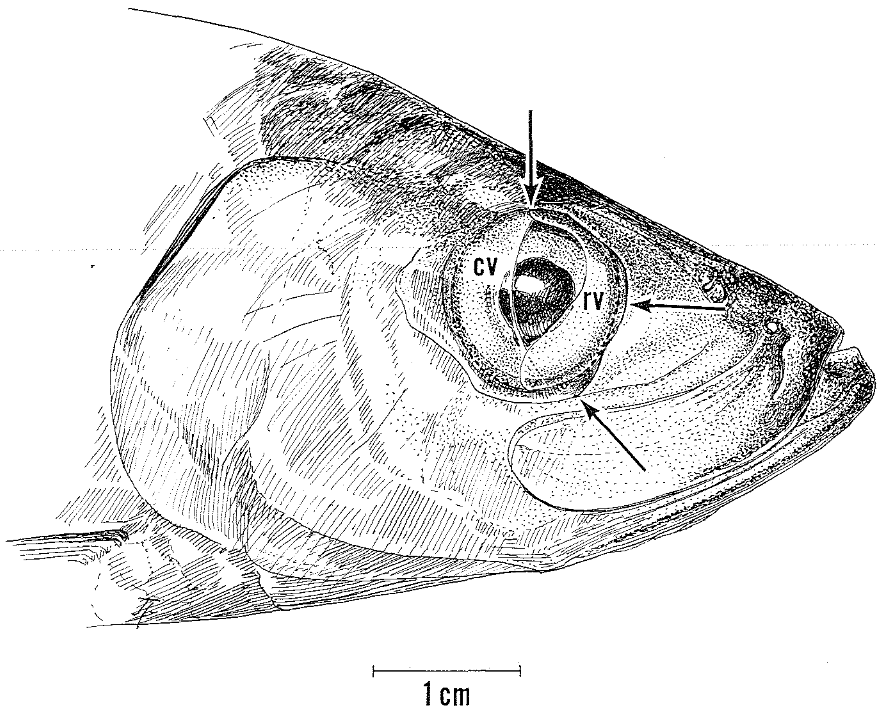

Fig. 4. Lateral view of head of herring, 235 mm in standard length. Three arrows point at margin of secondary skin-fold located rostral to eye, extension of fold in dorso-ventral direction being indicated by upper and lower arrows. Lettering: cv: caudal vertical lid; rv: rostral vertical lid.

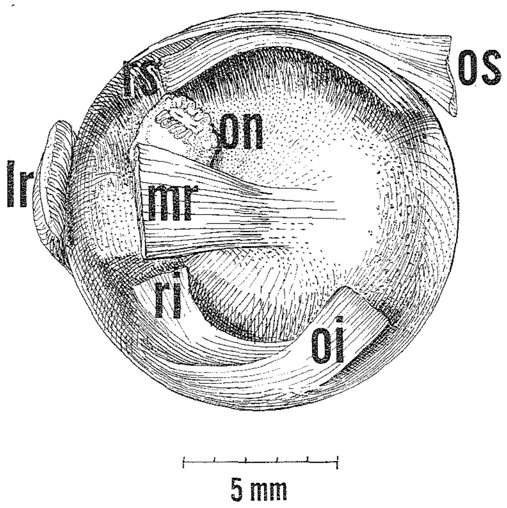

Fig. 5. Medial view of enucleated left eyeball of herring, 235 mm in standard length. Horizontal diameter of eyeball 12.5 mm. Lettering: lr: lateral rectus muscle; mr: medial rectus muscle; oi: inferior oblique muscle; on: optic nerve; os: superior oblique muscle; ri: inferior rectus muscle; rs: superior rectus muscle.

of various opisthoproctid deep-sea fishes have erroneously been described as orbital photophores. Histological examination of these structures has proved, however, that they are either retinal diverticula with unpigmented windows or modified parts of the sclera and cornea which may perhaps function as lenses (cf. PEARCY *et al.* 1965, MUNK in BERTELSEN *et al.* 1965, and MUNK 1966a, also for references). Another intraocular structure which might be considered a photophore is the annular ligament located in the angle of the anterior chamber. On intact specimens the annular ligament is in some cases seen as a whitish crescent-shaped structure on the iris, e.g., in *Nansenia groenlandica* (Reinhardt, 1839) and *Bathylagus stilbius* (Gilbert, 1890) (MUNK 1966a: 26 and 27). Dr. D. M. COHEN, of the Ichthyological Laboratory, U.S. National Museum, Washington, D.C., has informed me in a private communication that this whitish structure on the iris of *Bathylagus stilbius* appears when specimens are fixed.

The innervation of the medial eye muscle in *Bathylaco nigricans* is unfortunately unknown, but it is probably the medial rectus muscle, because this muscle according to HARMAN (1900: 30) inserts into the posterior pole of the eyeball slightly rostral to the optic nerve in *Argentina silus* and in clupeids (*Clupea harengus, C. sprattus, Alosa alosa*). Fig. 5 shows the insertion of the medial rectus muscle in the herring. Furthermore, the medial rectus muscle was in the same way seen to insert into the posterior pole of the eyeball both on the enucleated eyeball of the 84 mm specimen of *Platytroctegen mirus* and on the sections of the eye of the 78 mm specimen of the same species.

2. The Eye

It is probably a fair statement that the eyes of deep-sea fishes show greater variation as regards both gross anatomy and retinal structure than the eyes of all other vertebrates taken as a whole (cf. BRAUER 1908; PEARCY *et al.* 1965; MUNK 1966 a and b). As stated by BRAUER (1908), the development of the eyes of deep-sea fishes is independent of their systematic position. There is a very considerable variation in ocular anatomy in the isospondylous or clupeiform deep-sea fishes with normal eyes, most of which have pure-rod retinae. It may, for example, be mentioned that all species of opisthoproctids as defined by COHEN (1964) have tubular eyes except for the peculiar "four-eyed" *Bathylychnops exilis* Cohen, 1958 (PEARCY *et al.* 1965); several layers of rods are found in *Bathylychnops exilis* and in the main retina of *Winteria telescopa,* but not in *Opisthoproctus grimaldii* and *Rhynchohyalus natalensis* (PEARCY *et al.* 1965, MUNK 1966a). The omosudid *Omosudis lowei* has an almost pure-cone retina (MUNK 1965).

Eyes specialized in rostral binocular vision like those of *Bathylaco nigricans,* i.e., with a large rostral aphakic aperture and temporal areae or foveae, are found in several species of isospondylous deep-sea fishes, viz. the argentinid *Nansenia groenlandica* (Reinhardt, 1839) (cf. MUNK 1966a: 26), the bathylagids *Bathylagus stilbius* (Gilbert, 1890) (cf. MUNK 1966a: 27 and 50; classified as mesopelagic by CLARKE 1966), *B. pacificus* Gilbert, 1890 (cf. MUNK 1966a: 26-27), *B. benedicti* Goode & Bean, 1896 (probably a synonym of *B. euryops* Goode & Bean, 1896 according to COHEN 1964: 42-45; cf. VILTER 1954), the searsids *Platytroctes procerus* Brauer, 1906 (= *P. apus* Günther, 1878 according to PARR 1960; cf. BRAUER 1908: 192), and *Platytroctegen mirus* Lloyd, 1909 (cf. MUNK 1966a: 27-28). BRAUER (1908: 190) has furthermore described a temporal fovea in a species which he calls *Bathytroctes rostratus* Günther, 1878 (Fig. 6); as stated by MUNK (1966a: 27), it is not clear whether BRAUER's specimens belong to the alepocephalid species *Bathytroctes rostratus* or the searsid *Searsia koefoedi* Parr, 1937. All of these species have pure-rod retinae. *Nansenia groenlandica* and *Bathylagus stilbius* have an area temporalis retinae, small specimens of *Ba-*

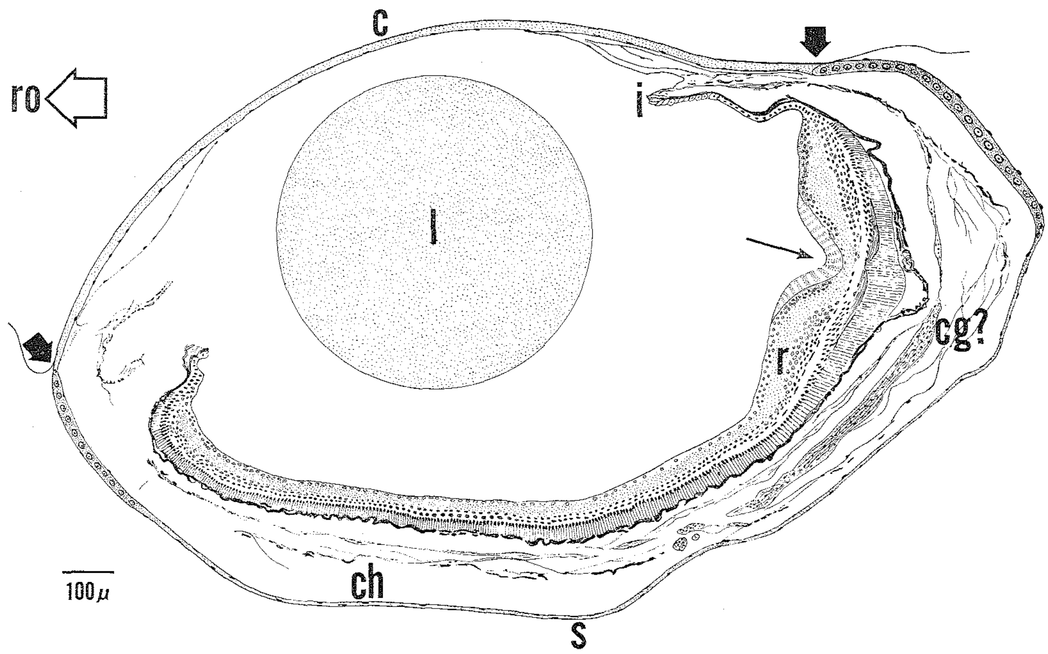

Fig. 6. Horizontal section of eye of alepocephalid or searsid deep-sea fish with convexiclivate temporal fovea (thin arrow). Thick arrows point at limbus corneae. Redrawn from BRAUER (1908). Lettering: c: cornea; cg?: choroid gland?; ch: choroid; i: iris; l: lens; r: retina; ro: rostrad; s: sclera.

thylagus benedicti and *B. pacificus* an area temporalis with a very shallow foveal pit. A fairly deep temporal fovea of convexiclivate type (WALLS 1937) is present in the two species examined by BRAUER and in *Platytroctegen mirus*. The species which BRAUER calls *Bathytroctes rostratus* probably has a choroid gland, although it is not mentioned by him (cf. Fig. 6); all six eye muscles are present and show a normal location (BRAUER 1908: 190).

It is difficult to assign a definite phylogenetic value to any particular ocular structure in deep-sea fishes; on the one hand great variation in ocular anatomy may be found within one family (e.g., the opisthoproctids), on the other essentially similar eyes may be present in species belonging to different families (e.g., the tubular eyes of *Argyropelecus* and *Opisthoproctus*). It may be pointed out, however, that the eye of *Bathylaco nigricans* has several structural features in common with that of the searsid *Platytroctegen mirus* (cf. MUNK 1966a: 27-28), viz., a convexiclivate temporal fovea, the location of the linear optic papilla and the short choroid fissure, and a choroid gland consisting of two separate limbs. Except for *Bathylaco nigricans* and *Platytroctegen mirus*, a pure-rod retina with a temporal convexiclivate fovea is known only in two species of deep-sea fishes described by BRAUER (1908), one of which is a searsid, the other either a searsid or an alepocephalid (see above). The searsids and the alepocephalids are closely related (PARR 1951). In the author's opinion a similarity in ocular anatomy which comprises several structural featurse of the nature mentioned above carries some weight. On the sole basis of ocular anatomy the bathylaconids may consequently be supposed to be rather closely related to the alepocephalids and searsids.

SUMMARY

The gross anatomy and the histological structure of the so-called preorbital light organ and the eye of *Bathylaco nigricans* are described. The structure described as the preorbital light organ in literature is actually the rostral part of the palpebral fold containing modified connective tissue which appears whitish on fixed specimens. The eye of *B. nigricans* has several structural features in common with that of the searsid *Platytroctegen mirus*, viz., a convexiclivate temporal fovea, a peculiar linear optic papilla and short choroid fissure, and a choroid gland consisting of two separate limbs. The ocular anatomy of *B. nigricans* suggests that the bathylaconids may be rather closely related to the alepocephalids and searsids.

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PLATES

Plate XI

Bathylaco nigricans

Fig. 1. Horizontal section through middle of rostral part of palpebral fold and secondary skin-fold of *Galathea* specimen. Two thin arrows point at pigment located in proximal part of palpebral fold. Large arrow points rostrad. 8 μ section. H-E-orange G. NA: 0.20. Reduced from 115×.

Fig. 2. Horizontal section through rostral part of eyeball at horizontal meridian of *Dana* specimen. Upper arrow points at scleral bone. Two lower arrows point at zones of scleral cartilage which are perhaps calcified. 30 μ section. H-E. NA: 0.20. Reduced from 110×.

Fig. 3. Horizontal section through medial wall of eyeball of *Galathea* specimen appr. at horizontal meridian. Scleral protuberance formed by scleral cartilage indicated by arrows. 15 μ section. PAS. NA: 0.10. Reduced from 33×.

Lettering:

a: angle of anterior chamber of eyeball
ch: choroid
e: artificially detached pigmented epithelium
f: fibrous sclera
li: limbus corneae
m: medial eye muscle
p: palpebral fold
r: retina
s: secondary skin-fold
sc: scleral cartilage