Ocular Morphology in Antarctic Notothenioid Fishes

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ABSTRACT Beneath the sea ice at McMurdo Sound, Antarctica, notothenioid fishes are subject to extreme seasonal variation in the annual light cycle including 4 months of continual darkness. Gross and microscopic anatomy of the eyes of 18 species revealed ocular morphology that was generally similar to that of coastal fishes elsewhere in the world, and unlike that of deep sea fishes living in perpetual darkness. The spectacle was well developed as were hyaloid arteries at the vitreoretinal interface. Fourteen species had a choroid body, and its presence was considered a primitive character state for notothenioids. The choroid body was absent in phyletically derived groups. The choroid body was especially large in Dissostichus mawsoni, the only species with a rod dominated retina. Retinæ were 154–279 μm thick with layering and sublayering typical for teleosts. Although all species had both rods and cones, there was marked interspecific variation in the ratio of cones:rods and in the total number of visual cells. Non-Antarctic notothenioids from New Zealand had more visual cells than most species from McMurdo Sound. Retinæ appeared balanced for vision under dim but seasonally variable light conditions and not specially adapted to the 4-month period of winter darkness. Retinal histology reflected the ecology and depth range of most species. Based on ecology and retinal histology, four groups of species were recognized: 1) Non-Antarctic, 2) cryopelagic (including two visually oriented benthic species), 3) pelagic and benthopelagic, and 4) benthic.

The fish fauna of Antarctica is dominated by a single group of 100 species of perciform fishes composing the presumably monophyletic suborder Notothenioidei (DeWitt, '71; Iwami, '85). It has been hypothesized that the ancestral notothenioid stock was associated with the continent since the waters began to cool 38 million years ago (Regan, '14; Norman, '38; DeWitt, '71). During a long period of isolation, notothenioids radiated to fill a variety of ecological niches normally occupied by taxonomically diverse fishes in temperate oceans (Eastman and DeVries, '81, '82, '85, '86; Eastman, '85a). Notothenioids are highly endemic, and constitute two-thirds of the fish species and 90% of the individuals in the Antarctic region (DeWitt, '71).

Notothenioids living under permanent sea ice in McMurdo Sound, Antarctica, experience a unique variety of environmental conditions at 78° south latitude. For example, the waters of the Sound have a nearly constant mean annual temperature of −1.87°C (Littlepage, '65). The body fluids of notothenioids are fortified with glycopeptide antifreeze compounds keeping them from freezing (DeVries, '82). There is extreme seasonal variation in the light regime consisting of 4 months of continual darkness in the austral winter and a comparable period of light in the summer. Surface irradiance is attenuated by snow, ice, and sea ice microbial communities (Sullivan et al., '84). Hence even at 1200 hours during the austral summer, the undersurface of the sea ice receives less than 1% of surface downwelling irradiance (Palmisano and Sullivan, '83; Sullivan et al., '84). Although teleost fishes occupy a large number of habitats, there have been few comparative morphological studies devoted to understanding ocular adaptation through structural variation (Powers and Easter, '83). The extreme conditions of McMurdo Sound provide an unusual setting for examining notothenioids and the ecological implications of their phenotypes. With the exception of studies on retinal organization (Meyer-Ro-
Fig. 1. Horizontal section from outer part of eye of *Pagotheria borchgrevinki*. Section is ventral to pupil, so iris appears complete. There is artifactual separation of the various layers. Bodian stain; ×19.0. 1, Epithelium of spectacle; 2, stroma of spectacle; 3, cornea; 4, retina; 5, chroidial stratum argentum; 6, cartilaginous sclera; 7, iridal stratum argentum; 8, iris; 9, skin of head.

Fig. 2. Cross section from inner part of eye of *Dissostichus mawsoni*, a species with a large choroid body. Hematoxylin and phloxine; ×13.2. 1, Retina; 2, chorio-capillaris; 3, choroid layer containing large choroid body; 4, rete mirabile of choroid body; 5, venous manifold; 6, branches of arterial manifold; 7, cartilaginous sclera; 8, fibrous sclera.

Specifically, I will present data on 1) the general anatomy of notothenioid eyes; 2) intraocular vascularization and the structure of the choroid body; and 3) retinal histology as related to ecology.

MATERIALS AND METHODS

Field work was conducted near the U.S. McMurdo Station on Ross Island in the...
Figs. 3, 4. Microfil in hyaloid arteries of right eye of *Pagothenia borchgrevinki* (Fig. 3) and left eye of *Gymnodiadraco aucticeps* (Fig. 4). Main vessel indicated by arrowhead; annular vein is also evident. ×5.4 and ×6.6, respectively. RL, Retractor lentis muscle.
Fig. 5. Scleral (medial) surface of formalin-preserved choroid body from *Dissostichus mawsoni* with attached choroid and retina. ×2.4. 1, Optic nerve; 2, ophthalmic artery; 3, rete mirabile of choroid body.

Fig. 6. Radiograph of inner (medial) aspect of eye of *Dissostichus mawsoni* demonstrating venous drainage of choroid body. Non-radiopaque Microfil was perfused through a cannula (1) in the ophthalmic artery and produced faintly visible filling of the arterial manifold (arrowheads). Subsequently radiopaque Microfil was perfused through a cannula (2) in the ophthalmic vein (2). Venous manifold (3) and ventral choroidal vein (4) are also evident. ×2.0.
Figs. 7, 8. Radiographs of inner (medial) aspect of eye of *Dissostichus mawsoni* showing arterial supply of chorioid body and the large rete mirabile occupying most of the choroid body. Non-radiopaque (white) Microfil was perfused through a cannula (arrowhead) in the ophthalmic artery. Branching of the arterial manifold and distribution of the arterial choriocapillaris are clearly visible. A portion of Figure 7 is enlarged as Figure 8 to show the arterial choriocapillaris originating on the lateral margin of the rete mirabile. ×2.2 and ×5.0, respectively.
southwestern Ross Sea. Using methods outlined by Eastman and DeVries (’82), 13 species were collected in McMurdo Sound during November 1978, 1979, and 1986. Notothenia larseni and N. kempi were captured near Sabrina Islet, Balleny Islands in a bottom trawl pulled by an ice breaker. Four species of channichthyids were obtained from trawls following uncommon McMurdo species was available: Bovichthys variegatus was netted in tide pools, and Notothenia angustata and N. microlepidota were caught in traps near Portobello.

Twenty-two species were used for gross morphological observations, and 18 of these species were analyzed histologically (Table 1). Sample sizes ranged from four to 14 specimens; however, only one specimen of the following uncommon McMurdo species was available: Pleuragramma antarcticum, Trematomous lepidorhinus, T. eulepidotus, and Pagetopsis macropterus. All specimens from McMurdo Sound were adults measuring 80–268 mm SL. Dissostichus mawsoni, the largest nototheniid species, was 820–1,480 mm SL. Entire specimens were preserved in 10% formalin and stored in 70% ethanol. Eyes were removed several years later for historical study.

The eyes of some anaesthetized adult specimens were removed and preserved especially for microscopy. Such eyes were divided into nasal and temporal halves by a dorso-ventral cut and then immersed in fixative (see below). Samples were taken from the central retina ventral to the optic disc, and histological descriptions pertain to this region. Although central and peripheral regions of the retina may differ, the general features are displayed centrally (Ali and Hanyu, ’63). Evaluation of this area was therefore considered appropriate for this survey of 18 species, and no attempt was made to evaluate regional variations in the types and density of retinal cells. Furthermore, there was insufficient well-preserved material for study of the visual cell mosaic.

Samples for light microscopy were fixed in Bouin’s solution, embedded in paraffin, sectioned at 5–7 μm, and stained using a variety of methods. Among these were Mayer’s hematoxylin and phloxine, Mallory’s phosphotungstic acid hematoxylin, McManus’ periodic acid-Schiff (PAS) with and without diastase control (Luna, ’68), 0.1% cresyl violet acetate for 45 sec, and Bodian’s Protargol for 24 hr at 50°C (Clark, ’81).

Samples from two specimens of Dissostichus mawsoni were prepared for electron microscopy. Choroid bodies and retinæ were perfused with saline (see below) followed by picric acid-paraformaldehyde in 0.15 M phosphate buffer. Small pieces were removed for postfixation first in Karnovsky’s paraformaldehyde-glutaraldehyde in 0.1 M cacodylate buffer and then in 1% osmium tetroxide. Samples were subsequently dehydrated in ethanol and propylene oxide and embedded in Araldite-Epon. Thick sections were stained with 1% toluidine blue in 0.1% sodiumborate. Sections with silver interference colors were stained with uranyl acetate and lead citrate before viewing with the electron microscope.

Microfil (Canton Bio-Medical Products), a liquid silicon rubber compound for microvascular injections, was used to demonstrate ocular blood vessels. After being anaesthetized with ethyl-m-aminobenzoate (Sigma Chemical Co.), fishes were placed ventral side up on a surgical board. An incision was made in the bulbous arteriosus, and the ventral aorta was cannulated with a 15-cm length of PE-50 tubing. This was in turn connected to a 23-G needle, an 84-cm extension tube, and a 10-ml syringe. The bottom of the syringe was 82 cm above the heart of the fish. Heparinized (250 U/ml) nototheniid saline solution (O’Grady et al., ’82) was perfused through the arterial system. The syringe was packed in an ice bath to maintain the saline at normal subzero body temperature. The hepatic veins were cut at the sinus venosus to facilitate washout of blood. The procedure was terminated after perfusion of 20–30 ml of saline. Ice-cold yellow, orange, or white Microfil was then perfused through the same apparatus for 60–90 min. A volume of 1–3 ml of Microfil filled the arterial system of specimens weighing 100–200 g. Fishes were subsequently fixed in 10% formalin, dehydrated in ethanol, and cleared in methyl salicylate. Some specimens were photographed or radiographed without being cleared. The large eyes of Dissostichus mawsoni were removed from the head, and the ophthalmic artery was cannulated. The perfusion of saline and Microfil was identical with the procedure outlined above.

Radiographs of eyes of Dissostichus mawsoni were produced using a Hewlett-Packard Faxitron soft X-ray machine (model 43805N)
with a dual cabinet. The machine was set at 30 kVp and 2.75 mA with an exposure time of 4.7 min. The 0.63-mm-thick beryllium window allowed the full spectrum of soft X-ray output. Radiographs were made on Kodak Industrex M film (M-5) placed in lead-backed cardboard cassettes. Film-to-source distance was 122 cm.

After calibration with a stage micrometer, ocular reticles were used in both dissecting and binocular microscopes to measure the diameter of blood vessels in Microfil specimens and the thickness of retinal layers and sublayers in histological sections. The thickness of the central retina was measured from the scleral tips of the outer segments of the visual cells to the internal limiting membrane. One to 13 slides from one to six individuals of each species were measured. Measurements were not corrected for shrinkage caused by fixation.

Nomenclature for ocular blood vessels was that used by Hanyu (‘62), Ali et al. (‘68), Anctil (‘68), Wittenberg and Wittenberg (‘74), and Copeland (‘80). Terminology for retinal layers was that of Ali and Anctil (‘76).

RESULTS

General description of the eye

The eyes of notothenioids are similar to those of other suborders of coastal Perciformes such as trachinoids and blennioids (Ali and Anctil, ‘76). They show no morphological evidence of either extreme specialization or reduction. The various coats of the eye (Figs. 1, 2) conform to the typical teleost condition (Walls, ‘42). The sclera is cartilaginous, and the embryonic fissure (hyaloid canal) is closed. In some species (Pagothenia), a partial or complete stratum argentum lies vitread to the sclera. In Pagothenia, this silvery reflective layer also is continued on to the anterior surface of the iris (Fig. 1). The pupil is fixed and all species have a well developed retractor lentis muscle attached midventrally to the inner surface of the iris (Fig. 4). The vascular and darkly pigmented choroidal layer lies between the sclera and the retina. Most species have a choroid body that occupies a fibrous interruption in the cartilage of the posterior aspect of the sclera (Fig. 2). Notothenioids lack other vascular specializations such as a falciform process and lentiform body. As the slightly oval optic disc is offset temporarily, the nasal field of the retina is larger than the temporal field in all species (Figs. 3, 4).

The spectacle

The spectacle is a stationary, transparent area of head skin that covers the eye in fishes (Walls, ‘42). All notothenioids have a secondary spectacle (Walls, ‘42) similar to that of the centrarchid Elassoma zonatum (Moore and Sisk, ‘63). Microfil injections and histological sections reveal that both the spectacle and cornea are avascular, relying on oxygen and nutrient diffusion from the ocular margin.

The outer surface of the spectacle (Fig. 1) is covered by a stratified squamous epithelium, which increases in thickness peripherally where the spectacle becomes continuous with the skin of the head. The epithelium contains many goblet cells peripherally, but not centrally. The epithelium is underlain by a thick connective tissue stroma with ordered parallel fibers. This layer, representing the dermis of the skin, forms the thickest part of the spectacle. Measurements on eight species showed that the spectacle is an average of 3.2 (± 0.30 SEM) times thicker than the cornea. In six specimens of Pagothenia borchgrevinki, for example, the epithelium of the spectacle averages 50 μm in thickness, the stroma of the spectacle is 214 μm, and the cornea is 91 μm. The resulting ratio of cornea:spectacle thickness is 1:2.9.

A network of thin connective tissue fibers connects the inner surface of the spectacle with the outer surface of the cornea. The spectacle and cornea are easily separated along this plane (Fig. 1). This arrangement allows the slack necessary for movement of the eye beneath the immobile spectacle. The cornea lacks epithelium, and its stroma is denser and more transparent than that of the spectacle. The periphery of the cornea is attached to the scleral cartilage.

Intraocular vasculature

After perfusion with Microfil, Gymnodraco acuticeps and Pagothenia borchgrevinki display an extensive series of blood vessels on the inside of the eye (Figs. 3, 4, 9). Trematomus hansonii and T. bernacchii have a similar but slightly less dense pattern. The efferent pseudobranchial artery continues into the orbit as the ophthalmic artery. This artery lies dorsal to the optic nerve (Figs. 5, 7) and supplies the outer surface of the retina through the rete mirabile of the choroid body (see below). In species without a choroid body, the ophthalmic artery ramifies directly into
The choroid body

The choroid body, a rete mirabile within the posterior part of the choroid coat of the teleostean eye (Walls, '42), occurs in 14 of 22 notothenioid species (Table 1). Examination of 25 specimens of species with and without a choroid body, showed that this structure does not vary intraspecifically among notothenioids. Therefore, in the case of rare notothenioid species, the presence or absence of the choroid body could be reliably ascertained by dissection of a single specimen. All notothenioids have a free pseudobranch on the inside of the operculum. The pseudobranch also occurs in species lacking a choroid body, an unusual situation (Walls, '42; Wittenberg and Haedrich, '74).

The choroid body of Dissostichus mawsoni is especially large; filling with Microfil made it suitable for study by radiography. It shows the typical horseshoe shape (Barnett, '51) with the opening directed ventrally between the two limbs (Fig. 5). The optic nerve lies dorsally in the space between the limbs. The ophthalmic artery enters the sclera dorsal to the optic nerve. After dividing, it runs along the central (medial) margin of each of the two limbs of the choroid body (Fig. 7). Forming an arterial manifold (Copeland, '80), these vessels subdivide into the arterial capillaries of the rete mirabile.

The rete is 1.7–2.1 mm wide and consists of parallel arterial and venous capillaries (Figs. 2, 8, 11). Electron microscopy reveals that the capillaries lie in an irregular pattern with three to five venous capillaries around each arterial capillary (Fig. 11). Consistent with the findings of Copeland ('74), venous capillaries are larger in diameter, more irregularly shaped, and have walls two to three times thinner than those of arterial capillaries (Figs. 11, 12). The generally oval arterial capillaries have a mean maximum internal diameter of 26.1 μm (+ 1.48 μm SEM; N = 21) as measured from electron micrographs. It is possible that the lumina of these vessels narrow to the diameter of typical notothenioid capillaries (9–15 μm) in a portion of the rete that was not sampled. Venous capillaries were too variable for reliable measurement.

Three to four nonfenestrated endothelial cells form the margin of the capillary lumina. Arterial capillaries are surrounded by a continuous basal lamina, which splits to enclose a discontinuous layer of pericytes.
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1 All are members of the family Nototheniidae except the five channichthyids, one bovichthyid (*), and one bathydraconid (+).
2 Eastman and DeVries ('82) for McMurdo specimens.
3 From qualitative examination of histological sections of central retina.
4 Excluding the retinal pigment epithelium.
Fig. 9. Ventral margin of eye of Microfil specimen of Gymnodraco acuticeps shown in Figure 4. Retractor lens is reflected by pin (arrowhead); branches of the main vessel supply this muscle. ×10. 1, Annular vein; 2, main vessel.

Fig. 10. Layers and sublayers of the cone dominated retina of Gymnodraco acuticeps. Hematoxylin and phloxine; ×454. 1, Retinal pigment epithelium; 2, visual cell layer; 3, external limiting membrane; 4, external nuclear layer; 5, external plexiform layer; 6, internal nuclear layer consisting of horizontal (a), bipolar (b), and amacrine (c) cells; 7, internal plexiform layer; 8, ganglion cell layer; 9, nerve fiber layer; 10, internal limiting membrane.
Fig. 11. Rete mirabile of choroid body of Dissostichus mawsoni fixed by vascular perfusion. Venous capillaries (V) have thin walls and irregular lumina, whereas arterial capillaries (A) have thick walls and oval lumina. The labeled arterial capillary at the top is surrounded by five venous capillaries, a common situation. ×1,160.
Fig. 12. Diffusion barrier between arterial (A) and venous (V) capillaries in rete mirabile of choroid body of *Dissostichus mawsoni*. Arterial capillary wall includes endothelium (E), a continuous basal lamina, and a discontinuous layer of pericytes (P) enclosed by basal lamina. Thickness of the diffusion barrier at double-headed arrow is 1.2 μm. ×11,165.

Fig. 13. Rods and an equal twin cone in the retina of *Dissostichus mawsoni*. Arrowheads indicate junction between inner and outer segments of rods. Pigment is present in cell processes of the retinal pigment epithelium. ×1,890. E, Ellipsoid; M, myoid; O, outer segment.
(Fig. 12). Venous capillaries lack a basal lamina. The endothelial cell cytoplasm shows few pinocytotic vesicles. Closely opposed capillary walls may facilitate diffusion of oxygen from arterial to venous capillaries (Fig. 12). Mean thickness of the diffusion barrier is 1.1 μm (± 0.08 μm SEM; N = 27).

The arterial choriocapillaris issues from the peripheral margins of the rete and is distributed predominantly to the ventromedial portion of the eye (Figs. 7, 8). The venous choriocapillaris join the limbs of the choroid body at its peripheral margin. They subdivide into venous capillaries of the rete that drain to the central margin of the limbs by a venous manifold (Fig. 6). Depending on its location in the limb, the manifold subsequently drains either directly to the ophthalmic vein or to the ventral choroidal vein, which continue as the ophthalmic vein. The venous manifold lies central (medial) to the arterial manifold in each limb (Fig. 6). In Dissostichus, the arterial and venous manifolds remain distinct (Fig. 2), and the arteries do not lie in a venous sinus as in some teleosts (Wittenberg and Wittenberg, '74; Cope-land, '80).

The retina

All notothenioids have a well-developed duplex retina ranging in mean thickness from 154 to 279 μm (Table 1), near the low end of the 100–500 μm range reported for fishes (Walls, '42). There is no obvious relationship between retinal thickness and habitat of the various species. With the exception of two benthopelagic and one New Zealand species (Trematomus lepidorhinus, T. loennbergii, and Bovichthys variegatus), retinal thickness is uniform throughout the eye. As judged by the thickness of the external nuclear layer, visual cell density is two to three times greater centrally than peripherally in these species.

Layering and sublayering of the retina is as typical for teleosts (Fig. 10) and conforms to the general pattern of eight layers and two membranes (Ali and Anctil, '76). Figures 15–17 present a sample of retinal morphology in this group of 18 species. A retinal pigment epithelium occurs in all species and is most prominent in non-Antarctic (Fig. 16A) and cryopelagic (Fig. 17A) species. Although the capacity for retinomotor movement was not investigated, some species have pigment granules in processes extending between outer segments of rods and cones (Figs. 16, 17). Pagotheria borchgrevinki reportedly exhibits retinomotor movement (Meyer-Rochow and Klyne, '82).

The visual cell layer ranges from 24% to 37% of retinal thickness (Fig. 14). Most of the thickness of this layer is attributable to the outer segments of the visual cells. In this character, notothenioids are intermediate between the ecological extremes of a goldfish (typical diurnal light cycle: 15%) and deep sea teleosts (continual darkness: 41%) (Locket, '75). Visual cells include single cones, equal twin cones, and rods (Fig. 15). Rods are thin and inconspicuous, except in Dissostichus mawsoni (Fig. 13, 15B). Species with numerous cones and many rows of nuclei in the external nuclear layer also have a large population of rods (Figs. 16A,B,D, 17D). Cone nuclei are easily recognizable as they protrude through the external limiting membrane. Cones do not contain oil droplets. Myoids and ellipsoids are distinct in the twin cones of Dissostichus mawsoni (Figs. 13, 15B).

There is considerable interspecific variation in the ratio of cones: rods (Table 2). Five species, mostly pelagic and benthopelagic, have low cone:rod ratios (1:14–57). Among these species only Dissostichus mawsoni has a rod-dominated retina. An additional five species, including some non-Antarctic and benthic forms have moderate cone:rod ratios (1:6–10). High cone:rod ratios (1:2–4) are characteristic of eight species including cryopelagic and some benthic ones.

The number of visual cells also shows marked interspecific variation (Table 2). The New Zealand bovichthyid Bovichthys variegatus (Fig. 16A) has 308 cells with 14 rows of nuclei in the external nuclear layer. At the other extreme, the deep living benthic notothenioids from McMurdo Sound (Fig. 17C) have 29–68 cells with nuclei arranged in two or three rows. Bovichthys variegatus has 10.6 times more visual cells than Trematomus centronotus, a benthic species from McMurdo Sound.

The external nuclear layer, containing the nuclei of rods and cones, is thicker than the internal nuclear layer in only four of 18 species: Bovichthys variegatus (Fig. 16A), Dissostichus mawsoni (Fig. 16C), Pleuragramma antarcticum (Fig. 16D), and Trematomus loennbergii (similar to T. lepidorhinus: Fig. 17D). This is a characteristic of the retinae of deep sea fishes with a high degree of summation (Munk, '84) and good sensitivity. The
<table>
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<tr>
<th>Species</th>
<th>Cones</th>
<th>Rods</th>
<th>Cones + rods</th>
<th>Ratio cones:rods</th>
<th>No. of cells in INL</th>
<th>No. of ganglion cells</th>
<th>Convergence ratio (cones + rods: ganglion cells)</th>
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</table>

1 Counts reflect number of nuclei in 100 \(\mu m^2\) of one Bodian-stained histological section viewed at \(\times 1,000\). For purposes of this study, cone:rod ratios are designated as high (1:2-4), moderate (1:6-10), or low (1:14-57). Similarly convergence ratios are high (58:1), moderate (30-12:1), or low (19-5:1).
remaining species have internal nuclear layers that are thicker than external nuclear layers, a feature usually associated with retinae of diurnal species (Munk, '84).

All species have the typical horizontal, bipolar, and amacrine sublayers of nuclei within the internal nuclear layer (Fig. 10). This layer constitutes 9–20% of the retinal thickness and is especially well developed in Gymnodraco acuticeps (Fig. 17B), a shallow water visual predator. The internal nuclear layer is poorly developed in Dissostichus mawsoni and sublayers are not distinct because there are so few cells (Fig. 16C). The horizontal cell sublayer contains only one row of cells in most species. Exceptions include Pagetopsis macropterus and Pagothenia borchgrevinki (Fig. 17A) which have two rows. Many teleosts have three rows of horizontal cells (Ali and Anctil, '76), a feature associated with a high degree of integration and good visual acuity (Wagner et al., '76).
Fig. 15. Retinae showing features of visual cell layer in various species. Photos aligned vertically along external limiting membrane; all stained with PAS except A (PTAH); ×454. A: Non-Antarctic Notothenia angustata with equal twin cones, single cones, and rods. B: Pelagic Dissostichus mawsoni with rods and one equal twin cone showing myoid, ellipsoid, and outer segment. C: Pelagic Pleuragramma antarcticum with single cones showing well-developed outer segments. Many rods are present but not visible. D: Benthic Trematomus hansoni with equal twin cones, single cones, and rods.
Fig. 16. Bodian-stained retinae showing development of layers and sublayers in various species. Photos aligned vertically along external limiting membrane (except for A); ×454. A: Non-Antarctic Bouichthys variegatus. B: Non-Antarctic Notothenia angustata. C: Pelagic Dissostichus mawsoni. D: Pelagic Pleuragramma antarcticum.
The nuclei of Müller's cells, the retinal neuroglial cells extending from external limiting membrane to internal limiting membrane, are prominent in the internal nuclear layer of some species. These cells display a positive reaction for glycogen upon staining with periodic acid-Schiff.

The thickness of the internal plexiform layer is 13–34% that of the retina and is especially well developed in Trematomus bernacchii, T. loennbergii, and Pagetopsis macropterus. It is distinctly sublayered in Notothenia angustata (Fig. 16B).

DISCUSSION

Ocular evolution in the Antarctic marine environment

Trachinoids and blennioids, possible sister groups to notothenioids (Andersen, '84), are coastal fishes with well-developed duplex retinae containing many cones (Ali and Antcil, '76). Similarly Bovichtys variegatus from New Zealand, a primitive notothenioid (Regan, '14; Eakin, '81; Iwami, '85; Prirodina, '86), possesses a generalized eye with a retina suitable for vision over a wide range of illumination. In McMurdo Sound, notothenioids live at the extreme southerly boundary of marine life. In spite of the atypical light cycle, the small amount of solar radiation reaching the subice habitat and millions of years of evolution in isolation, their eyes are generally similar to those of coastal fishes elsewhere in the world.

Ali ('75) identifies a number of problems associated with vision at low temperatures including slowing of retinomotor movements and bleaching rates of visual pigments. Nothing is known about either of these processes in notothenioids (Ali and Wagner, '75a,b). However given the absence of marked daily fluctuations in light, retinomotor movement may prove to be less important in notothenioids than in temperate fishes. Ali ('75) also mentions that under cold conditions the visual threshold goes up and both visual acuity and the ability to perceive moving objects are reduced. Whereas these specific processes have not been studied, the effects of low temperatures may not be as significant in notothenioids as the nervous system exhibits evolutionary (i.e., genetic) cold adaptation. Thus, both sensory and motor nerves are resistant to blockade at low temperatures, and show compensatory increases in excitability and conduction velocity compared with values extrapolated from temperate fishes (Macdonald, '81; Montgomery and Macdonald, '84).

It is possible that senses other than vision are important in the detection of prey during the darkness of the austral winter. Montgomery and Macdonald ('87) have demonstrated that vibrations produced by swimming crustaceans are important natural stimuli to the cephalic lateral line system of Pagotheria borchgrevinki. In addition, enlarged and open cephalic lateral lines with prominent pores, pits, or free neuromasts are common in other notothenioids, including Aethotaxis (DeWitt, '62), Pleuragramma (DeWitt and Hopkins, '77), and Cryothenia (Daniels, '81).

Significance of hyaloid arteries

Ali et al. ('68) found that the extent of intraocular vascularization is positively correlated with retinal development, pelagic or coastal habitat, and elevated levels of activity. Notothenioids lack both a falciform process and lentiform body. They have, however, an extensive series of hyaloid arteries—possibly representing the primitive character state for intraocular vasculature in teleosts (Hanyu, '62). Their density is comparable with or exceeds that of well-developed hyaloid arteries in coastal and pelagic teleosts from temperate waters (Ali et al., '68). The pattern of hyaloid arteries in notothenioids may simply represent the persistence of a primitive vascular pattern, perhaps similar to that of the perciform stock that gave rise to notothenioids. Unfortunately the hyaloid arteries of Dissostichus were not perfused with Microfil, hence nothing is known about the condition of these vessels in a notothenioid with a rod dominated retina.

Loss and significance of the choroid body

Through counter-current multiplication, the choroid body produces elevated oxygen tensions in the choroid adjacent to the outer surface of the retina (Wittenberg and Witternberg, '62, '74; Fairbanks et al., '74). The avascular retina, especially the visual cell layer, can then be supplied with oxygen by diffusion. After surveying the distribution of the choroid body in fishes, Wittenberg and Hae-drich ('74) concluded that there was little correlation between habitat and presence or absence of the choroid body. They also decided that this structure was too widely distributed and too easily lost to be of use in phylogenetic analysis.

In the presumably monophyletic notothenioids, presence of the choroid body is considered to be the primitive character state because of its widespread occurrence among
Fig. 17. Bodian-stained retinae showing development of layers and sublayers in various species. Photos aligned vertically along external limiting membrane; ×454. A: Cryopelagic Pagathenia borchgrevinki. B: Benthic (but visually orientated) Gymnодraco acuticeps. C: Benthic Trematomus hansoni. D: Benthopelagic Trematomus lepidorhinus.
both blennioids (Wittenberg and Haedrich, '74), an outgroup, and primitive notothenioids (bovichthyids). The choroid body has been lost in phyletically derived families (channichthyids, harpagiferids, bathydraconids) and in some derived genera (Pagothenia) of notothenioids. The limited sample suggests that most species without a choroid body live in relatively bright surface waters. Their retinae have fewer visual cells, higher cone:rod ratios, and are thinner than those of species with a choroid body. There is no obvious relationship between retinal thickness and presence or absence of a choroid body among notothenioids.

Dissostichus mawsoni, the species with the largest choroid body, has a rod-dominated retina. Outer segments of rods are longer than those of cones and are therefore farther away from the hyaloid arteries at the vitreoretinal interface. Furthermore, rods have more visual pigment than cones (Weiss, '83), and discs in the outer segments are rapidly turned over (Fawcett, '86), suggesting that rods may have a greater demand for oxygen than cones. Although there is no experimental proof that rods are more aerobic than cones in fishes, this hypothesis is compatible with the existence of an exceptionally large choroid body in Dissostichus.

Ecology and retinal histology

The well-documented association between retinal organization and habitat depth (Ali and Hanyu, '63; Anctil, '69; Ali and Klyne, '85) is also valid for notothenioids. This finding is in agreement with the data of Meyer-Rochow and Klyne ('82) relating retinal structure to habitat in three species. Notothenioid retinae appear to be balanced for vision under dim but seasonally variable light conditions and not specially adapted to the 4-month period of winter darkness. Their retinae may represent a compromise to the average yearly light conditions. Although notothenioids are ecologically comparable to some deep sea fishes, their eyes are devoid of the extreme specializations associated with life in perpetual darkness. For example, pure rod retinae, long rod outer segments, banded rods, retinal diverticula and tubular eyes (Munk, '66, '84) are unknown in these fishes.

Ecology and retinal histology suggest that there are four groups of notothenioids represented among the 18 species comprised by this study.

Non-Antarctic species

The Non-Antarctic notothenioid species live in shallow, rocky inshore waters or, in the case of Bovichthys, in tidepools (Ayling and Cox, '82). They range south only as far as the sub-Antarctic islands. Their retinae have well-developed pigment epithelia, large numbers of visual cells compared to the Antarctic species, moderate ratios of cones:rods, and moderate convergence ratios. Therefore, both visual acuity and sensitivity are reasonably well developed. Their retinae may be considered arhythmic (Ali and Klyne, '85), since they function over a wide range of illumination, and typical of those of many coastal fishes from temperate waters.

Cryopelagic and two visually oriented benthic species

The cryopelagic (and two visually oriented benthic) species live in shallow, relatively bright waters of McMurdo Sound. Cryopelagic species such as Pagothenia live immediately beneath several meters of ice including 2–3 m of annual sea ice and an additional 0.5–4 m of platelet ice. They feed on copepods and amphipods (Eastman and DeVries, '85). Gymnodraco are piscivorous (Eastman, '85b), employing an ambush feeding strategy, and are the only benthic fish in McMurdo Sound that will rise in the water to strike an artificial lure. Pagetopsis perch on sponges to ambush fishes and crustaceans (Robilliard and Dayton, '69). Retinae of these species have high ratios of cones:rods and low convergence ratios indicating good visual acuity necessary for movement detection.

Meyer-Rochow and Klyne ('82; Figs. 7, 8) indicate that Pagothenia have a tapetum lucidum. However, I interpret the equivalent structure in my specimens as an ocular stratum argentum consisting of guanine crystals (Somiya, '80). The tapetum lucidum depicted by Meyer-Rochow and Klyne is located sclerad to the retinal pigmented epithelium, an unusual and ineffective position for a tapetum lucidum in fishes. Furthermore, a tapetum lucidum is usually considered an adaptation for a dim rather than a bright environment (Walls, '42; Lythgoe, '79; Ali and Klyne, '85).

The stratum argentum (Fig. 1) is a silvery reflective layer external to the iris and choroid in Pagothenia (Eastman and DeVries, '85). The black iridal and choroidal pigment provides undesirably high visual contrast in a bright environment. When camouflaged by
the stratum argentum, however, the eye is rendered inconspicuous. Predators in McMurdo Sound approach *Pagothenia* from below (Eastman and DeVries, '85), and thus the stratum argentum provides effective camouflage when *Pagothenia* are viewed against a light background of platelet ice.

Pelagic and benthopelagic species

The pelagic and benthopelagic species live in low light levels at depths of at least 300–550 m. *Dissostichus* is a large predator primarily feeding on fishes, especially *Pleuragramma*, and mysid shrimp (Eastman, '85a). *Pleuragramma* feed on copepods, mysids, and fishes (Eastman, '85b). Benthopelagic species prey on amphipods near the bottom at depths greater than 450 m (Eastman, '85b). At locations other than McMurdo Sound, *Trematomus loennbergii* and *T. lepidorhinus* have been captured at depths of 830 m (DeWitt, '71).

Pelagic and benthopelagic species have large numbers of visual cells and low ratios of cones:rods. *Dissostichus* is the most extreme example and is the only species with a rod-dominated retina. Rods are adapted for low-intensity illumination (Levine and MacNichol, '82). Convergence ratios are high, indicating a high degree of summation. Whereas this increases the sensitivity of the retina, acuity is reduced (Ali and Hanyu, '63; Lythgoe, '79).

The rod-dominated retina of *Dissostichus* is especially sensitive and well suited to respond to dim light at 300–500 m. It is similar to the retinæ of bigeyes (Priacanthidae), nocturnal, deep water shore fishes (Ali and Anctil, '76) having only a few cones. Cones are generally associated with color vision, but, more importantly, they enhance visual contrast and enable both dark and bright objects to be discriminated against the background light (Levine and MacNichol, '82). In this respect they may be important in the detection of bioluminescence emanating from prey organisms (see below).

*Pleuragramma* live throughout the water column in McMurdo Sound to depths of 500 m. Elsewhere in the Southern Ocean they range from depths of 0 to 900 m (Gerasimchuk, '86). Unlike *Dissostichus*, the retina of *Pleuragramma* contains many closely packed cones and is not adapted primarily for vision at depths of 300–500 m. It is unique among this sample of 18 species in also possessing a combination of numerous rods, a well-developed internal nuclear layer, and many ganglion cells. Although the ratio of cones:rods is lower in *Pleuragramma*, it is 3½ times greater than that of *Dissostichus*. Furthermore, the convergence ratio, while moderate, is nearly five times greater than in *Dissostichus*. Hence, the acuity and sensitivity of its retina allow *Pleuragramma* to feed discriminately on small mobile prey throughout the water column, a niche underutilized in the Southern Ocean. In both McMurdo Sound and elsewhere, *Pleuragramma* is a numerous and ecologically important notothenioid playing a vital role in the midwater ecosystem (Eastman, '85a,b).

Pelagic and benthopelagic species share another morphological feature related to vision—shielding the bioluminescence of prey items in the gut. In *Pleuragramma*, *Aethotaxis mitopteryx* (another pelagic notothenioid) and most benthopelagic species, the parietal peritoneum and walls of the esophagus, stomach and rectum are heavily pigmented. This black pigment may reduce transmittance of bioluminescence from gut contents to the exterior of the body thereby rendering these fishes less visible to potential predators (McAllister, '61; Eastman, '81). Raymond and DeVries ('76) describe bioluminescent dinoflagellates, copepods, ostracods, and fish fecal pellets from McMurdo Sound. During the darkness of the austral winter, or at any time of year, in water more than 30 m deep (Lythgoe, '72), bioluminescence is brighter than downwelling daylight and would probably be visible through the thin body walls of fishes. *Dissostichus* is the only pelagic or benthopelagic species lacking a darkly pigmented gut. The thick body wall (to 5 cm) of this large fish may effectively mask bioluminescence.

Benthic species

The six benthic species live at moderate depths (30–550 m—see Table 1) and are generalized bottom feeders on slow-moving or sessile organisms. *Trematomus bernacchii* is active and feeds all winter in McMurdo Sound (Wohlschlag, '61). The benthic trematomids eat primarily polychaete worms (Eastman, 85b). Their retinæ are intermediate between the extremes of the cryopelagic (group 2) and the pelagic species (group 3).

Retinæ are moderately to poorly developed and similar to those of temperate wolfishes (Anarhichadidae) living at 200–500 m (Ali and Anctil, '76). Ratios of cones:rods are moderate to high, and convergence ratios are moderate to low. Numbers of visual cells,
cells in the internal nuclear layer, and ganglion cells are relatively low compared to the other groups. Although not as well developed as those of non-Antarctic species or Pleuragramma, the retinai of benthic species may represent a compromise between modest acuity and sensitivity.

**Significance of cones in benthic species**

Although rods outnumber cones in all species (Table 2), histological sections reveal that cones are qualitatively abundant in the retina of 16 out of 18 species (Table 1; Figs. 15–17). There is no clear ecological separation among species with single cones and twin cones. Twin cones are most prevalent in non-Antarctic, cryopelagic, and shallow-living benthic species, although they are also found in deeper-living benthic and pelagic species. Both types of cones must therefore have some adaptive significance even in the benthic species. The majority of notothenioids are benthic and most diverse between 200 and 600 m (Andriashev, '65); thus, a retina with cones may represent a successful solution to the detection of bioluminescence and to the problem of vision in the dim but seasonally changeable light cycle prevailing at this depth. Additional insights must await examination of the visual pigments of nototheniid cones.

**Final considerations**

In McMurdo Sound notothenioids are subject to a unique photic regime. Four-month periods of continual darkness in the winter and continual light in the summer are separated by 2-month transition periods during which the photoperiod increases or decreases by 20 minutes a day (Rivkin and Putt, '87). Ice cover, sometimes persisting for several years without significant breakup, also affects light penetration in the water column. However, there is no obvious correlation between the unusual light conditions in McMurdo Sound and ocular morphology among ecologically diverse notothenioids. The key evolutionary adaptations for visual function in this habitat are probably related to temperature. These adaptations are molecular and involve all systems of the body. Glycopeptide antifreezes confer resistance to freezing, while homeoviscous adaptations allow normal cellular function, including nerve conduction and muscle contraction, at sub-zero temperatures. Apparently light penetration in McMurdo Sound is sufficient to permit normal ocular function in cold-adapted, but morphologically unspecialized eyes.

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ANTARCTIC FISH EYES

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