Acta Zoologica (Stockholm) **82**: 89–105 (April 2001)

Outer retinal fine structure of the garfish *Belone belone* (L.) (Belonidae, Teleostei) during light and dark adaptation – photoreceptors, cone patterns and densities

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Keywords:
Atheriniformes, retina, photoreceptor, regional retinal differences, fine structure, hexagonal pattern, adaptations to photic habitat

Accepted for publication:
31 July 2000

Abstract

Reckel, F., Melzer, R. R. and Smola U. 2001. Outer retinal fine structure of the garfish *Belone belone* (L.) (Belonidae, Teleostei) during light and dark adaptation – photoreceptors, cone patterns and densities. — *Acta Zoologica* (Stockholm) **82**: 89–105

In the present EM study, we investigate the retina of *Belone belone*, a visually-orientated marine predator living close to the water surface. In the duplex retina, four morphologically different cone types are observed: unequal and equal double cones, long single cones and triple cones. In the light-adapted state, five different cone patterns occur: row, twisted row, square, pentagonal and hexagonal patterns. High double cone densities are found ventro-nasally, ventro-temporally and dorso-temporally. Throughout the retina the double cone/single cone ratio is 2 : 1, in the ventral part, however, a 1 : 1 ratio occurs. In the vitreous body we found a curtain-like intraocular septum dividing the retina into two morphologically different regions. In most areas of the dark-adapted retina the cone patterns are absent at the ellipsoid level, with long single cones standing more vitreally in the light path than double cones. The mosaics are retained, however, in the outer nuclear layer. Typical dark adaptation, i.e. the retinomotor movements of the retinal pigment epithelium and photoreceptors in response to the dark adaptation (light change) is not present in the peripheral ventral and parts of the central ventral area. In both regions we found a twisted row pattern of cones having a vitreal position. The findings are discussed with respect to the photic habitat and feeding habits of this species.

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Introduction

In contrast to many other vertebrates, the teleost retinal structure often varies distinctly between the allied families, sometimes even between genera within a family (Engström 1963a). The retina can contain rods and different cone types such as short single or long single cones, double cones and even triple or quadruple cones, the cones being arranged in different patterns. In some cases, certain photoreceptor types are missing, for example the retinae of deep sea teleosts contain mainly or exclusively rods (Ali and Klyne 1985). In addition, regional differences may occur within the retina with considerable variations in photoreceptor types, densities and patterns. These intra- and interspecific variations in retinal structure reflect the feeding habits and photic habitat conditions of the respective species (Ahlbert 1969).

In the present study we investigate the retina of *Belone belone* (Linnaeus 1761), using light and electron microscopy. We studied the photoreceptor types, cone patterns, the cone densities and regional differences of the retina in the light- and dark-adapted state and compared our findings to those in other genera within the Belonidae. Light microscopical descriptions of belonid retinae are given in Friis (1879) and Ali and Anctil *et al.* (1976). Moreover we tried to find out to what extent the retina of *B. belone* shows adaptations to its special feeding habits and light conditions in its habitat.

Belonidae are marine epipelagic visually-orientated predators which live very close to the surface, and therefore are exposed to high light intensities from above. They can be found in tropical and temperate waters also. *B. belone* is the most abundant belonid species in the Mediterranean Sea. Belonids form large shoals and mainly prey on smaller fish, e.g. Atherinidae, either during sunrise, in the early morning hours or in the late afternoon, even after sunset (Bauchot 1987; personal observations).

This investigation is part of a comparative EM-study dealing with the morphology and fine structure of the retina of Atheriniformes, i.e. belonids, exocoetids, hemiramphids, atherinids and colleagues, including ecological aspects as well as their phylogeny. A short account of the findings presented here is given in Reckel *et al.* (1999a).

Materials and Methods

Animals

All specimens were caught just beneath the surface by rod and line in the Adriatic Sea at Poreç (Croatia). The fish caught during daylight were kept alive under daylight conditions for several minutes, then the eyes of the freshly killed fish were enucleated and fixed for electron microscopy. For studying the dark-adapted state of the retina, one fish caught after sunset was kept in complete darkness for 3 h, after which the eyes were fixed for electron microscopy. The studied specimens (n = 4) were from catches of three different days all having a body size between 41 and 42 cm total length, with eye diameters of 1.2 cm horizontally and 1.1 cm vertically. For morphological analysis of the intraocular curtain-like structure, five extra fish were examined. Transmission of the isolated curtain (whole tissue pieces of 3–4 mm^2) was measured with a Uvikon 810 spectrophotometer. The species' names were determined after Bauchot (1987).

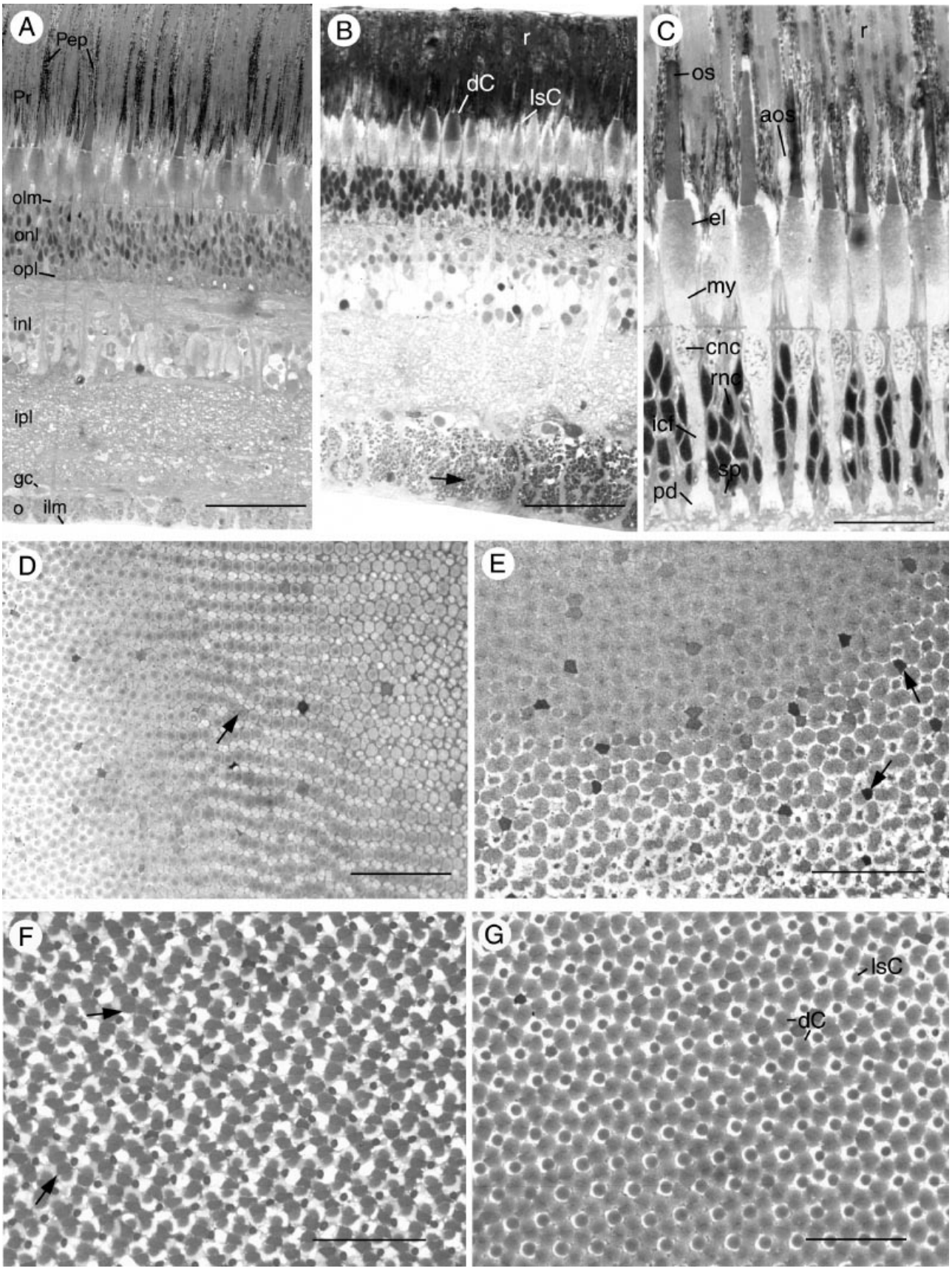
Transmission EM and light microscopy

Just after being dissected from the freshly killed fish, the eyes were perforated around the lenses using fine needles or scissors to allow a thorough infiltration with the primary fixative (4% glutaraldehyde im 0.1 M sodium cacodylate buffer (pH 7.3), at 4 °C). Back in the lab, the lenses and vitreous bodies were removed from the eyecups and the retinae were dissected into dorsal, ventral, ventro-temporal, nasal and temporal parts. Each of these pieces was divided into a peripheral and a central part, thus improving the infiltration with the applied chemicals. After rinsing in buffer, the parts were postfixed in 1% OsO_4 in 0.2 M buffer (2 h, 4 °C). After rinsing in buffer, the specimens were dehydrated in a graded acetone series, and after infiltration with epoxy resin, they were cut into pieces of 2–3 mm^2 of well-defined orientation (28 pieces in one specimen (n = 1) which was selected for the detailed basic examination and 8 pieces in the additional specimens (n = 3)) for a detailed mapping of the photoreceptor patterns and densities in each eye region. Finally the retinal pieces were embedded in epoxy resin. Radial and tangential ultrathin sections of the retinae were cut on a RMC Ultrotome III with a Diatome diamond knife and mounted on formvar-coated copper grids. The specimens were observed with a Philips CM 10 transmission electron microscope at 80 kV. In addition, semithin sections (1.5 µm) were made using glass knives, stained with toluidine blue and inspected under a Zeiss Axioplan microscope. To investigate regional variations of visual cell densities and cone patterns, tangential sections in the centre of each retinal piece were made. The number of double cones per 0.0225 mm^2 was then counted from photographs taken at the ellipsoid or nuclear level. To allow comparison with other species the number was converted into double cones per mm^2. For preparing the density map, the converted double cone numbers were placed in an eye graphic at their corresponding position. Missing data of cone densities was replaced by linear interpolation and all points of the same densities connected with each other. Finally the obtained density lines were revised on a computer with Adobe Photoshop 3.1.

Results

In *Belone belone*, we find a typical duplex retina made of rod and cone photoreceptors with all its layers well-developed within the four quadrants of the eyecup (Fig. 1A–G). However, considerable regional differences regarding cone patterns, cone densities and the dimensions of the respective photoreceptor types occur (Figs 1A–G, 2). In addition, our light adaptation experiments indicate that the photoreceptors make light-induced retinomotor movements which influence the actual photoreceptor patterns.

Fig. 1— Gross morphology and regional differences in the light-adapted retina, light microscopy. A–C, radial, D–G, tangential sections. —**A**. Dorsal periphery. —**B**. Temporal periphery; note the very thick layer of optic nerve fibers (*arrow*) which would be typical of more central regions. —**C**. Dorsal retina, near centre. —**D**. Twisted row pattern, ventro-temporally, near centre; *arrow* forking long single cone row. —**E**. square pattern in the temporal periphery; *arrows* darker stained members of double cones. —**F**. pentagonal pattern in the dorsal peripheral area of the retina (*arrows*) between numerous transitions to a hexagonal pattern. —**G**. Hexagonal pattern, dorsal, periphery. Bars: A, B, D–G 50 µm; C 25 µm – *aos*, accessory outer segment.–*cnc*, cone nucleus. – *dC*, double cone. – *el*, ellipsoid. – *gc*, ganglion cell layer. – *icf*, inner cone fibre. – *ilm*, inner limiting membrane. – *inl*, inner nuclear layer. – *ipl*, inner plexiform layer. – *lsC*, long single cone. – *my*, myoid. – *o*, optic nerve layer. – *olm*, outer limiting membrane. – *onl*, outer nuclear layer. – *opl*, outer plexiform layer. – *os*, outer segment. – *pd*, cone pedicle. – *Pep*, pigment epithelium processes. – *Pr*, photoreceptor layer. – *r*, rods. – *rnc*, rod nucleus. – *sp* rod spherule.



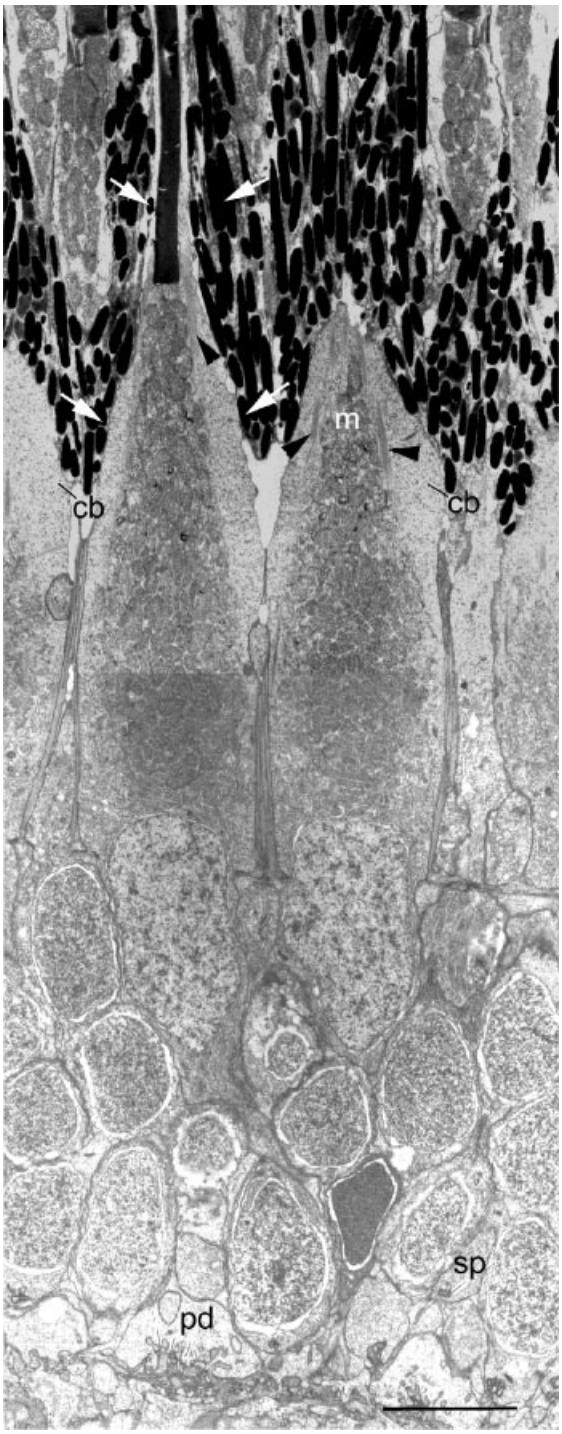


Fig. 2—Photoreceptor fine structure in the light-adapted retina, electron microscopy, radial section. The section shows to the left a longitudinally-cut long single cone; note the vitreally concentrated melanin granules (*arrows*) almost forming a 'bag' around the cone outer segment. Bundles of longitudinal filaments (*arrowheads*) are situated between mitochondria (*m*) and cytoplasmic bulge (*cb*). Rod spherules (*sp*) terminate more sclerally than cone pedicles (*pd*) in the outer plexiform layer. Bar: 5 μm.

Radial arrangement of photoreceptors in the light-adapted state

In the light-adapted state, the rods are positioned scleral to the cones with their myoids elongated and their outer segments reaching deep into the pigment epithelium (Figs 1A–C, 2). In this state, rod-shedding can often be observed which indicates the regeneration of rod disks during the day. By contrast, the cone myoids are contracted. This brings the cones into a more vitreal position within the light path. Long pigment epithelium processes, densely packed with pigment granules, extend vitreally and form finger-like 'bags' around the scleral parts of the cone ellipsoids and their outer segments (Figs 1A–C, 2, 3A,C). The different cone types are positioned at the same level within the visual cell layer. Their nuclei can be found at the level of the outer limiting membrane with the prevailing portion of vitreally located heterochromatin (Figs 1B,C, 2).

Photoreceptor types

Altogether, six morphologically different photoreceptor types occur: rods, equal and unequal double cones, long single cones, and triple cones of both the triangular and the linear variety. The rods have long and slender outer segments and ellipsoids (Figs 1A,C, 4D). In all regions they are arranged in a single layer of varying thickness, ranging between 38% of the whole retina dorsally and 21% temporally. No regular rod mosaic was found within the photoreceptor layer.

The equal double cones consist of two identically shaped members which are positioned at the same level (Fig. 1B). Subsurface cisternae run parallel to the cell membranes in the apposition zone of the inner segments of the two members. As a consequence, the parts of the nuclei which are scleral of the outer limiting membrane have neighbouring subsurface cisternae (Fig. 3D), which are absent more vitreally (Fig. 3D). The unequal double cones show the same fine structural features. However, in most cases, one of the two members is located slightly more vitreal than the other (Fig. 1A). In cases where they are positioned at the same level, one of the partner cells has a higher electron density, not being mistaken with the appearance of putatively degenerating photoreceptor cells (Fig. 1E).

The second main type of cone, in addition to the double cones, is long single cones. Their size, shape and morphological features are the same as those of a single member of double cones (Figs 1B,C, 2). Only in a few regions do their cross-sectional diameter and length appear to be slightly smaller (Fig. 3C). Their outer segments terminate at approximately the same level within the retina as those of double cones, sometimes slightly more vitreally (Fig. 1B). Triple cones occur only sporadically. They consist of three photoreceptors with subsurface cisternae at their apposition zones (Fig. 4B). Two different types could be distinguished. The first type are the triangularly arranged triple cones (Fig. 4B), the inner segments of the three cells adjoining each other in

the centre of the complex. The second type are the linearly arranged triple cones, the inner segments of which are lying in a row, one inner segment on each side of the central one. The triple cones are situated at the same level within the retina as the double and long single cones and consist of three equally sized photoreceptors, the outer and inner segments of which are positioned at the same level (Fig. 4B).

As to the fine structure, the cones of the garfish show the basic features of this photoreceptor type. The outer segment discs are orientated perpendicularly to the longitudinal axis of the outer segment. An accessory outer segment, being a sclerad continuation of the eccentrically located connecting cilium joining the cone inner and outer segment, is situated along the outer segment proper (Figs 1C, 3A, 4C). In the double cones these accessory outer segments can be positioned in the cis position (at the same side) (Fig. 3A) or in the trans position (at the two opposite sides of the two outer segments).

Cone ellipsoids are filled with mitochondria. Especially in the dorsal region, we found a vitreo-scleral gradient, the density of the mitochondria increasing in the sclerad direction, the mitochondria at the same time attaining a more regular arrangement (Figs 1C, 4A,C).

From the scleralmost to the middle portion of the cone ellipsoids, a cytoplasm of low electron density forms a kind of ring around the mitochondria which are concentrated in the centre of the ellipsoids (Figs 1C, 2, 3B,C, 4C). Close to the mitochondria this cytoplasm contains bundles of longitudinally-orientated filaments extending sclerally to the distalmost part of the inner segment (Fig. 2). A number of calycal processes originate from the sclerad part of the inner segment and surround the vitread part of the outer segment (Fig. 3A); each calycal process contains a single longitudinal bundle of cytoplasmic filaments.

Cone patterns and regional differences of the retina

Contrary to the rods, the cone photoreceptors exhibit distinct and highly geometrical patterns in the light-adapted state, with double cones and long single cones as the main elements (Figs 1D–G, 3A–D, 4A). Five distinct patterns can be identified but also transitory patterns between the different types of mosaics are found:

- pure row pattern (ventro-temporally, peripherally): the equally arranged double cones form parallel rows with long single cones standing equidistantly between the double cone rows (Fig. 3A).
- twisted row pattern (whole ventral region; nasally, peripherally; ventro-temporally, peripherally): the double cones, more or less twisted along their main axes form parallel rows. The position of long single cones is as in the pure row pattern (Figs 1D, 3B–D). Sometimes the double cones are twisted approximately 45° along their longitudinal axis which gives the impression of a square pattern (Fig. 1D).
- square pattern (dorso-temporally; centrally): four double cones are arranged in a square with one long single cone in the centre (Fig. 1E).
- pentagonal pattern (occurring sporadically in small areas dorso-nasally, centrally; temporally, peripherally): five double cones are arranged around one central long single cone (Fig. 1F).
- hexagonal pattern (dorsally): six double cones are arranged around one central long single cone with each double cone being also part of two other neighbouring hexagonal units (Figs 1G, 4A).

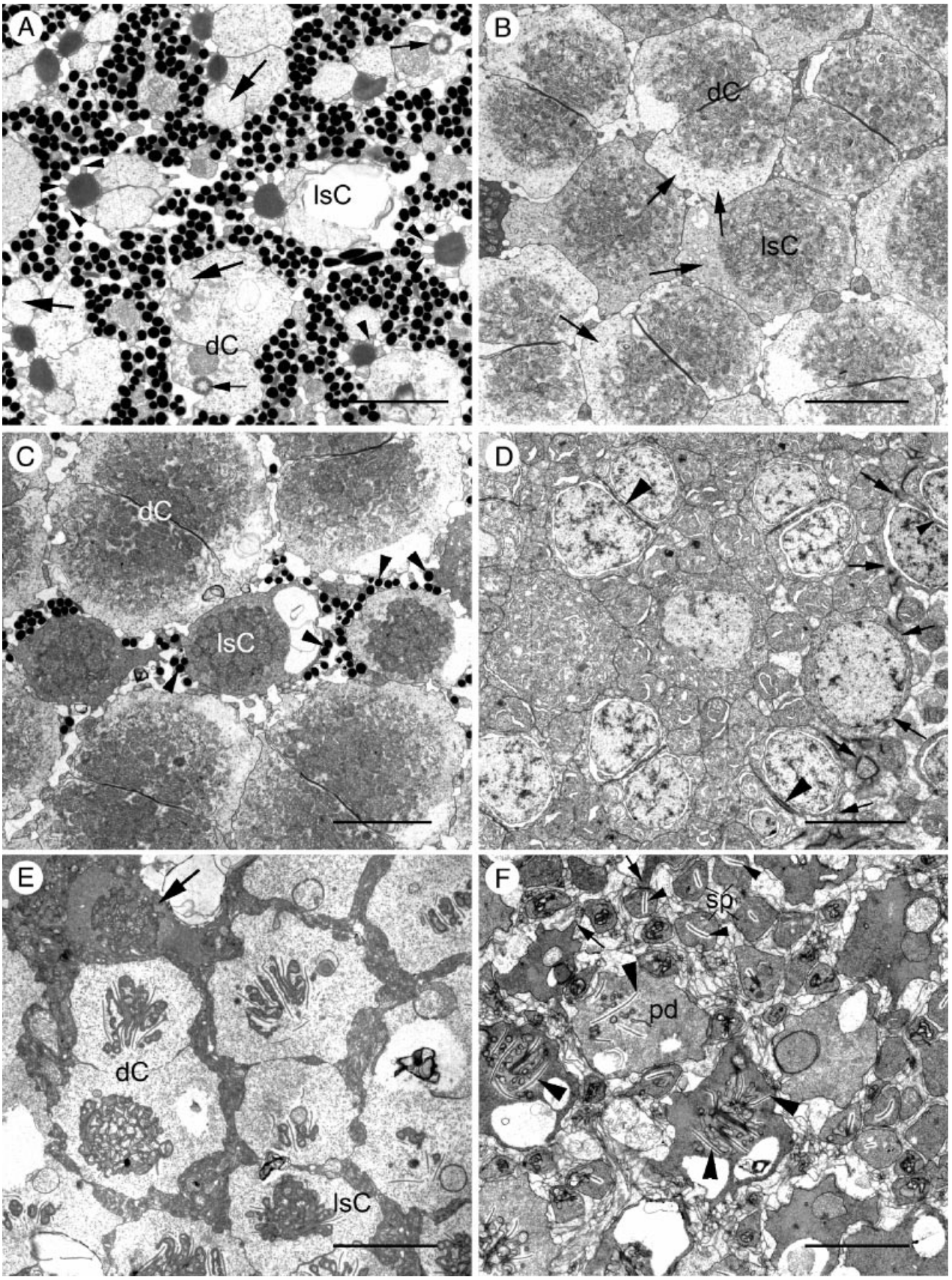
The exact distribution of the different cone patterns is shown in Fig. 5(A).

The ratio between double cones and long single cones is 2 : 1 throughout the retina (each double cone is counted as a single functional unit) except for the whole ventral region where the ratio is 1 : 1 (Fig. 5A).

As well as the distribution of the different pattern types across the retina, the shape and density of the cone photoreceptors varies between the different regions (Figs 1A–G, 2, 3B,C, 5B). Three maxima of double cone density were observed: ventro-nasally and ventro-temporally we counted 18000 double cones/mm^2, and dorso-temporally 14000 double cones/mm^2. This parallels an increase in relative thickness of the inner nuclear layer in these regions (13.8% up to 16.4% of the whole retina) compared to other areas with less cone densities (4.9% to 11% of the whole retina). The lowest double cone densities, however, were found in the dorso-nasal area, with 6000 double cones/mm^2. The exact distribution of densities can be taken from Fig. 5(B). Generally, in the peripheral regions there are higher cone densities than in the corresponding central areas. This is in accordance with the different shapes and dimensions of the cones: in the periphery the cones are more slender and densely packed than in the centre where cones are usually longer and more bulky. This can be noted in the central dorsal region especially, where not only the cone ellipsoids but also their outer segments are very large (Fig. 1C) compared to the more slender but extraordinarily long outer segments of the ventral and ventro-temporal cones (Fig. 2) which can reach up to 130% of the ellipsoid's length. An exact measurement of the total cone length is difficult because usually the tips are broken off and complete cones are very rarely found in our specimens. The exact sizes of rods and cones in selected regions are shown in Table 1.

Intraocular septum

The ventral region is covered by an intraocular septum, a curtain-like structure which has its origin in the optic disc. At its base, the septum has a type of stalk consisting of fibers of the optic nerve and choroidal tissue penetrating the choroidal fissure accompanied by a collar of the pigment epithelium extending vitreally and forming a sheath around parts of the curtain. From this stalk the septum spreads horizontally



into the vitreous body in the lower third of the eyecup (Fig. 6A,B,F). Centrally in the eyecup this tissue is fixed to the retina. Here the retina shows a little notch in the area of mutual contact which appears as a weakly stained 'line' running horizontally (Figs 5A, 6B). Dorsal to this 'line' the retina is thicker (ranging between 280 and 490 μm) than in ventral retina (ranging between 170 and 250 μm) and without any conspicuous difference concerning the different retinal layers. Laterally, on both sides of the pupil, the curtain is fixed at the ventral iris with two ligaments. It surrounds the lens at its lower fifth section leaving open some kind of semicircle allowing light from dorsal to reach the retina (Fig. 6B). From the curtain, a thin pigmented blood vessel extends ventrolaterally to the lens muscle. In the intraocular septum, traversed by blood vessels, we found pigmented cells containing many melanin granules of the same type and shape as those found in the pigment epithelium (Fig. 6C). In the extracellular matrix, collagen fibrils were abundant (Fig. 6D). Spectrophotometric analysis revealed the curtain to be nearly impermeable for wavelengths between 350 and 870 nm.

Structure of the outer plexiform layer

In the light-adapted state, we found regular cone patterns in the outer nuclear layer corresponding well to the respective ellipsoid patterns (Fig. 3B–D). In the outer plexiform layer, however, the only regular arrangement which occurred was a row pattern with double cone pedicles arranged in parallel rows and long single cone pedicles alternating between them (Fig. 3E). An identification of the different pedicle types was very difficult, therefore we cannot exclude other cone patterns at the level of the outer plexiform layer.

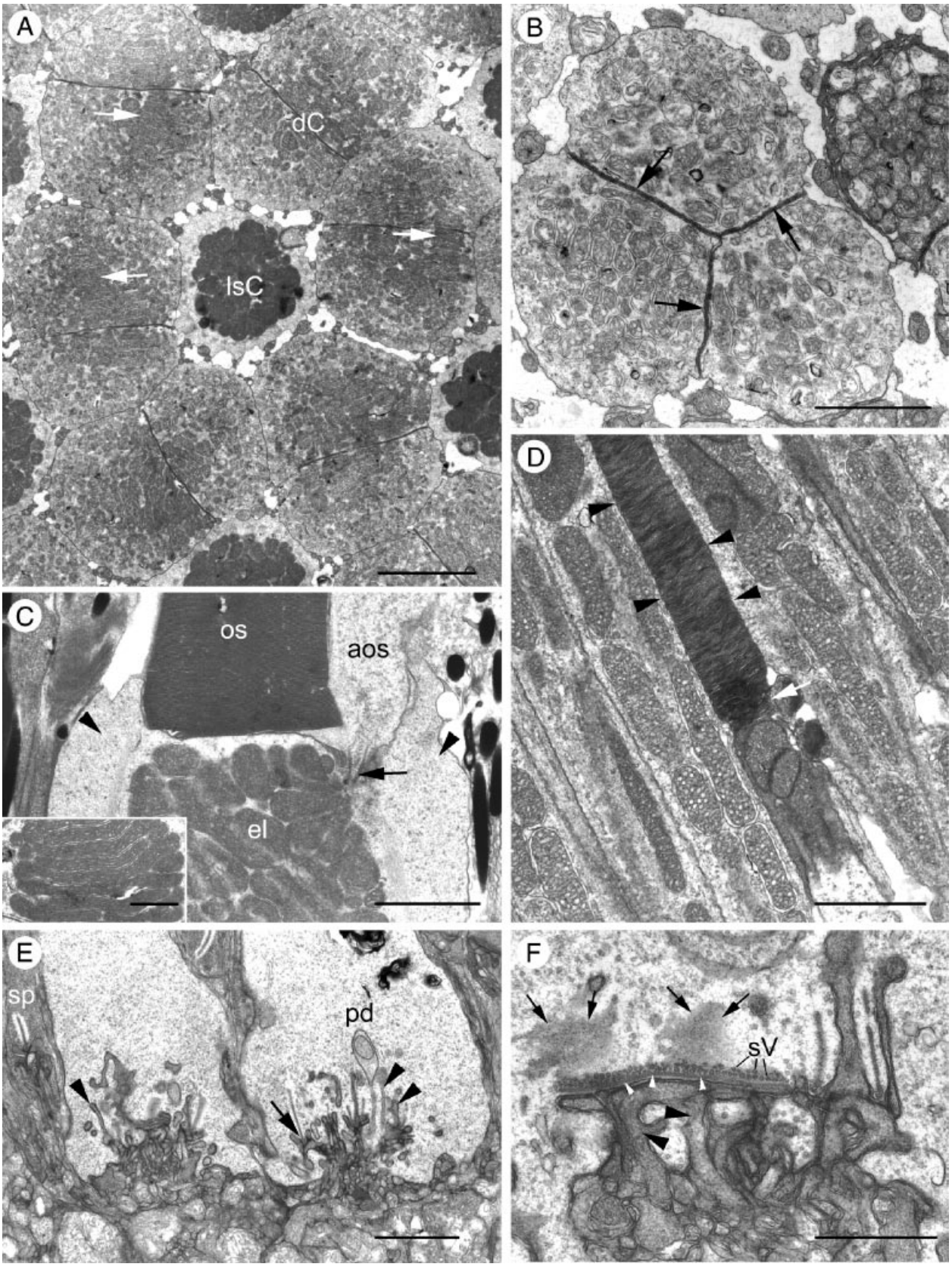
However, there are typical morphological and fine structural features which allow the distinction between cone pedicles and rod spherules. Rod spherules are rather small and of higher electron density than cone pedicles (Figs 3F, 4E). Furthermore, they terminate more sclerally compared to cone pedicles (Figs 2,4E). Spherules are also characterized by a single synaptic ribbon and a single subsynaptic invagination containing the fibers of horizontal and bipolar cells, the second order neurones (Figs 3F, 4E). Contrary to the rod spherules, the cone pedicles are much larger, with those of double cones being closely apposed (Fig. 3E). They possess telodendrites projecting to the neighbouring cells (Fig. 3E,F) and have several invaginations rather than a single one (Figs 2, 3E,F, 4E). Here one finds the so-called triad, two lateral cell processes probably from horizontal cells, and one central cell process probably from a bipolar neurone (Fig. 4E). At the base of the synaptic ribbon, just sclerally of the arciform density, an aggregation of synaptic vesicles can be found (Fig. 4F). In transverse sections, no differences between long single cone pedicles and those of individual members of double cone pedicles could be seen. All cone pedicles have the same relative position within the outer plexiform layer (Figs 3E,F, 4E). We also found several pedicles with higher electron densities (Fig. 3E) but we were unable to make a correlation to a special cone type.

The dark-adapted retina

Compared to the light-adapted state, the dark-adapted retina shows some basic differences. The melanin granules of the retinal pigment epithelium are concentrated within the somata of the cells, and its processes are withdrawn sclerally (Fig. 7A,B). Rod myoids are contracted bringing the rods into a more vitreal position compared to the cones. Cone myoids, however, are elongated and their outer segments reach sclerally into the pigment epithelium (Fig. 7A,F). Looking at the photoreceptor layer, one can see that there are two strata of cones with double cones having a more scleral position than long single cones which reach about half the length of rod outer segments (Fig. 7A,C,E). As a consequence, no regular arrangement of the cone ellipsoids was found in most of the regions (Fig. 7E). Any regular pattern present is a row pattern (Fig. 7C). Though in the outer nuclear layer, we observed regular cone patterns corresponding well to the respective ellipsoid patterns seen during light adaptation.

Typical dark adaptation is missing in the peripheral and in part of the central ventral retina (Fig. 7B,D). Here, a twisted row pattern of cones is found at both the ellipsoid level and the outer nuclear layer (Fig. 7D). The cones are elongated,

Fig. 3—Photoreceptor fine structure in the light-adapted retina, electron microscopy, tangential sections. —**A**. Pure row pattern area sectionned at the level of the connecting cilia (*small arrows*) of the cones, large accessory outer segments (*large arrows*) in 'cis' position can be seen. Note the calycal processes (*arrowheads*) surrounding the vitread part of the outer segment. —**B**. Twisted row pattern in the central ventral area at the ellipsoid level. In this region the long single cones have about the same size as a single member of a double cone. Note the low electron density cytoplasmic bulges (*arrows*) around the mitochondria. —**C**. Same as in B but in the peripheral temporal region. At this level the long single cones have a smaller cross-sectional diameter than a single member of a double cone. Note the melanin granules (*arrowheads*) occurring even at this vitreal level. —**D**. Same as in B but close to the membrana limitans externa (*arrows*). Subsurface cisternae (*large arrowheads*) are seen in between the parts of the double cone nuclei located sclerad to the external limiting membrane, but absent vitread to this membrane (*small arrowhead*). —**E**. Tangential section in the outer plexiform layer. Double cone pedicles and long single cone pedicles arranged in a pure row pattern show the same fine structural features. Note the single cone pedicle with high electron density (*arrow*). —**F**. Same as in E. Rod spherules have only one synaptic ribbon (*small arrowheads*), in cone pedicles the ribbons (*large arrowheads*) are more abundant. Note the telodendrites (*arrow*) projecting to neigbouring cells. Bars: 4 μm – *dC*, double cone. – *lsC*, long single cone. – *pd*, cone pedicle. – *sp* rod spherule.



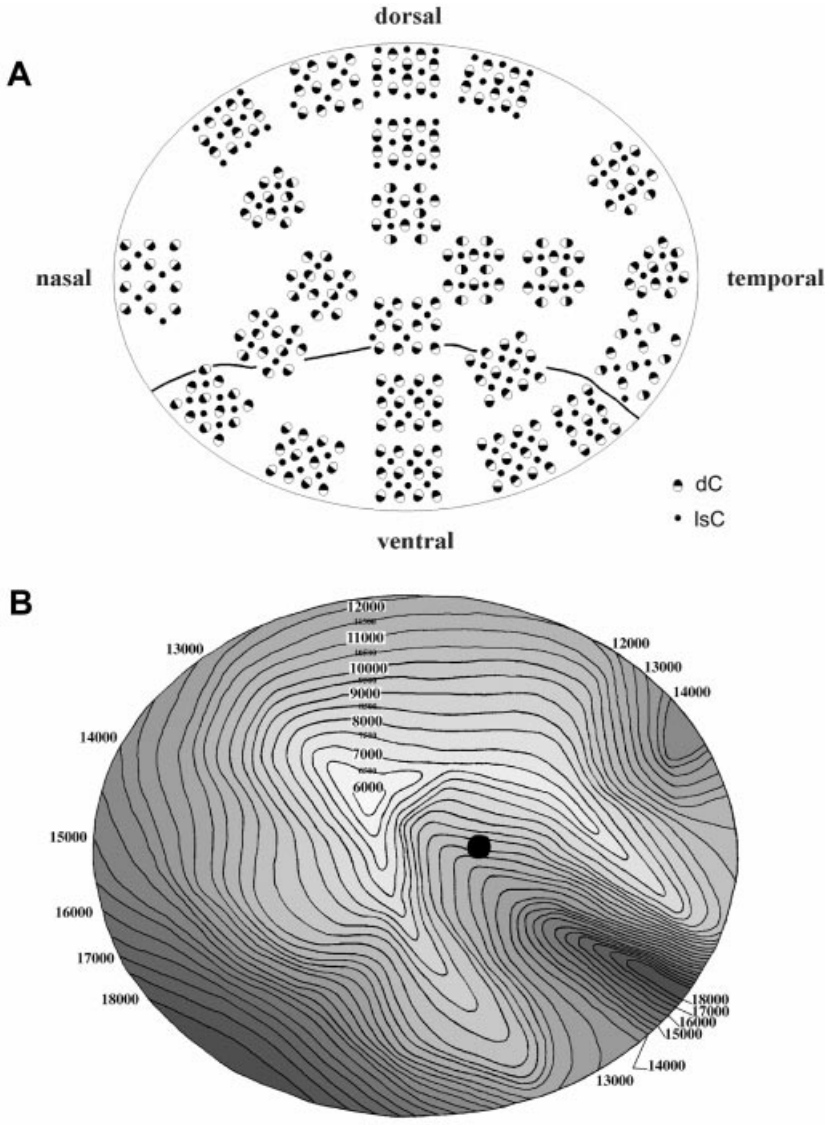


Fig. 5—Diagrams of regional variations in cone patterns and densities, both from left eye. —**A**. Distribution of the different cone patterns within the retina of *B. belone*. The solid line represents the border between a double cone/long single cone ratio of 2 : 1 dorsally and of 1 : 1 ventrally. The curtain is inserted at the retina at about the same place. —**B**. Distribution of double cone densities indicated as double cones/mm^2. Intervals between neighbouring lines represent a difference of 500 cones/mm^2. The black spot represents the optic disc. – *dC*, double cone. – *lsC*, long single cone.

Fig. 4—Photoreceptor fine structure in the light-adapted retina, electron microscopy, tangential (A, B) and radial (C–F) sections. —**A**. Hexagonal unit in the dorsal periphery at the ellipsoid level of the double cones, six double cones (*dC*) surround one centrally located long single cone (*lsC*). Note the regular mitochondrial arrangement (*arrows*) in the ellipsoid's core region. —**B**. Triple cone of the triangular type with subsurface cisternae (*arrows*) in the apposition zones of the neighbouring cells. —**C**. Cone longitudinal section of the transition between ellipsoid (*el*) and outer segment (*os*). Note the connecting cilium (*arrow*) joining the cone inner and outer segment and its sclerad continuation into the large accessory outer segment (*aos*). Around the mitochondria the large cytoplasmic bulge (*arrowheads*) can be seen; insert: densely packed, regularly arranged mitochondria. —**D**. Rod longitudinal section. The outer segment contains a stack of individual disks situated within the plasma membrane (*arrowheads*), only the vitreadmost disks being continuous with the plasma membrane and open to the extracellular space (*arrow*). —**E**. Two cone pedicles (*pd*) probably from a double cone unit. Apart from numerous synaptic invaginations (*arrowheads*) a so called triad can be seen (*arrow*). Note the rod spherule (*sp*) terminating more sclerally. —**F**. Detail of a longitudinally sectioned cone synaptic ribbon. The darker stained areas (*arrows*) are part of the side of the synaptic ribbon. Scleral to the arciform density (*small arrowheads*) one can see an aggregation of synaptic vesicles (*sV*). Note the dendrites of second order neurones (*large arrowheads*). Bars: A 4-µm; B–E 2 µm; C insert 1 µm; F 1 µm.

	dorsal						**ventro-temporal**					
	periphery			central			periphery			central		
	dC	lsC	r	dC	lsC	r	dC	lsC	r	dC	lsC	r
n	40	40	30	30	30	30	40	40	16	40	40	30
md	11.0	8.6	1.4	11.5	6.3	1.4	5.8	3.1	1.3	7.2	5.2	1.4
SD	0.8	0.8	0.2	1.2	1.0	0.2	0.9	0.7	0.2	0.6	0.6	0.1
n	20	10	–	13	4	–	–	2	–	6	6	–
ml	66.4	50.8	124–140[1]	65.2	56.3	128–140[1]	mnp	69	60–70[1]	60	56.7	88–105[1]
SD	4.2	5.0	–	3.1	3.2	–	–	–	–	7.4	1.7	–

[1]rod layer was approximately measured from the vitread limit of the nuclear membrane of the scleralmost nuclear layer to the sclerad limit of the outer segment.

Table 1 Photoreceptor sizes of selected regions in *B. belone*. *dC* double cone, *lsC* long single cone, *md* mean diameter in µm (measured in the middle of the ellipsoid in cones and in the middle of the outer segments in rods), *ml* mean length in µm (measured from the vitread limit of the nuclear membrane to the sclerad limit of the outer segment), *mnp* measurement not possible, n number of measured cones, *r* rod, *SD* standard deviation

but no genuine rod-cone stratification can be seen, since the rods are standing between the cones. Even the pigment epithelium has small processes reaching the cone outer segments (Fig. 7B,D).

Discussion

Our results indicate that both the general features of the eye and the fine structural characteristics of the retina, e.g. pronounced regional differences of the retina comprising variations in cone patterns and cone types, can be interpreted as adaptations of *B. belone* to its habits as a visually orientated predator foraging under bright light conditions just below the surface.

Cone densities

The garfish has very high cone densities, which is one of the prerequisites for a high visual acuity, compared to bottom-living or non predatory teleosts and even predatory cyprinids like the asp (Zaunreiter *et al.* 1991). They are similar to other visually orientated predators, e.g. the walleye (Ahlbert 1969) or coregonids (Reckel *et al.* 1999b) but far less than in certain reef fishes feeding on very small prey like, e.g. polyps (Munz and McFarland 1973). Classical areae with a marked increase in thickness of the retina as have been described by Munk (1970), are missing. However, the three maxima of cone density (ventro-nasally, ventro-temporally and dorso-temporally) are seen in regions which process visual stimuli from the dorsal and anterior parts of the visual field, which are especially important to the visually guided predation. This assumption was verified by personal observations of the belonid feeding behaviour, made by the authors who observed belonids attacking their prey, mainly schools of small fish, from below and from behind (Fig. 6E). Therefore, the ventral and ventro-temporal region of the retina in particular requires adaptations for movement detection and high visual acuity. In addition, the ventro-nasal peak might help the garfish to detect predators, e.g. birds attacking from above.

Density peaks in the retina of teleosts mainly occur in two different forms: round or oval and horizontal band-shaped areas. The former are thought to improve resolution in small but important sections of the visual field and are often used in binocular vision. The latter are discussed to provide a lower threshold for movement perception (Munk 1970; Collin and Pettigrew 1988a,b). Among numerous examples of this phenomenon, the Florida garfish *Lepisosteus platyrhincus* deserves peculiar attention. In studying the 'garfish', which represents a fish group not closely related to belonid garfish but with similar habitus and life habits as a predator living close to the surface, Collin and Northcutt (1993) observed retinal specializations and peaks of ganglion cell densities in similar parts of the retina for which we have shown maxima of photoreceptor density in *Belone*.

Cone patterns

The retina of *B. belone* is characterized by pronounced regional differences in retinal structure, not only regarding photoreceptor densities, but also their patterns, i.e. there are different cone patterns specifically distributed within the different areas of the retina.

In regions of highest cone densities, a twisted row pattern predominates, which differs from the square pattern which many other teleosts have in these areas (Lyall 1957a; Ahlbert 1973). Obviously not only square patterns are related to an improved sensitivity to movement and to similar functions (Kunz 1980; Collin and Collin 1999), but also twisted row patterns, such as those detected in the garfish. Furthermore, this pattern can be viewed as an effective tool for packing together the different cone types in high density regions. This supports the suggestion of Fernald (1988), that row mosaics are an adaptation for enhanced motion detection. Typical predatory blue water fish like the mackerel (*Scomber scombrus*) also have this cone pattern (Engström 1963a). However, the gradual change from row (periphery) to square pattern (near fundus) in many regions corresponds with other observations (Lyall 1957a). Another remarkable observation is the hexagonal pattern viewed in the peripheral dorsal

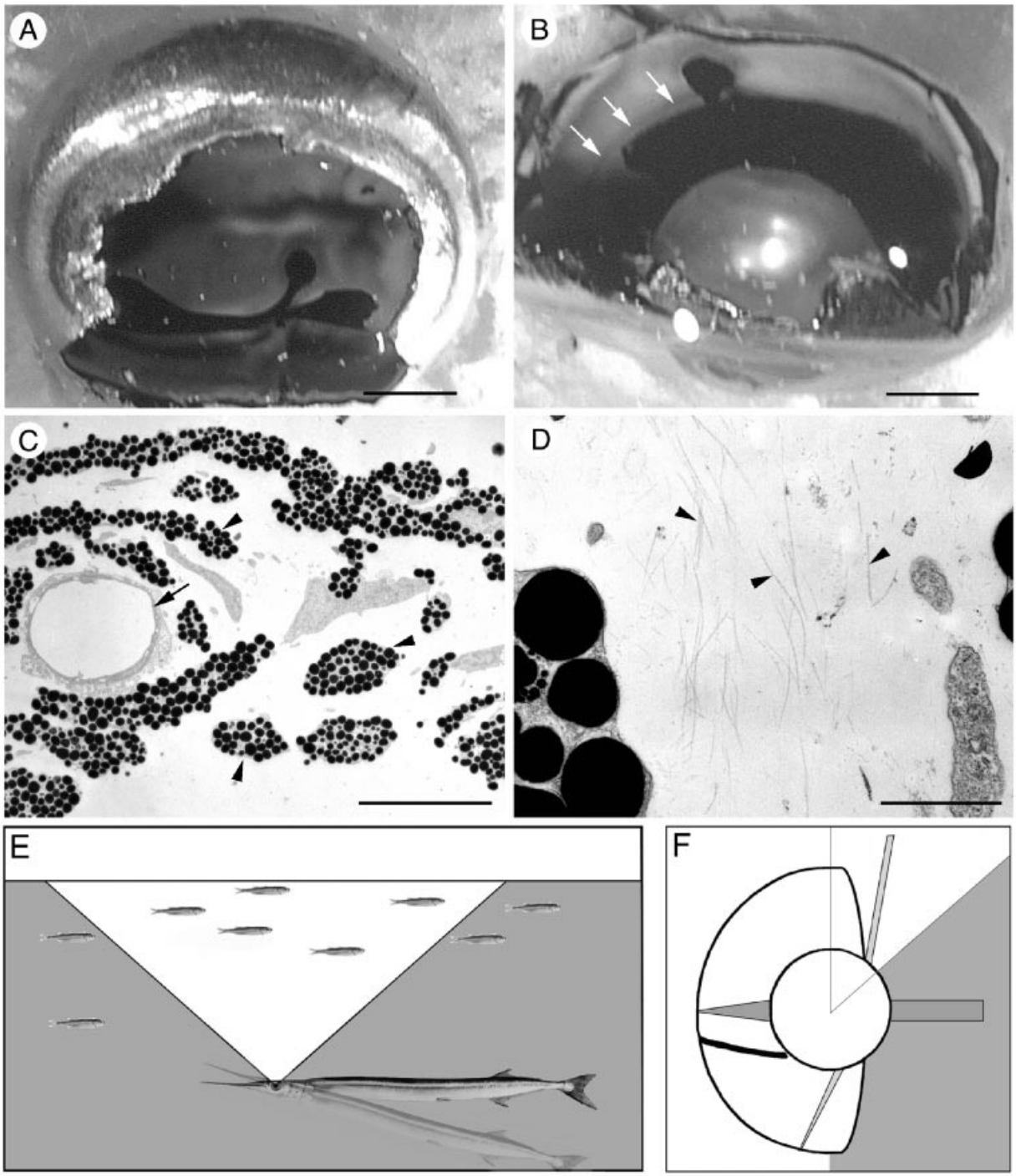
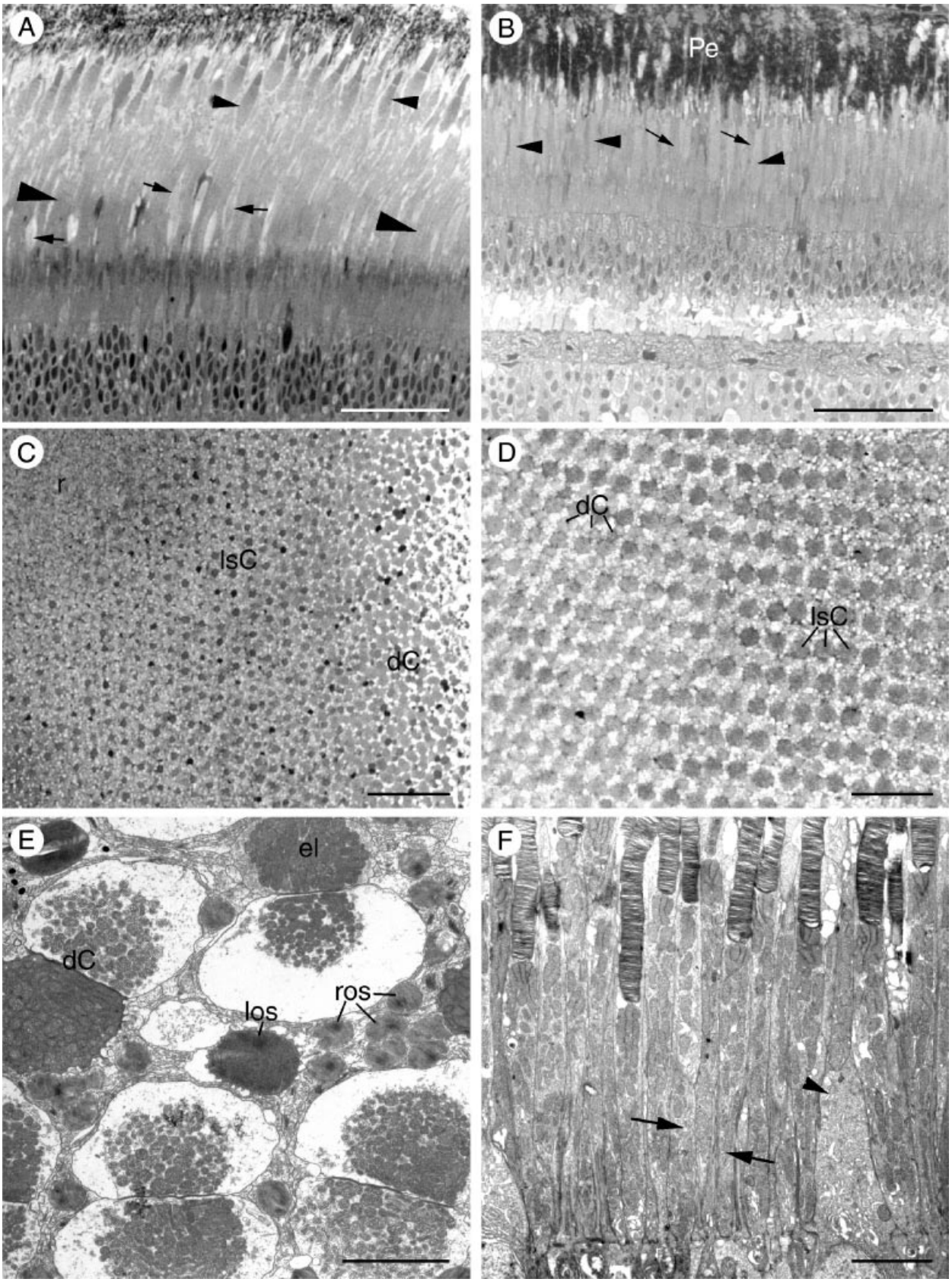


Fig. 6— Curtain-like structure in the eye. A and B are from dissected eyes, C and D are TEM-pictures; E and F are schematical illustrations of Snell's window and its effects on the vision of the garfish. —**A**. Lateral view of the left eye, cornea and lens removed. —**B**. Dorsal view of the right eye, dorsal part of the eyecup removed. Note the weakly stained line indicating the notch in the retina (*arrows*). —**C**. Cross section of the curtain with blood vessel (*arrow*) and packs of melanin granules (*arrowheads*). —**D**. Detail of collagen fibrills (*arrowheads*) in the extracellular matrix. —**E**. *B. belone* preying on silversides (small fish) and the position of Snell's window in calm water near the surface. The white triangle represents the high brightness area in the centre subtending an angle of 97°. The shaded area shows the region with lower light intensities outside the window. The transparent image demonstrates a second observed position of the garfish before attacking its prey. —**F**. Vertical meridional section of the left eye (frontal view) to explain how Snell's window is projected onto the retina with the curtain-like structure (solid black line) at the window's border. Bars: A and B 2,5 mm; C 10 µm; D 1 µm.



retina where cones face the lowest light intensities during the day. Hexagonal patterns are very rare in teleost retinae. Lyall (1957a) described some form of hexagonal pattern found in the northern pike *Esox lucius*, which can be derived from triangular units with double cones having a starlike arrangement around one central single cone. Yet the hexagonal pattern of the garfish is different. It can be derived from pure row patterns with double cones regularly being shifted against each other. Two of these shifted rows with long single cones between them are the basis for hexagonal units which can be formed by a twist of the double cones along their longitudinal axis. As a consequence, the double cones of *B. belone* within the hexagonal pattern are twisted between 45° and 90°, with respect to those of *E. lucius*. This pattern resembles the hexagonal arrangement of rhabdomeres, i.e. the microvillous portions of the photoreceptors containing the chromophores in the ommatidia of compound eyes (Meinertzhagen 1991). Each double cone of a hexagonal unit is also part of two other units, which explains the double cone/long single cone ratio of 2 : 1 in this region. The significance of this pattern for dim-light vision is not yet clear. Collin *et al*. (1998) suggests that rod hexagonal patterns maximize photon capture in the deep-sea pearleye *Scopelarchus*. The high share of the rod layer in the dorsal retina, looking down into lower light intensities, shows general adaptation of this retinal part for high light sensitivity.

Another point to be considered is the development of cone patterns. Teleost retinae grow throughout life by addition of cones from a peripheral growth zone (Lyall 1957b; Fernald 1991). In *B. belone*, we observed that peripheral and central cone arrangements vary, and even in adjacent peripheral retinal regions the mosaics differ. This indicates that mechanisms responsible for cone pattern formation may be loci-dependent. Cameron and Easter (1995) suggest that either interactions between central and peripheral retina, signals given by the ora serrata itself or induction by the pigment epithelium are possible mechanisms for controlling the spatial mosaic organization. Direct interactions between cone subtypes are proposed by Raymond *et al*. (1995) for changing the protomosaic found at the retinal margin into the fully developed cone pattern. The findings presented here indicate that the general mechanism of pattern formation can be specifically expressed in relatively small retinal areas, which results in different cone arrangements even in adjacent peripheral regions.

Cone types

Apart from the varying cone pattens and cone densities throughout the different regions of the retina, the well-developed cone repertoire of *B. belone*, mainly double cones (equal and unequal) and long single cones, is one of the characteristics for vision-based feeders. In many teleost groups, the different cone morphologies also reflect different receptor-specific wavelength sensitivities, which are often the same even between different families. In certain double cones, the principal member of a double cone pair contains a red sensitive pigment and the accessory member a green sensitive pigment (Marc and Sperling 1976 for goldfish; Bowmaker and Kunz 1987 for brown trout; Robinson *et al.* 1993 for zebrafish). Ali *et al.* (1977) reported an absorbance maximum for twin cones in the red part of the spectrum at 630 nm in the yellow perch and at 620 or 630 nm in *Stizostedion* sp. Long single cones often have their maximal sensitivity in the blue part of the spectrum (Bowmaker and Kunz 1987; Robinson *et al.* 1993). Munz and McFarland (1973) report a visual pigment of 501 nm in *Strongylura incisa*, another representative of the belonids, but unfortunately without any relation to a special photoreceptor type. While these cone types, using structural criteria, can be identified in the adult garfish, short single cones, which serve as UV- or blue receptors in many teleosts, (Marc and Sperling 1976; Bowmaker *et al.* 1991; Raymond *et al.* 1993) seem to be absent.

A further cone type observed sporadically in *B. belone* is the triple cone. In general, there is little known about this photoreceptor type, even if they are repeatedly found in teleost retinae (Engström 1963a; Ali and Anctil 1976; Collins and MacNichol 1978; Heß *et al.* 1998). The opinion about their possible function and origin ranges from 'macroreceptors' of increased sensitivity (Kunz *et al.* 1985) to a result of mechanical disturbance of the retina (Cameron and Easter 1995). A function of triple cones as single and double cone precursors during ontogeny is discussed in Shand *et al.* (1999).

Our study reveals that each photoreceptor type can be identified from the outer segment level vitreally to the outer nuclear layer and, with some difficulties, even to the outer plexiform layer. Here, morphological features such as the relative position in the layer, electron density and number/

Fig. 7— Gross morphology, regional differences, and fine structure of the dark-adapted retina, light (A–D) and electron (E, F) microscopy. A, B, F, radial, C–E, tangential sections. —**A**. Dorsal periphery; typical dark adaptation. Rods (*large arrowheads*) are positioned vitreally of the cones. Note the cone stratification with long single cones (*arrows*) standing more vitreally than double cones (*small arrowheads*). —**B**. Ventral periphery; incomplete dark adaptation. The pigment epithelium is concentrated sclerally but the rods (*arrows*) are standing between the cones (*arrowheads*). —**C**. Temporal periphery; typical dark adaptation. Note that cones are forming a row pattern instead of a square pattern as seen during light adaptation. —**D**. Same as in B. Cones are arranged in a typical twisted row pattern. —**E**. Retinal zone lacking a regular cone pattern. Rod outer segments (*ros*) and long single cone outer segments (*los*) are located between double cone ellipsoids (*el*). —**F**. Vitreally positioned rods near the membrana limitans externa. Rod myoids (*arrows*) are contracted whereas cone myoids (*arrowhead*) are elongated. Bars: A–C 50 μm; D 25 μm; E and F 5 μm – *dC*, double cone. – *lsC*, long single cone. – *Pe*, Pigment epithelium. – *r*, rod.

arrangement of synaptic ribbons can be used for identification of the pedicles (see Goede and Kolb 1994, 1995). To distinguish between long single cone pedicles and those of individual members of double cones, it is necessary to consider their position in the pattern because there are no distinct morphological differences between them (see also Braekevelt 1992).

In multi-layered tissues such as the retina, there are many ways to influence and modify the path of light to the photosensitive regions. For example, Novales Flamarique *et al.* (1998) propose that membraneous partitions in paired cones function as dielectric mirrors and play a decisive role in detecting polarized light. In *Strongylura timucu*, a relative of *B. belone*, Ali and Anctil (1976) found oil droplets at the scleral ellipsoid end. Generally, these elements are supposed to act as colour filters (Borwein 1981) or as microlenses with light-gathering functions (Young and Martin 1984). In *B. belone*, we did not find any oil droplets, but we did find ellipsoid mitochondria arranged in a highly-ordered grouping, combined with a vitreo-scleral density gradient, especially in the dorsal region. Such a light gathering system would correspond well with the large size of dorsal cones, as also described by (Bathelt 1970) for several teleosts, since the light-collecting surface is enlarged in a region where cones face the lowest light intensities. This assumption is supported by the observation of Munz and McFarland (1973, 1977) who found that diurnally feeding teleosts often have smaller and more slender cones than nocturnal ones. In the adult killifish, Anctil and Ali (1976) also found a vitreo-scleral density gradient of mitochondria, but in connection with a maturation process of the mitochondria resulting in oil droplets at the scleral end of the cone ellipsoid.

A possible function of the cytoplasmic bulge around the ellipsoid's mitochondrial core region is not known. A role as a cytoplasmic reservoir, e.g. for cone elongation during retinomotor movements, as has been discussed for cone inner segment fins (Burnside 1978) can be excluded, since the bulges occur both in light-and dark-adapted states in the same extension.

Special features of the ventral retina and dark adaptation

Obviously the ventral region facing upward towards the surface plays an important role in the vision of the garfish. Here one finds the highest general cone densities and a double cone/long single cone ratio of 1 : 1. Within the eye, the curtain-like structure containing pigment granules divides the retina into two areas. Dorsally of this intraocular septum, the double cone/long single cone ratio is 2 : 1, the cone ellipsoids are longer, their outer segments are thicker, and also the retina is thicker than ventrally. Hanyu (1959) found a similar structure in *Ablennes hians*, another member of the belonids and Schwartz (1971) and Saidel (1987) in *Pantodon buchholzi* and other Osteoglossidae, ancestral surface living teleosts. At first it seems to be contradictory to the eye's function to have a large pigmented structure within the vitreous cavity. What then, could be the function of such a strange curtain?

In calm water near the surface lies a sharp boundary at Snell's window between high brightness in the centre and lower light intensities outside the window due to the angle of 48.5° for total reflexion of light at the water/air surface (Lythgoe 1979). Considering the lens which focuses downward directed light onto the ventral retina and light from a lateral direction onto the central retina, plus the different morphologies of the two regions, one can assume that the ventral retina is specialized for bright light vision within Snell's window and the rest of the retina for vision at lower light intensities in the remaining part of the visual field, with the septum absorbing light stimuli from the border of Snell's window. Therefore, the curtain's function can be viewed as a shield separating two morphologically different regions.

For *Pantodon*, a species preying directly at or even above the water surface, Schwartz (1971) suggested that the curtain enables the fish to look through the water surface within Snell's window with its specialized ventral retina, e.g. to detect passing prey. *Belone*, however, forages exclusively below the water surface and hence has to detect prey passing in front of or against Snell's window with its higher light intensity and contrast (Fig. 6E), features for which *Belone's* ventral retina seems to be well-adapted by having relatively small cones arranged in a high density. Apart from this, the higher amount of single cones might also reflect the optical properties of Snell's window. In order to settle this question, the spectral sensitivity of ventral cones have to be measured. At the border of Snell's window the visual requirements change abruptly. Here, in the respective part of the retina which processes signals from this border, the curtain is inserted. Schwartz (1971) suggested that the intraocular septum divides the visual field with the water surface being projected directly onto the septum. Assuming a change in photoreceptor sensitivity, which is necessary to optimize vision at the border of Snell's window, one can conclude that the curtain might allow adequate light stimulus to enter the proper retinal region without disturbances, and protect the part of the dorsal retinal region which processes light stimuli from the border of Snell's window against glare, (Fig. 6E,F) therefore minimizing the part of the retina being dazzled. An additional function of the curtain could be the absorption of scattered light. See also Saidel and Bradford (1985).

In *Aplocheilus lineatus* and *Epiplatys grahami* two horizontal band-shaped areas are found, the ventral being thought to look into Snell's window and the central for lateral vision (Munk 1970). This corresponds to the two temporal density peaks observed in *Belone*, one being dorsal to the curtain and the other one being ventral. This seems to combine the demands for preying forward or upward under the optical requirements of Snell's window. Examples for further adaptations to Snell's window are provided in Horváth and Varju *et al.* (1995) for the grass shrimp *Palaemonetes vulgaris* and rainbow trout *Oncorhynchus mykiss*. A division of

the retina into different areas not only due to regional differences in photoreceptor populations but additional structures in the eye has also been observed in deep sea teleosts, e.g. in Scopelarchidae (Locket 1971; Collin *et al.* 1998) and in the 'four-eyed' fish *Anableps anableps* (Borwein and Hollenberg 1973).

Considering the fine structure of the curtain containing many blood vessels and connective tissue, its origin in the choroidal fissure and its position in the eye, a choroidal origin is likely. It might have developed from the falciform process, a thin plate of connective tissue projecting in the vitreous body (Locket 1977) occurring in many teleosts (Fiedler 1991). A role of this modified falciform process in controlling the retinal organization as is disscussed for other pigmented tissues (Silver and Sapiro 1981) is unlikely in the garfish, since *Pseudotylosurus angusticeps* and *Xenentodon cancila*, both fresh water forms of the belonid family, are lacking this structure. The falciform process is thought to be homologous to the conus papillaris, which can be found in many reptiles, and pecten oculi, which can be observed in several species of birds. These two organs are thought to have nutritive functions (Braekevelt 1989, 1994; Braekevelt and Richardson 1996). However, form and dimensions of the garfish's curtain can not sufficiently be explained by this.

Another remarkable fact is the lack of a full dark adaptation of the ventral retina, which also faces the highest light intensities during dim light conditions. The retained twisted row pattern could perhaps enable the garfish to prey even at night. This seems to correspond with our observations. We have caught garfish after sunset in darkness and watched them preying at night in the light of sardine fishing boats. Obviously moon- or starlight is sufficient to make the ventral region retain an almost light-adapted state.

The lack of cone mosaics in the dark-adapted state in several regions does not correspond to observations made by Kunz (1980) and Kunz and Ennis (1983) in *Poecilia reticulata.* In the latter fish, row patterns were always found during dark adaptation in regions containing square patterns in the light-adapted state. This is true for *B. belone* only in a few regions. A more definite determination of cone patterns independent of the state of retinal adaptation can be found at the level of the outer nuclear layer. While patterns obviously change with myoid elongation of cones during retinomotor movements, their nuclei remain fixed, probably stabilized by the network of Müller cell processes reaching scleral to the outer limiting membrane (Burnside 1978; Kunz 1980). The fact that cone nuclei form patterns which correspond well with the respective ellipsoid patterns in the same region during light adaptation, has also been observed in other teleosts, e.g. Labridae (Engström 1963b) and the guppy (Kunz 1980).

For the more vitreal position of the long single cones compared to the double cones during dark adaptation, there are two conceivable explanations. First, the two different cone types may form two different strata for spatial reasons. Secondly, the long single cones may take part in the scotopic vision during dim light conditions and thus have a better position relative to the light focused on the retina. To clarify this, it would be necesserary to know the spectral sensitivity and threshold of belonid long single cones. In certain teleost groups, this cone type belongs to the same red or green spectral class as one partner double cone, e.g. in the goldfish (Marc and Sperling 1976), pike perch or yellow perch (Ali *et al.* 1977). In other teleosts, however, they are blue sensitive (Lythgoe 1979; Bowmaker and Kunz 1987). Cone stratification during dark adaptation also occurs in other teleosts. In the guppy, Kunz (1980) observed short single cones retaining their vitreal position near the outer limiting membrane and long single cones extending sclerally but not as far as the double cones. She suggested a functional significance for this arrangement with vitreal cone ellipsoids acting as optical light guides for the overlying rods.

Epilogue

Our present study is part of an inquiry into the retinas of Atheriniformes which considers not only phylogenetic but also ecological aspects, such as habitat, light conditions and feeding habits of the respective species. Even though several well-known representatives belong to this group of teleosts, e.g. flying fishes or half-beaks, our knowledge of their retinal structure and differences between the families is rather poor. For the half-beaks *Zenarchopterus* sp. and *Dermogenys pusillus*, Waterman and Forward (1970) and Forward and Waterman (1973) have shown for the first time the perception of polarized light in vertebrates, a phenomenon whose morphological foundations are still not well-known (Novales Flamarique *et al.* 1998).

Only a few examinations of the belonid retina have been made so far. Friis (1879) mentions single and double cones in *Belone belone*, but no further descriptions are provided. In addition, the studies of Ali and Anctil (1976) on *Strongylura timucu*, revealed large numbers of rods and cones with single and double cones arranged in square patterns.

The findings presented here correspond well with these observations. Yet *B. belone* is far from having a 'normal' teleost eye. Detailed mapping of the whole retina shows that the retina's basic structure is modified in a very subtle way in these fish and can be seen as an optimization of photoreceptor equipment, patterns and densities. The latter are prerequisites for successfully foraging in the visual environment of the garfish. Furthermore, the upper few decimeters of the marine water column – the preferred hunting grounds of the garfish – deserve peculiar consideration. Here, one finds high light intensities coming through Snell's window, plus the light of the red and UV part of the spectrum unaffected by absorption as a result of the organic matter in the water column (Lythgoe 1979; Ali and Klyne 1985). The specialized ventral retina and the curtain might be only part of the solutions the garfish has found to surviving in his visual habitat.

Mechanisms of contrast enhancement would be appropriate additional tools for *B. belone* when looking for prey forward and upward.

Acknowledgements

We thank Hedwig Gebhart (Munich) for her excellent technical assistance and Terry Saks and Heidi Hefele for improving the English of the text.

This study was partly supported by the Graduiertenförderung Bayern.

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