

Ultrastructure of photo-sensory cells and pigment epithelium
in the retina of the Antarctic fish
Notothenia neglecta Nybelin (Nototheniidae)

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南極産の魚 *Notothenia neglecta* Nybelin (ノトセニア科)
網膜の光受容細胞と色素上皮の微細構造

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要旨: 南極産の魚 *Notothenia neglecta* はキングジョージ島, アドミラルティ湾の生息域では優先的に出現する魚である。本種は捕食者であり, しばしば, 正確な視覚を用いた待ち伏せ採餌を行う。そこで網膜の光受容細胞と色素上皮の微細構造を電子顕微鏡を用いて解析することとした。網膜には色素上皮と桿体, 短い独立型錐体, 長い独立型錐体, 不等双子型錐体, 三子型錐体の5種の光受容細胞とニューロン, 支持細胞が存在する。色素上皮はたたみ込まれた基底膜, 基底ミトコンドリア, 平滑な網状体, 大量の微小管, メラニン顆粒, 食作用胞, 光受容細胞の剝離膜で特徴づけられている。錐体には外節の二重膜状板, 楕円体・筋様体の副錐体, 連結繊毛, 微絨毛が, 楕円体中には中心小体, そして筋様体・楕円体域には掌状筋様体, ミューラー細胞の頂上微絨毛が存在する。これら総ての状態は, *N. neglecta* に環境の光条件の変化に対するあらゆる種類の適応を可能にし, *N. neglecta* を, 水平, 垂直方向に調整可能な10層に配置された細胞を持つという, 複雑な網膜を備える魚類の1種としている。このことが, 周年, 十分な視覚による行動と餌と環境との認知を可能にしているのである。

Abstract: The Antarctic nototheniid *Notothenia neglecta* is the dominant fish in its habitat in Admiralty Bay, King George Island. They are predators, often ambush feeders, with accurate visual behaviour. For that reason, the ultrastructure of retinal photoreceptive cells and the pigment epithelium was analysed through electron microscopy. Their retina has a pigment epithelium, five different photoreceptors: rods, short single, long single, double, and triple cones, and neurones and support cells. The pigment epithelium is characterised by infoldings of the basal membrane, basal mitochondria, smooth reticule, large amount of microtubules, melanin granules, phagosomes and detached membranes of photoreceptors. Cones show bimembranous discs in the outer segment, an accessory outer segment, a connecting cilium, calycal processes, microtubules in the inferior ellipsoid and myoid, centrioles in the ellipsoid, interdigitating myoid fins and

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apical microvilli of Müller cells in the myoid and ellipsoid region. All these features allow all sorts of adaptations to the environmental photic variations, and situate *N. neglecta* among fish with a complex retina, with cells that are arranged in ten layers, allowing horizontal and vertical integration among them. This allows optimal visual behaviour and perception of food and environment in every Antarctic season.

1. Introduction

Among the sensory systems, vision has a major role for fish that live in the photic region of the ocean. Several studies associate visual capacity with morphology and behavioural ecology in Antarctic fish (Eastman, 1988, 1993; Fanta *et al.*, 1994, 1999, 2001; Grötzner and Fanta, 1998; Macdonald and Montgomery, 1991; Meyer-Rochow and Klyne, 1982; Pankhurst and Montgomery, 1989).

Notothenia neglecta is a circumpolar demersal coastal species (DeWitt, 1971; Fischer and Hureau, 1985; Kock, 1989), frequently observed in middle of algae or in shelter (Burchett *et al.*, 1983; Daniels, 1982; Daniels and Lipps, 1982; Moreno and Zamorano, 1980). It is basically an ambush feeder that eventually feeds on the water column (Daniels, 1982; Moreno and Zamorano, 1980). Because it selects the food actively (Barrera-Oro and Casaux 1990; Fanta, 1999; Fanta and Meyer, 1998; Rios and Fanta, 1998), *N. neglecta* has prominent eyes, great interorbital distance, capacity of independent fast eye movements, and several different cones and rods (Fischer and Hureau, 1985; Grötzner and Fanta, 1998).

The structural analysis of the retina in some Nototheniidae suggests that there are no retinal adaptations that are specific for fish that live in shallow waters, or for vision in low light levels (Eastman, 1988; Meyer-Rochow and Klyne, 1982), but that there is considerable interspecific variation in the relative number of visual cells and some morphological features (Ali and Anctil, 1976; Eastman, 1988; Grötzner and Fanta, 1998).

The aim of this study was to analyse the ultrastructure of the pigment epithelium, and of cones and rods, to evaluate which structural features could explain the great ability that *N. neglecta* has to survive in different environments, and to detect and select varied food items, year-round.

2. Materials and methods

N. neglecta were collected in Admiralty Bay (King George Island, South Shetlands) with trammel nets, from 20 m depth. They were identified as *N. neglecta* Nybelin, 1951, according to Fischer and Hureau (1985), being considered different from *N. coriiceps* Richardson, 1844, which are also present in the bay (Fanta *et al.*, 2000). At the Brazilian Antarctic Station Comandante Ferraz, some healthy adult individuals of mean standard length 38.4 cm (33.7–47.2 cm) were selected and sacrificed, and the retina dissected out for morphological studies.

For transmission electron microscopy, the retina was cut in small pieces and fixed at 4°C in modified Karnowski for 3 hours (Culling *et al.*, 1985), followed by treatment with 2% osmium tetroxide in buffered 2% solution of 0.2 M cacodylate (pH 7.2), contrasted with

2% uranyl acetate. After dehydration in ethanol, embedding was in Epon-812 (Luft, 1961). They were examined under a JEOL-JEM 1200 EXII Electron Microscope.

3. Results

3.1. Pigment epithelium

In *N. neglecta* the retinal pigment epithelium is a single layer of cuboidal cells. They rest on and are firmly attached to the choriocapillary layer of the choroid. The hyaline Bruch's membrane or basal lamina provides the connection of the retina and the choroid, and consists of sparse collagen fibres (Fig. 1A).

The cells of the pigment epithelium are specialized in their apical or vitreal surface, which has a large number of microvilli that extend toward the neural retina to interdigitate with the outer segments of the photoreceptors, surrounding them. However, there is no connection between the membranes of pigment cells, and of photoreceptors. The basal region of the pigment epithelium cells shows many irregular infoldings. These infoldings of the membrane form a net of vesicles in the whole extension of the pigment epithelium (Fig. 1B).

Tight junctions such as zonulae adhaerens followed by maculae adhaerens sealed the intercellular spaces of adjacent pigment epithelium cells (Fig. 1C). The cytoplasm of these cells contains vesicles of smooth and of rough endoplasmic reticule, and a spherical nucleus. There is an abundance of oval and elongated mitochondria, and a Golgi complex, both located mainly in the basal region (Fig. 1A, C). Dispersed in the cytoplasm, there are detached membranes from the external segment of photoreceptors, lamellar phagosomes (Fig. 1C), and a high concentration of microtubules (Fig. 1C; 2B). The pigment granules or melanin granules are present in the whole cytoplasm. Their shape varies between spherical and oval (Fig. 1C, D; 2). Rod-shaped melanosomes (Fig. 2A, B) are parallel to the axis of the apical microvilli and the photoreceptors.

3.2. Photoreceptors

N. neglecta has four types of cones: short single and long single cones, double cones, and triple cones (Fig. 3; 4A, C), and rods (Fig. 3B). The nuclei of the photoreceptors are seen in the outer nuclear layer (Fig. 3A; 6D), and are placed at different levels, being elongated in cones, and are more spherical and dense in rods.

3.2.1. Cones

The cones of *N. neglecta* show morphological variability, but all of them are elongated and with two distinct segments: an inner and an outer segment, that vary in size and shape (Fig. 3A, C, D; 4A, C). The inner segment of cones has mitochondria that vary in shape and density, depending on the functional state of the cell (Fig. 4B, D). The double cones of *N. neglecta* can be classified as symmetric double cones, because they consist of two halves morphologically of the same type and size, fused along their inner segments (Fig. 4A). The triple cones consist of three portions of the same type and size, fused along their inner segments (Fig. 4C). The membranes of both halves were not connected by any membrane specialisations, such as desmosomes or gap junctions, but have only some slight interdigitations. The intercellular space is relatively constant (Fig. 3A, C). The single

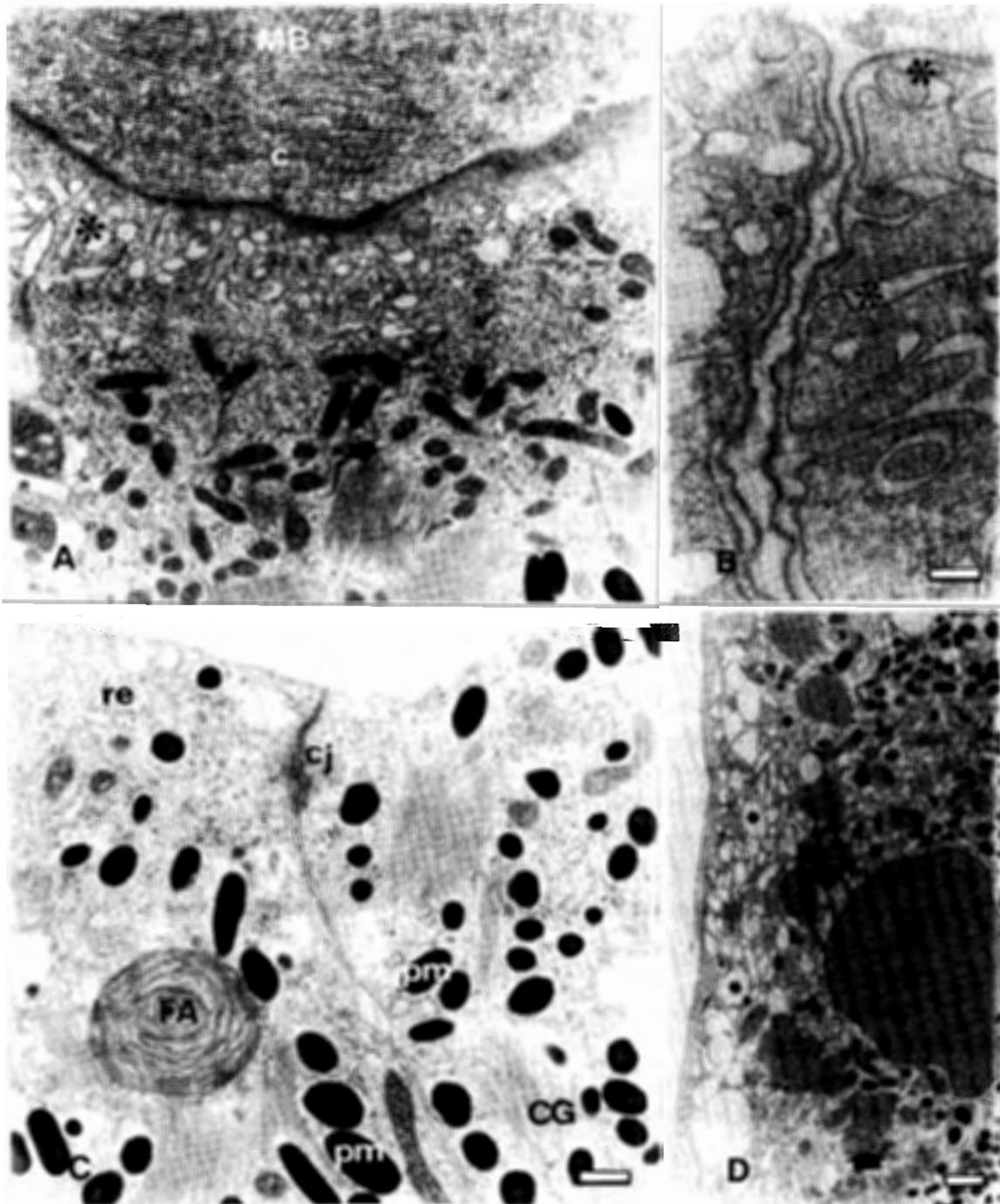


Fig. 1. Retinal pigment epithelium of *Notothenia neglecta*. A. Basal region with Bruch's membrane (MB) with collagen (c), mitochondria (★), detached membranes from the external segment of photoreceptors (♣) and infoldings of plasmatic membrane (*) (scale: 500 nm); B. detail of infoldings of plasmatic membrane (*) (scale: 200 nm); C. Junctional complex (cj) between two adjacent epithelial cells, phagosomes (FA) in the cytoplasm of one of the cells, smooth endoplasmic reticule (re), Golgi complex (CG) and melanin granules (pm) (scale: 500 nm); D. basal region of the pigment epithelium with myeloid bodies (↓), associated to lipid vesicles (⊛), the nucleus (N) and the detached membranes of the external segment of photoreceptors (♣) (scale: 1000 nm).

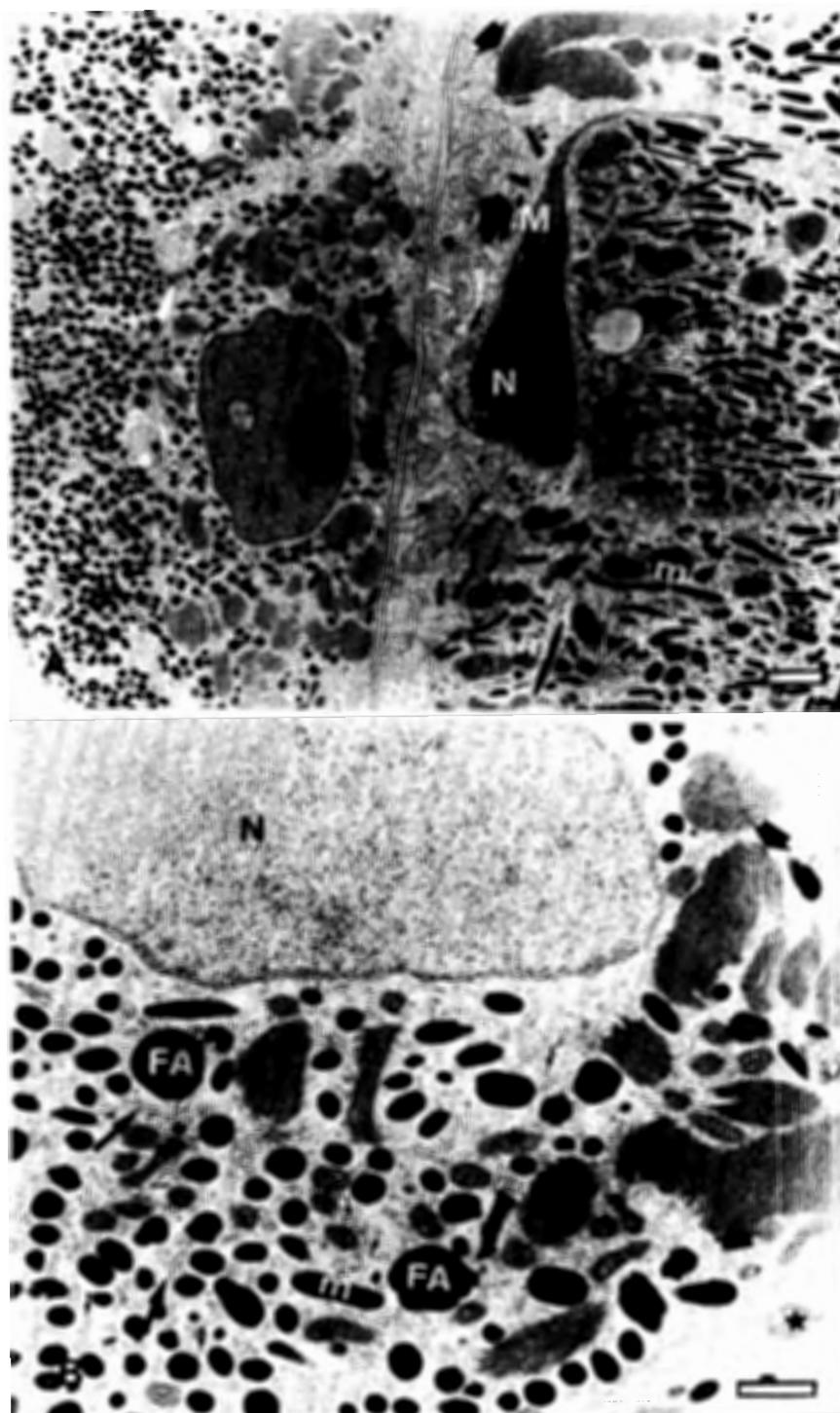


Fig. 2. Retina pigment epithelium in *N. neglecta*. A. general aspect of the pigment epithelium. Notice the infoldings of the plasma membrane (*), melanin pigment (*), melanosomes (m), and detached membranes of the external segment of photoreceptors (black arrowhead), the nucleus (N) and nucleolus (Nu) of the epithelial cells (scale: 2000 nm); B. Basal region of the pigment epithelium with phagosomes (FA), melanosomes (m), detached membranes of photoreceptors (black arrowhead), nucleus (N), mitochondria (★), smooth endoplasmic reticulum (↓) and microtubules (↓) all over the cytoplasm. (scale 1000 nm).

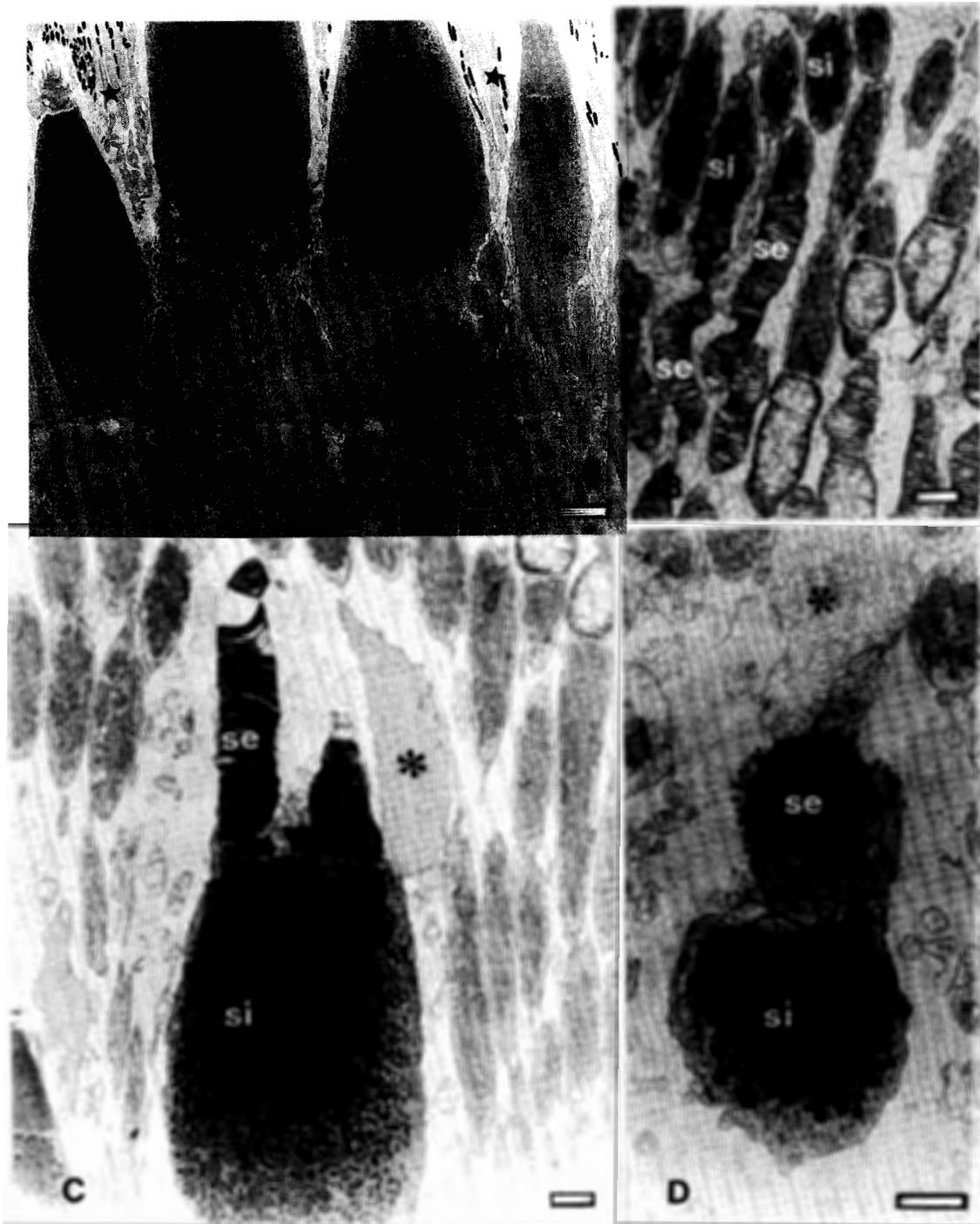


Fig. 3. Detail of the retina in *N. neglecta*. A. general view of some photoreceptors with outer nuclear layer (black arrowhead), outer limiting membrane (black arrow), cones (black star) and rods (black star) (scale: 7000 nm); B. Rods with inner segment (si) and outer segment (se) (scale: 2000 nm); C. Double cones with inner segment (si), outer segment (se), and accessory outer segment (*) (scale: 2000 nm); D. Single cones with inner segment (si), outer segment (se), and accessory outer segment (*) (scale: 2000 nm).

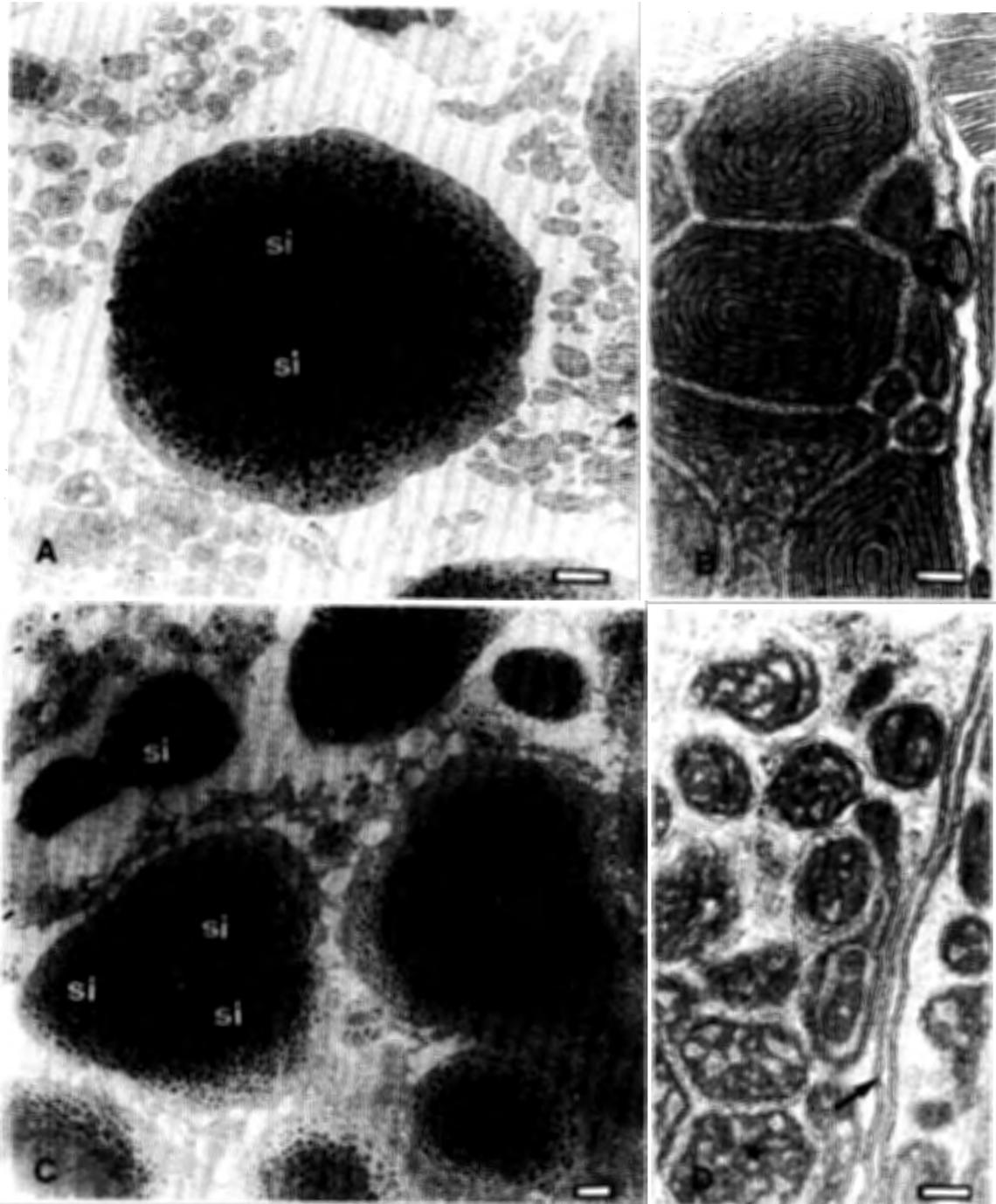


Fig. 4. Some photoreceptors in the retina of *Notothenia neglecta*. A. Transverse section of double cones with the two halves of the inner segments (si) with mitochondria (★) (scale: 2000 nm); B. Mitochondria (★) in the cytoplasm of the inner segment, with the membrane (⤴) that limits the two halves of a double cone (scale: 200 nm); C. triple cones in transverse section (*) with three inner segments (si), and a single cone (***) with its inner segment (si) (scale: 2000 nm); D. mitochondria (★) in the cytoplasm of the inner segment with membrane (⤴) that limits the two halves of a double cone (scale: 200 nm).

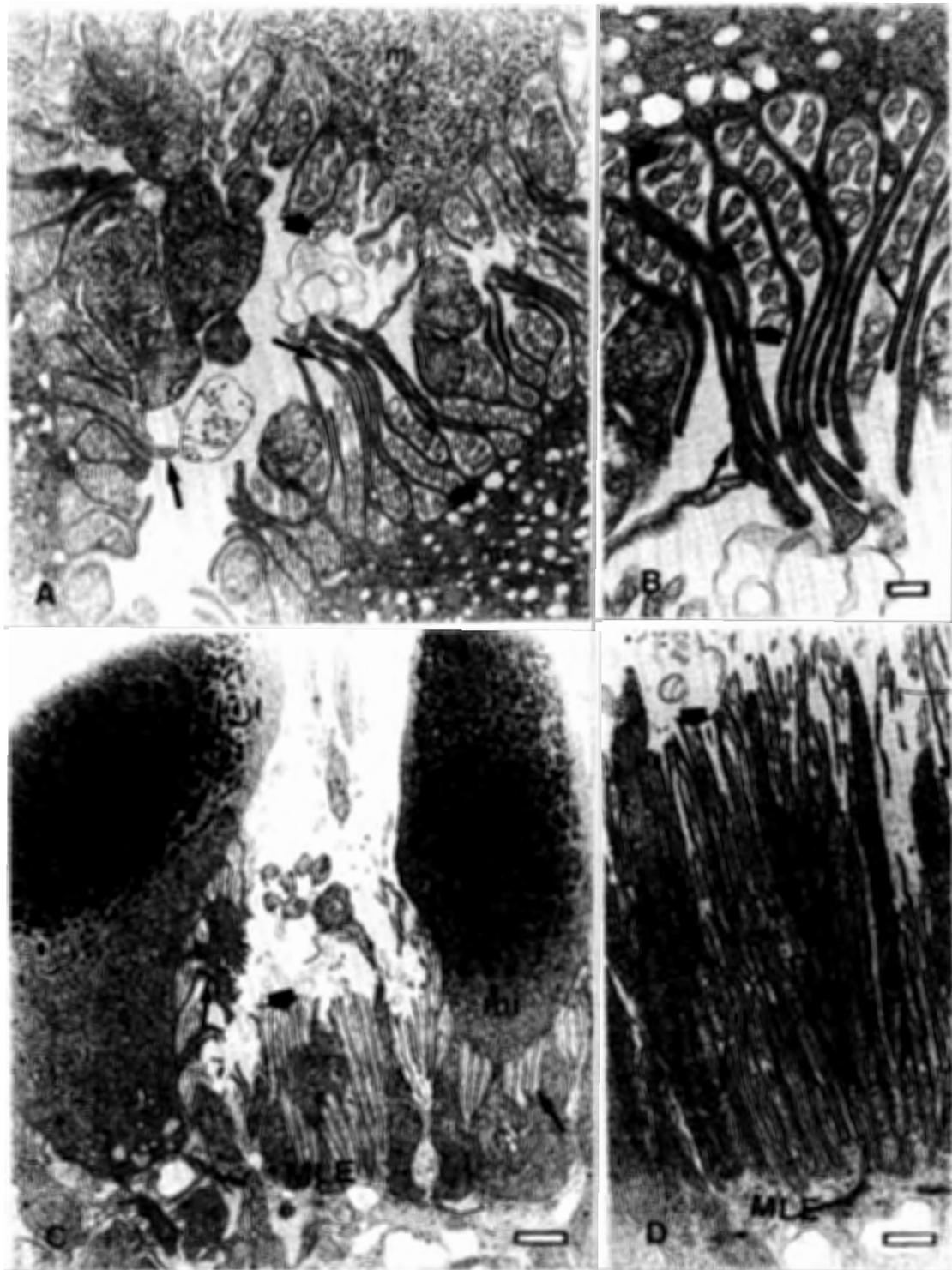


Fig. 5. Inner segments of cones in *Notothenia neglecta*. A. Inner segment with myoid region (mi) rich in fins (♣) and Müller cells appendices in transverse direction (♣) (scale: 500 nm); B. Detail of fins (♣) and the appendices of Müller cells (♣) (scale: 200 nm); C. Region of outer limiting membrane (MLE) with appendices of Müller cells (♣), fins (♣) at the myoid (mi) of cones, and mitochondria (★) in the ellipsoid (el) of cones (scale: 2000 nm); D. detail of appendices of Müller cells (♣), and of outer limiting membrane (MLE) (scale: 1000 nm).

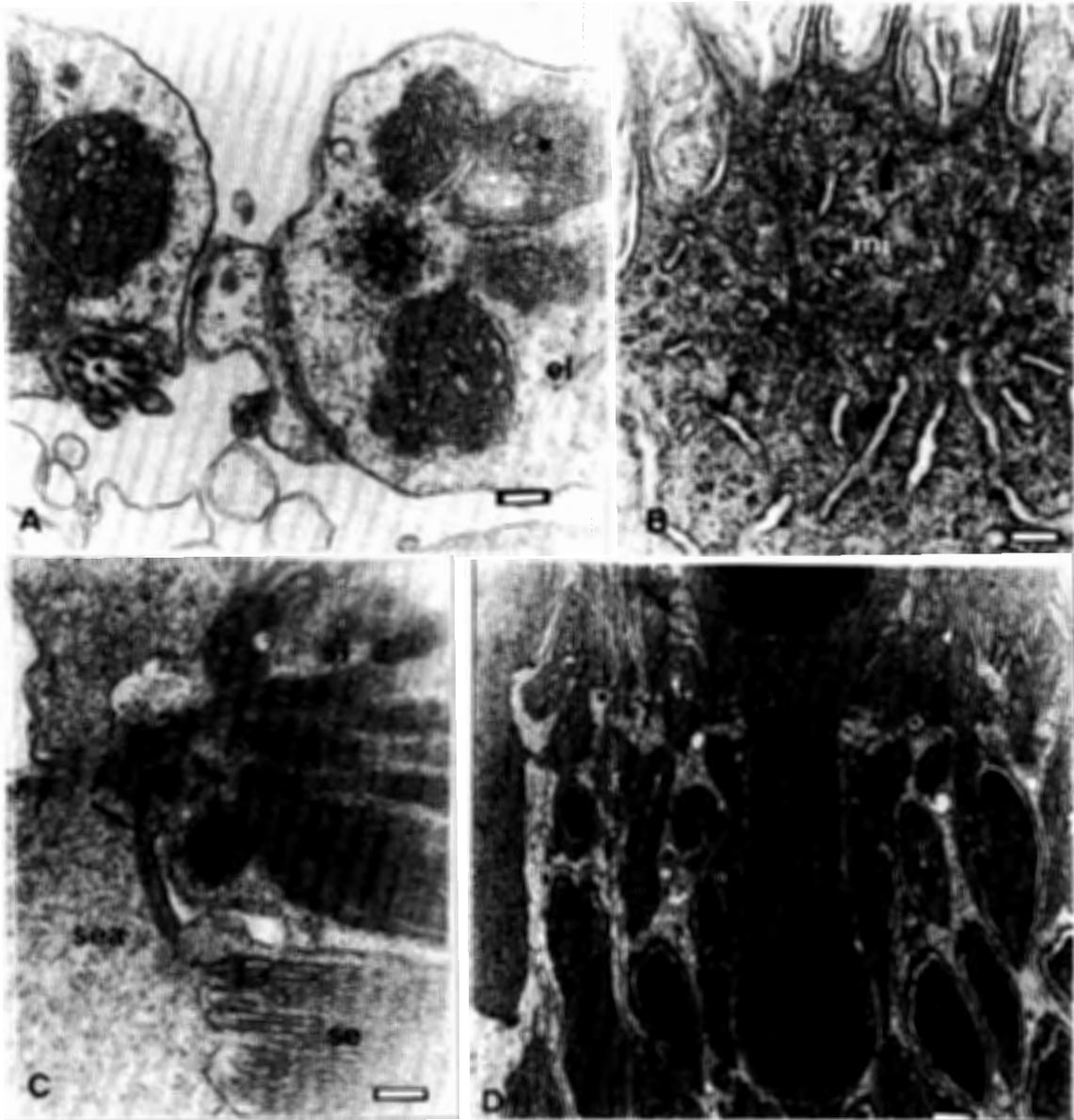


Fig. 6. Microtubules in the inner segment of cones in *Notothenia neglecta*. A. centrioles (★) in the region of the ellipsoid (el) of a cone, with mitochondria (★) (scale: 200 nm); B. Microtubules (↑) in the region of the myoid (mi) of a cone with smooth endoplasmic reticulum (↑) (scale: 200 nm); C. Microtubules in the region of the connecting cilium (↓), accessory outer segment (sea), inner segment (si), and outer segment (se) of a cone (scale: 200 nm); D. cell body (★) and nucleus (n) of a cone. Notice the outer limiting membrane (↓), mitochondria (★) and fins (↓) (scale: 2000 nm).

cones possess one single inner segment (Fig. 3D; 4C).

At the proximal or myoid region of the inner segments, there are many lateral elongated thin fins that interdigitate with the fins of neighbouring cones at the same level (Fig. 5A, B, C; 6D). Crossing the space between these cells, at an angle of 90° to them, there are apical microvilli of Müller cells, which support the myoid region of the cones

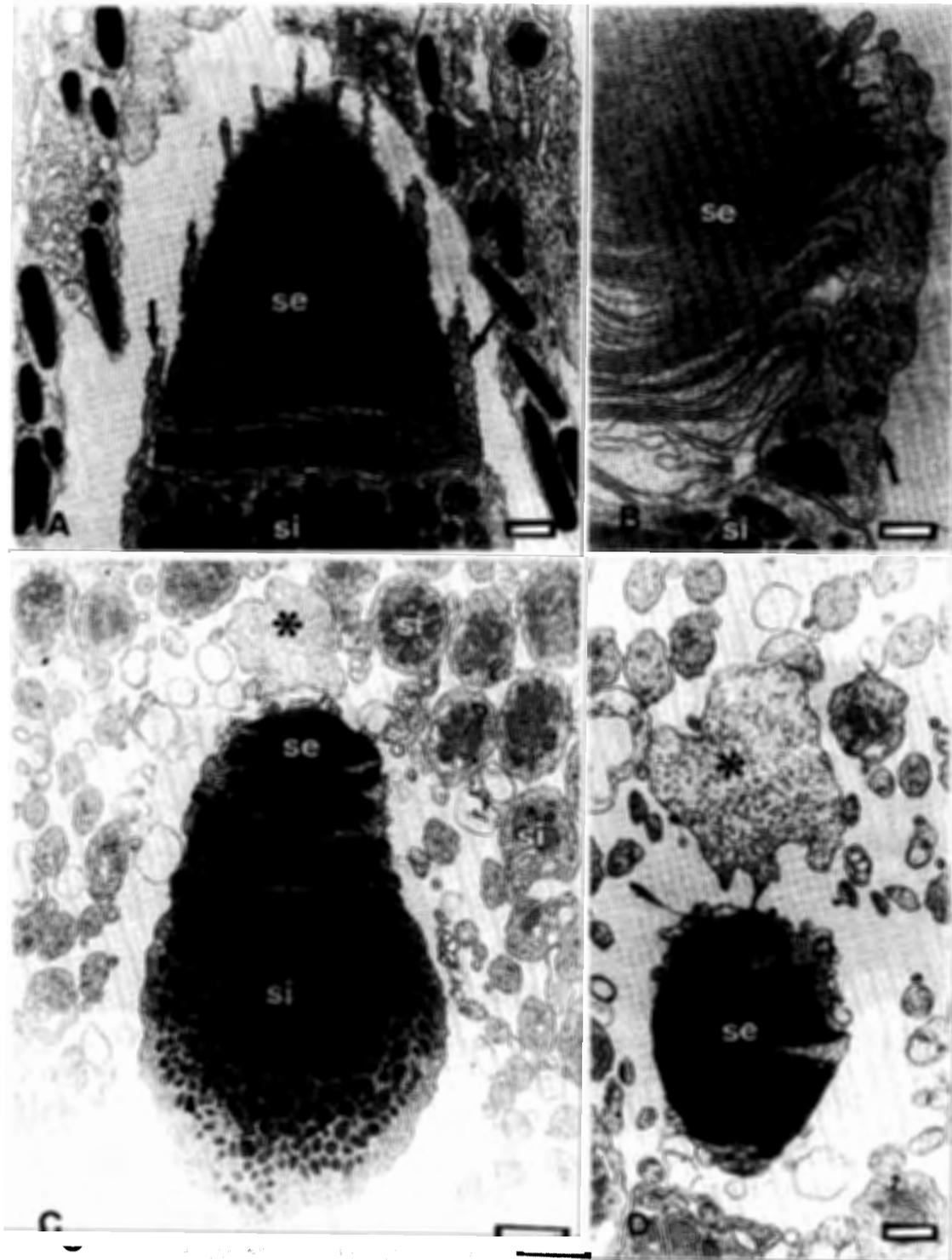


Fig. 7. Calycal processes and accessory outer segments in cones of *Notothenia neglecta*. A. Calycal processes (\downarrow) surrounding the outer segment (se) of a cone. Notice the inner segment (si) rich in mitochondria (\star) and the outer segment with bimembranous lamellae (\blacklozenge) (scale: 500 nm); B. detail of the calycal process (\uparrow), inner segment (si) and outer segment (se) (scale: 500 nm); C. outer accessory segment (\star), outer segment (se) and inner segment (si) (scale: 2000 nm); D. outer accessory segment (\star) and its connection with the outer segment of the cone (se) (scale 1000 nm).

(Fig. 5). These regions of interaction among photoreceptors form the outer limiting membrane (Fig. 5C, D).

Microtubules are observed in the vitread region of the myoid and the ellipsoid, which form the inner segments of cones (Fig. 6). Centrioles are seen in the region of the ellipsoid (Fig. 6A). In the sclerad region, microtubules are only in the connecting cilium of the accessory outer segment (Fig. 6C).

In cones, there is a barrier of thin calycal processes that emerge from the apical region that surrounds the distal portion of the inner segments. The calycal processes surround the outer segments of the cones, without any contact between them. These processes support the outer segments (Fig. 7A, B).

Together with the outer segments of the cones, an accessory outer segment emerges from the region of the connecting cilium (Fig. 7C, D). This accessory segment is a lateral process that extends along the outer segment. At its basal portion this structure does not make any contact with the outer segment, but at its median and apical region a contact is established, and their membranes fuse with the membranes of the outer segments. There is also continuity between the cytoplasm of both structures (Fig. 7D)

The accessory outer segment contains an amorphous substance with a slightly granular matrix, but without the presence of biological membranes (Fig. 7C, D). The calycal processes do not surround the accessory outer segment.

The outer segments of cones consist of a pile of bimembranous discs, or double membrane lamellae (Fig. 7A). These membranes are parallel and are oriented transversally to the axis of the cones. The insides of these membranous discs show continuity with the extracellular space.

3.2.2. Rods

Rods in *N. neglecta* are elongated cells with outer and inner segments. They are slender fragile cylindrical structures (Fig. 3B). Their outer portion can be surrounded by melanin pigments present in the pigment layer, and by the outer segments of different types of cones. They show calycal processes that are morphologically similar to those of cones. The accessory outer segment of rods has the same origin as that of cones, but extends directly toward the outer segment, eccentrically inside the limiting membrane. Therefore, the outer accessory segment of rods is not so easily visible as in cones. Ultrastructurally the outer segment of rods is similar to that of the cones, consisting of sacules of the double membrane in form of discs. However, these double membranes show no continuity with the extra cellular space.

4. Discussion

N. neglecta are domineering fish among the fishes in their habitat. They use their vision in a very competent way, carrying out complex behavioural strategies, mainly for feeding, and for mating or avoiding predators (Donatti and Fanta, 2002; Fanta and Meyer, 1998; Fanta, 1999).

N. neglecta is active and capable of visual food detection in light and also in relative darkness (Donatti and Fanta, 2002; Fanta, 1999; Fanta and Meyer, 1998). This ability can be explained by the presence of two types of photoreceptors: rods that mediate scotopic

vision, and cones that mediate photic vision (Levine and MacNichol, 1982; Nicol, 1963; Paulus *et al.*, 1986). Their retina is complex (Grötzner and Fanta, 1998), when compared to the retina of other Nototheniidae (Eastman 1988; Meyer-Rochow and Klyne, 1982).

Rods can facilitate the perception of differences in light intensity, and movement of prey, predators or co-specifics, as can be noticed in those fish that show only rods (Fanta *et al.*, 2001), corresponding to the behavioural reaction of *N. neglecta* to escape prey (Fanta and Meyer, 1998), and their visual capacity to detect food at night (Donatti and Fanta, 2002).

Single and double cones are common for some other Nototheniidae (Eastman, 1988; Fanta *et al.*, 1994; Grötzner and Fanta, 1998; Meyer-Rochow and Klyne, 1982; Pankhurst and Montgomery, 1989). However, the presence of two types of single cones, double, and even triple cones, is probably responsible for the detection of a wider range of wave lengths, based on Levine and MacNichol (1982), who suggested that Perciformes have short wave and long wave receptors in the two halves of double cones, and Miyazaki *et al.* (2001), who described ultraviolet sensitive cones in some Nototheniidae. Accordingly, one can assume that the triple cones in *N. neglecta* might have receptors for three different ranges of wavelengths.

Membranous discs transversal to the axis of the photoreceptors probably exist in teleosts in general (Braekevelt, 1992; Dickson and Graves, 1979; Januschka *et al.*, 1987; Sillman *et al.*, 1990), being responsible for the photochemical processes (Levine and MacNichol, 1982; Wheeler, 1979, 1982). To develop colour vision, fish must have different visual pigments, and interneural connections that allow the comparison of the signals that come from the different photoreceptors (Levine and MacNichol, 1982). If *N. neglecta* had only one type of photo sensor, their vision would be as limited as observed for other Antarctic species, such as the zoarcid *Ophthalmolycus amberensis* (Fanta *et al.*, 2001).

Cones and rods of *N. neglecta* have an accessory outer segment. In cones this process is placed along the external segment and maintains contact with it by a cytoplasm bridge. In rods, it extends directly inside the external segment. One may suggest that one of its functions is to give support, and another to be a route for the transport of material between the inner and the outer segments (Locket, 1999), that can be necessary mainly in periods of higher stimulation of the photoreceptors. This would allow the transport of the necessary materials for the reconstruction of bimembranous discs of the external segments.

N. neglecta has a pigment epithelium made up of a single layer of cylindrical cells that show microvilli at their apical portion, giving structural support to the outer segments of the photoreceptors, as well as guiding the incoming light. Because *N. neglecta* lives in variable luminous environments, this epithelium protects the outer segments of the photoreceptors, mainly of rods, from excessive exposure to direct light with consequent bleaching of photo pigments in this region. The polarisation of the epithelial cells of *N. neglecta*, and the augmented membrane surface by infoldings, favours the entrance of nutrients into the retina.

The luminosity in the marine environment in Antarctica is seasonally variable, often limiting the visual function in nototheniids, in which there is often dominance of chemo and mechano receptors (Montgomery and Macdonald, 1987; Macdonald and

Montgomery, 1991; Meyer and Fanta, 1998). The visual function and eye structure of Nototheniidae seem not to have changed in answer to the specific needs of the Antarctic environment (Pankhurst and Montgomery, 1989; Macdonald and Montgomery, 1991).

However, in *N. neglecta*, the multitude of photoreceptors and the ultrastructural features of these cells and of the pigment epithelium place them among fish with high visual development and competence. They show the morphological and metabolic capacity to adapt to different photic situations. This explains their behaviour in relation to other species that share the same habitat in the shallow coastal regions where they may live, in all seasons of the year.

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