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Structure and function of the retinal pigment epithelium, photoreceptors and cornea in the eye of *Sardinella aurita* (Clupeidae, Teleostei)

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Abstract The structure of the pigment epithelium, photoreceptors and the cornea in the eye of a teleost, *Sardinella aurita* was examined by light and electron microscopy. The retinal pigment epithelium forms a single layer of cells joined laterally by cell junctions. Centrally in the retina these cells are columnar, while more peripherally they become cuboidal in shape. The basal (scleral) border of the pigment epithelial cells is not infolded but is relatively smooth. Phagosomes containing lysosome-like bodies are also common features of the retinal pigment epithelium. Numerous melanosomes (pigment granules) are abundant throughout the epithelial cells. These melanosomes probably absorb light which has passed through the photoreceptor layer. Four photoreceptor cells were identified; rods, long single cones, short single cones and double cones. The presence of these types suggests a diversity of photoreceptor function. Square mosaic pattern of cones and well-developed choroid gland are also main features of the eye. The inner segment of rods and cones were rich in organelles indicating much synthetic activity. Calycal processes projecting from cone outer segments are also observed. The cornea includes an epithelium with a complex pattern of surface microplicae, a basement membrane, dermal stroma, an iridescent layer, scleral stroma, Descemet's membrane and endothelium. The autochthonous layer which is seen in some teleosts has not been observed in the cornea of this species. These and other observations were discussed in relation to the photic environment and habits of this fish.

Introduction

Fish and other aquatic animals live in a different light environment than terrestrial species. Therefore, fish possess various kinds of sense organs and use them to detect many kinds of information in the ambient environment. Ali and Klyne (1985) classified the sense organs in fishes into three groups; (1) organs of chemical sense which comprise the olfactory organs, taste buds and Jacobson's organ, (2) organs of vision which include the eyes, and (3) organs detecting pressure change and the movement of the medium which comprise the inner ear, lateral line organs and pit organs. The eye of the fish has been chosen as a focus, in an effort to illustrate how aquatic animals can overcome visual barriers.

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The eyes of vertebrates show many adaptations that can be related to specific visual tasks or the intensity and spectral composition of light in which species are active (Beaudet and Hawryshyn, 1999). The teleost fishes have been extensively studied and, due to the diversity of light environments and habitats in which they are found, have provided numerous examples of visual specialization in optics, retinal structure, and physiology (Collin, 1997). It has been reported that vision in fish depends on: size and position of the eyes, morphology and types of retinal photoreceptors, structure of the pigment epithelium, structure of the cornea and lens, and on the visual pathways and integrating areas in the brain (Zaunreiter et al., 1991; Schmitt and Dowling, 1999). In the present study, the cornea, the retinal pigment epithelium and the photoreceptors were chosen.

In most vertebrates, the cornea plays an important role in providing protection for the inner structures of the eye and acts as a light collector in refracting incident light into the retina. The fish cornea does not have such a large refractive index relative to the surrounding water medium. However, it still constitutes a protective cover for the eye and provides an optically smooth surface and a transparent window. In comparison with the mammalian cornea many specializations have been reported. These include spectacles and corneal filters (Kondrashev et al., 1986), iridescent layers (Lythgoe, 1976; Collin and Collin, 1998), and an autochthonous layer (Jermann and Senn, 1992), all of which are thought to provide some visual advantage to the animal.

Although the retinal structure is basically the same as in vertebrates, the teleostean retina has been, and still is, a focus for the attention of many researchers due to a number of features that characterize it. Of these features are: (1) the presence of retinomotor movements in response to changes in light conditions (Donatti and Fanta, 2007), (2) the presence of large photoreceptor outer segments and prominent ellipsoids to improve absorption of light (Reckel and Melzer, 2003), (3) the existence of double cones which increase the area available for the absorption of light (Shand, 1997), (4) regular cone mosaic pattern (Reckel et al., 2002), (5) the existence of a well developed retinal pigment epithelium (Braekevelt, 1982), (6) presence of foveae or areas with an increase in photoreceptors and other neurons (Wagner, 1990), and (7) a marked synaptic plasticity as is demonstrated by the formation of spinules (Schmitz and Kohler, 1993) during light adaptation and their disappearance during dark-adaptation, and others. In summary, these features demonstrate the importance of vision in the mode of life and survival of the species.

In contrast to many other vertebrates, the teleost retinal structure often varies distinctly between the allied families, sometimes even between genera within a family (Ali and Klyne, 1985). It contains highly specialized types of photoreceptors, i.e., rods, single long and short cones, double cones and triple cones, that are arranged in distinct row, square or hexagonal patterns (Reckel et al., 2002; Darwish et al., 2015). The interspecific variations in retinal structure reflect the feeding habits and photic habitat conditions of the respective species. Rod cells provide high visual sensitivity, being used in low light conditions, while cone cells provide higher spatial and temporal resolution than rods and allow for the possibility of color vision by comparing absorbances across different types of cones which are more sensitive to different wavelengths (Flamarique and Harosi, 2000; Al-Adhami et al., 2010). The ratio of rods to cones depends on the ecology of the fish species concerned, e.g., those mainly active during the day in clear waters will have more cones than those living in low light environments (Wagner, 1990; Collin et al., 1996).

A basic structural plan seems to be common to all vertebrate photoreceptors with the typical photoreceptor consisting of an outer segment (light-capture area) joined to an inner segment (synthetic area that is often further subdivided into compartments) by a non-motile cilium, a nuclear region, and a synaptic end piece (Rodieck, 1973). In addition, in a number of teleosts a well-defined repeating mosaic in the arrangement of the cone photoreceptors has been reported (Garcia and De Juan, 1999; Reckel and Melzer, 2003; Salem, 2004).

The retinal pigment epithelium normally consists of a single layer of cuboidal to low columnar cells forming the outermost (scleral) layer of the neural retina. The retinal pigment epithelium is an essential layer of the vertebrate retina charged with several specialized roles indispensable to the visual process and as such has been described in a variety of teleost species (Es-Sounni and Ali, 1986; Braekevelt et al., 1998; Donatti and Fanta, 2007; Darwish et al., 2015). The pigment epithelium along with the choriocapillaris and Bruch's membrane is intimately involved in several processes vital to the proper functioning of the photoreceptor cells and hence to vision itself. Among the best known functions of the pigment epithelium are: (1) the storage and modification of vitamin A precursors of the visual pigments (Braekevelt et al., 1998); (2) the architectural support and proper orientation of the photoreceptor outer segments during light and dark adaptations (Bernstein, 1961); and (3) the selective transport of materials to and from the photoreceptors (Es-Sounni and Ali, 1986). This layer is normally pigmented to absorb light which has passed through the photoreceptor layer.

The round sardinella, *Sardinella aurita* (Clupeidae, Teleostei) is a mid-sized pelagic fish that represents one of the most important commercial fishery resources in the Egyptian Mediterranean Sea (Madkour, 2011) and one for which no TEM data on the eye are currently available. Therefore, the purpose of this study was to investigate the morphology and fine structure of the retinal pigment epithelium, photoreceptors and cornea in the eye of *S. aurita* to provide more data of the vision of a predatory fish in order to increase our understanding of the morphology and structure of the eye and its relation with the ecology of the species.

Materials and methods

The specimens of the round sardinella, *S. aurita* were obtained from Mediterranean Sea at Port Said coasts. The extraocular muscles were cut and the eyes were excised, and following the removal of the lens and vitreous, small pieces from the cornea and various regions of the retina were cut and fixed in 2% glutaraldehyde in 0.1 M phosphate buffer for 2 h and post-fixed in 2% osmium tetroxide in 0.1 M phosphate buffer for 1 h. Tissues were then dehydrated in ascending ethanol series and embedded in epoxy resin. Some thick sections were cut by the Porter-Blum ultramicrotome using glass knife and stained with toluidine blue. For transmission electron microscopy observations, thin sections were cut and stained with lead citrate and uranyl acetate and examined under a JEOL 100 CX transmission electron microscope at 80 kV.