

Univerzita Karlova v Praze
Přírodovědecká fakulta

Studijní program: Biologie
Studijní obor: Biologie



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PHYSIOLOGY OF SPECIAL MIRROR EYES OF MOLLUSCS, CRUSTACEANS AND DEEP-SEA FISH
FYZIOLOGIE SPECIÁLNÍCH ZRCADLOVÝCH OČÍ MĚKKÝŠŮ, KORÝŠŮ A HLUBINNÝCH RYB

Bakalářská práce

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Praha 2016

Prohlašuji, že jsem závěrečnou práci zpracovala samostatně a že jsem uvedla všechny použité informační zdroje a literaturu. Tato práce ani její podstatná část nebyla předložena k získání jiného nebo stejného akademického titulu.

V Praze 16. srpna 2016

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Acknowledgements

I would like to express my gratitude to my advisors doc. RNDr. René Hudec, CSc. and Mgr. Zuzana Musilová, Ph.D. for their assistance, patience and valuable guidance during my work on this thesis.

I am also very grateful to my family and close friends for their unceasing encouragement, support and attention.

Abstrakt

Většina optických systémů zvířecích očí funguje na principu lomu světla. Některé typy očí však využívají pro tvoření obrazu biologická zrcadla, protože jsou označovány jako zrcadlové oči. Biologická zrcadla jsou zvláštním typem tkáně, která odráží světlo prostřednictvím konstruktivní interference na vrstvách se střídavým indexem lomu. Zrcadlové oči se obvykle vyskytují u živočichů žijících v zakalených a hlubokých vodách. Různé typy zrcadlových očí byly popsány u měkkýšů, korýšů a ryb. Mimo to, zrcadlové superpoziční oči korýšů desetinožců posloužily jako inspirace pro rentgenové teleskopy (tzv. lobster-eye X-ray telescopes) využívané v astrofyzice. Tato práce popisuje různé typy zrcadlových očí. Přehled živočichů se zrcadlovými očima je doplněn o popis jejich habitatu. Závěrem jsou jednotlivé typy zrcadlových očí porovnány a je diskutována jejich případná biomimetická aplikace, zejména v opticko-technických systémech.

Klíčová slova

Zrak, zrcadlové oči, měkkýši, korýši, hlubinné ryby.

Abstract

The majority of image forming systems in animal eyes are based on refractive optics. However, there are several eye types that use as a main image forming devices biological mirrors hence they are called mirror eyes. Biological mirrors are special type of tissue that reflects light beams usually by means of the constructive interference on multi-layers of alternating refractive indices. The mirror eye arrangement can be found mostly in animals living in the dim or deep water. Different types of mirror eyes have been described among molluscs, crustaceans and fishes. Moreover, the reflective superposition eyes of decapod crustaceans served as an inspiration for construction of the lobster-eye X-ray telescopes used in astrophysics. In this thesis, various types of mirror eyes are described. The overview of animals with mirror eyes is supplemented by description of their habitat. Finally, different types of mirror eyes are compared and their possible biomimetic application especially in optical technology is discussed.

Key words

Vision, mirror eyes, molluscs, crustaceans, deep-sea fishes.

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Introduction

Vision is one of the most important senses that allow animals to connect with surroundings. Unlike chemoreception (e.g. taste) or mechanoreception (e.g. touch), it does not require direct contact with the detected objects. Vision is a capability of detecting shapes, colours, hues and brightness, as well as dimensions, distances and other features. Therefore visual perception allows animals to keep safe and avoid danger, to build and maintain relationships with others, to navigate in space and to find resources to feed on.

The visual information is carried by light. Light is electromagnetic radiation with particle and wave properties. It travels through space and interacts with matter in different ways, which are transmission, reflection, absorption and scattering. Light behaves as waves when it travels; however, it behaves as particles when it is emitted or absorbed (Björn, 2015).

In general, photons (fundamental particles of light) heading into an eye are focused on retina and detected by photoreceptors located there. Consequently, the information about the presence of light is converted into neuronal impulses, which are then led into a brain. In the brain, the information is further processed and the signals are converted to images. Finally, these images are recognised and interpreted through cognitive processing (Nilsson, 2013).

Each part of the visual pathway – from the light detection through the information processing to the image interpretation – may be modified in many ways. In this bachelor thesis, I mostly focus on the morphological modifications of the optical systems, particularly on the so-called mirror eyes. The mirror eye type is an image-forming arrangement based on reflection of a biological mirror, which is very unique since the majority of the eye systems utilise refraction of lenses (Land, 2000).

Biological mirrors are special type of tissue usually made of many layers of material with alternating high and low refractive indices. Light reflects from the upper and lower surfaces of each layer; the reflections interfere and create images (Land, 1972).

The mirror eye arrangement can be found mostly in animals living in the dim or deep water, such as scallops, shrimps, prawns or even some fishes (Land & Nilsson, 2012). The first documented mirror eyes were optical systems of scallops, demonstrated by Land in 1965, and of shrimps, described by Vogt in 1975. The latest discoveries show that mirror eyes can be found even in vertebrates, such as fishes *Dolichopteryx longipes* (Wagner et al., 2009) and *Rhynchohyalus natalensis* (Partridge et al., 2014).

The mirror optics used in these special eyes is also applicable in technical area. Already in past century, Angel (1979) came up with an idea of technical application of the mirror eye arrangement. He proposed to imitate principle of decapod eye imaging to construct a high-energy responsive telescope with wide field of view. Eventually, this so-called lobster-eye X-ray

telescope was assembled and it is nowadays used in astronomical satellites, such as VZLUSAT-1 (Pina et al., 2015).

The aim of this thesis is to create an overview of animals with mirror eyes, to summarize the current knowledge about these types of eye and to discuss possible biomimetic applications.

1. Optical Systems in Animal Eyes

The fundamental requirements for light sensation are light sensitive molecules and a signalling mechanism (Land & Nilsson, 2012; Nilsson, 2013). Those can also provide non-directional photoreception that might be useful e.g. for control of circadian rhythms (Adler, 1970; Nilsson, 2013). For directional photoreception, important for phototaxis, shielding pigment is required (Jékely et al., 2008; Nilsson, 2013). If different photoreceptors simultaneously monitor different directions, spatial vision is possible (Land & Nilsson, 2012; Nilsson, 2013). Spatial vision improves control of locomotion and navigation (Muntz & Raj, 1984). For high spatial resolution which enables further connection with surroundings, such as communication, a focusing device is required (Land & Nilsson, 2012; Nilsson, 2013).

In almost all phyla, some type of optical system has evolved. However, their construction and ontogenesis varies greatly, as shown in Figure 1 by four examples (Nilsson, 1996). The most complex types of eyes can be found in vertebrates, arthropods and molluscs (Land & Nilsson, 2012). Despite the huge variety in optical designs and eye attributes, all of them provide similar information about wavelength and intensity of light (Fernald, 2000). Eyes occur not only on head but on other body parts too, moreover, one individual can have several of them (Nilsson, 1996); for example starfish have a compound eye at the tip of each arm (Garm et al., 2014). Furthermore, one individual can even have more types of eyes at once, such as fish *Dolichopteryx longipes* (Wagner et al., 2009).

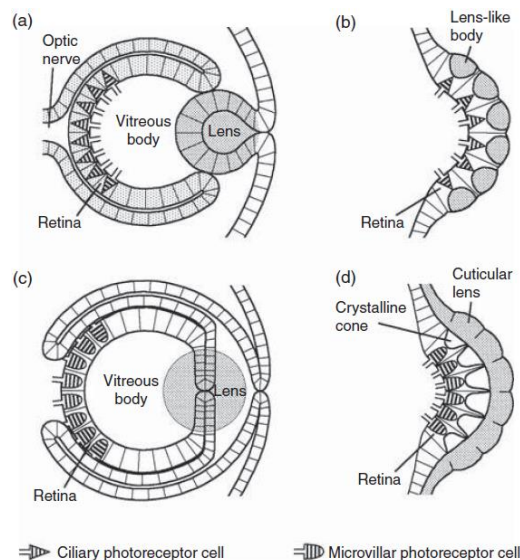


Figure 1 The Composition of Eyes in (a) Vertebrates, (b) Polychaete Fan Worms, (c) Octopus and Squid, (d) Insects and Crustaceans. Although there are only few ways of making functional eyes, the tissues and morphological components that are recruited vary greatly between animal phyla. The vertebrate retina (a) is produced by the neural epithelium of the brain (light shading) and the lens is formed by an invagination of the epidermal epithelium. In squid and octopus (c) the entire eye is formed as a double epidermal cup, with the bottom of the inner cup being the retina and its fused opening producing the lens. The compound eyes of fan worms (b) and arthropods (d) have likewise vertebrates (a) and octopus and squid (c) recruited different types of visual receptor cells, but more importantly they are formed on different parts of the body: as paired structures on the first segment of the head in arthropods and as multiple structures on the feeding tentacles of fan worms (figure and legend modified after Land & Nilsson, 2012).

Salvini-Plawen & Mayr (1977, as cited in Land & Fernald, 1992*) concluded from their complex study involving morphological, physiological, developmental and phylogenetic approaches that eyes evolved at least 40 times independently. However, recent genetic studies show that the same transcription factors for eye development can be found in all bilaterian phyla (Gehring, 2014; Nilsson, 1996). Homologues of *Pax6* (*paired box 6*) – the so-called master control gene – regulate eye morphogenesis in all major types of eyes, such as primitive eyes of brachiopod larvae, camera types of eyes in vertebrates and cephalopods, mirror eyes of scallops or compound eyes of arthropods (Callaerts et al., 2006; Gehring, 2014; Hartmann et al., 2003; Ogino & Yasuda, 2000; Passamaneck et al., 2011). From the fact that the same morphogenetic transcription factors can be found within every bilaterian phylum, Gehring & Ikeo (1999) concluded that all the different eye types originated monophyletically and consequently diversified. However, number of authors have repeatedly questioned this hypothesis (Fernald, 2000; Kozmik, 2008; Land & Nilsson, 2012; Morton, 2008; Nilsson, 2009). For example, Fernald (2000) points out that *Pax6* is not a master control gene of eye development since the genetic control of eyes construction is more complex and works rather as a gene network. Kozmik (2008) further adds that there are several exceptions among bilaterians which have eyes developing even in absence of *Pax6*. Fernald (2000) also shows that even though all types of eyes use the same proteins (opsins) to collect photons, by contrast, the light refracting proteins are not homologous. Moreover, the fact that the way of making lenses is similar even when different proteins are used, points to the concept of convergent evolution (Fernald, 2000). Nilsson (2009) also argues that some of the eye structures are not necessarily homologous, even if they may be controlled by homologous genes, as shown in work of True & Carroll (2002) on crystallins (structural proteins of lens).

Nevertheless, it is obvious that the process of eye evolution consisted of four stages that overlap and interact: evolution of molecular components, evolution of cell structures, evolution of cell types and evolution of organ shapes (Nilsson, 2009). The first two stages (evolution of molecular components and of cell structures) follow concept of 'tree thinking' – a complex network, while the second two processes (evolution of cell types and organ shapes) follow a linear evolutionary model – gradual progression (Nilsson, 2009; Plachetzki & Oakley, 2007). Absolute and spectral sensitivity, speed and intensity adaptation were the evolutionary drivers of the first two stages (Nilsson, 2009). The driver of further evolutionary development was visually guided behaviour (Nilsson, 2013).

In evolution, eyes appeared together with modern animal phyla during the so-called Cambrian explosion – a very rapid evolutionary event happening 540 million years ago. However, light sensitive cells existed even before it (Land & Nilsson, 2012; Nilsson, 1996). It is possible that a few species possessing spatial vision and improved mobility in Precambrian era

drove evolution of others resulting in the Cambrian explosion (Land & Nilsson, 2012). *Pax6* homologues that control genes initiating eye development existed even long time before the Cambrian period (Nilsson, 1996). However, their evolutionary origin is still unknown (Gehring, 2014).

In this thesis, I distinguish simple eyes (including those with just one cell, couple of them, or eye pits) from more complex eyes. The more complex eyes can be designed in two different ways depending on if the receptor surface is concave or convex. The concave receptor surface leads to single chambered eyes, the convex receptor surface then can be found in compound eyes (Land & Nilsson, 2006).

1.1. Simple Eyes

Photoreceptive organelles can be found even in some unicellular organisms, such as the alga *Chlamydomonas eugametos*, the flagellate protist *Euglena granulate* or the eubacterium *Leptolyngbya* (Albertano et al., 2000; Walne & Arnott, 1967). Moreover, in unicellular protists dinoflagellates eyespots called ocelloids can be found. Ocelloids are very similar to the camera-type eyes since they contain structures analogous to a cornea, a lens, an iris, a retina and a pigment cup but all of them within one single cell (Gavelis et al., 2015; Gómez, 2008; Greuet, 1978; Hayakawa et al., 2015).

The minimum requirement for a structure to be called an eye is the close association of a photoreceptor cell with a pigment cell (Kozmik, 2008; Land & Nilsson, 2012). This simple arrangement can be found in trochophore (a larva) of the annelid worm *Platynereis dumerilii*. Each of its eyespots is composed from only two cells – a sensory cell and a pigment cell, as shown in Figures 2 and 3 (Rhode, 1992).

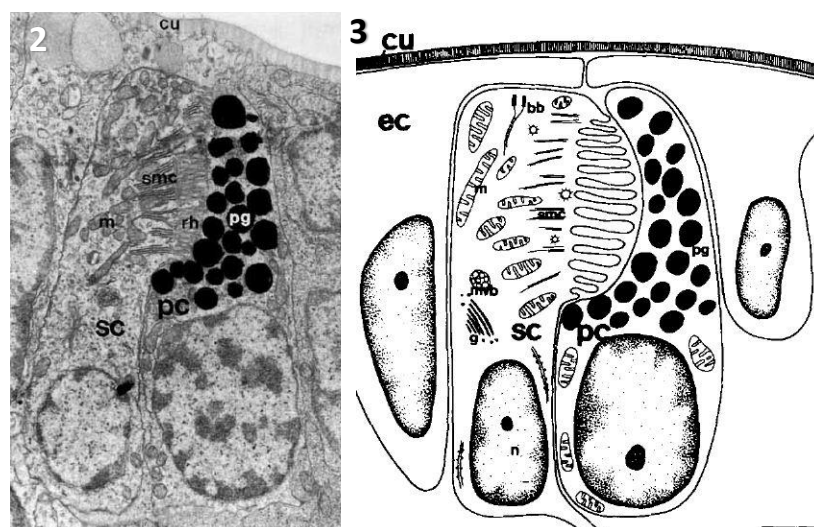


Figure 2 Transmission Electron Microscopy of the Eye in a Two Days Old Trochophora *Platynereis dumerilii*. $\times 11,000$.

Figure 3 Schematic Reconstruction of the Trochophoral Eye of *Platynereis dumerilii*. $\times 11,000$. Scale bar = 1 μm .

bb, basal body; cu, cuticle; ec, epidermal cell; g, Golgi cisternae; m, mitochondrion; mvb, multivesicular body; n, nucleus; pc, pigment cell; pg, pigment granule; rh, rhabdomere; sc, sensory cell; smc, submicrovillar cisternae (figures and legend adapted from Rhode, 1992).

Similar eye arrangement can be found in other planarians, such as in *Planaria maculata* (shown in Figure 4); however, these eyes are composed of multiple cells. Moreover, retina of *Prorhynchus applanatus* consists of three parts – directive, refractive and sensory one – which is a very similar structure to more complex eyes of vertebrates (Taliaferro, 1920). These types of eyes are used by planarians for light orientation leading to negative phototaxis (a movement away from the light source) (Asano et al., 1998).

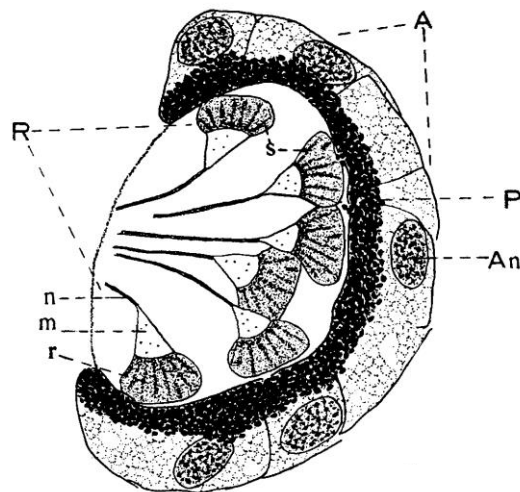


Figure 4 Camera-Lucida Drawing of a Transverse Section of the Eye of *Planaria maculata*. × 1,500.

A, accessory cells; An, nucleus of accessory cell; P, pigment-cup containing visual cells or retinulae, some of which have been omitted; R, retinulae; r, rhabdom; s, striae in the rhabdom; m, middle region of the retinula; n, portion of the nucleus-bearing region of the retinula (the nucleus as well as the greater part of this region lie outside of the pigment-cup and are not shown in the drawing) (figure and legend adapted from Taliaferro, 1920).

Another type of optical system without any special refractive or reflective compound is a pin-hole eye of the cephalopod mollusc *Nautilus pompilius*. Not only it does not have any lens or cornea, furthermore, it lacks optic chiasma; nerves leaving retina pass directly to the brain (Muntz & Raj, 1984). *Nautilus pompilius* also has no ocular muscles. In the retina, there are two types of cells – retinula cells (receptors) and supporting cells (epithelial cells), both present on a basal lamina, whereas other cephalopods have the supporting cells only distally to the lamina. Moreover, *Nautilus pompilius* has well-developed optomotor response (Barber & Wright, 1969b).

The pin-hole type of eye appears also in the giant clam *Tridacna* that exhibits many types of visual responses, such as retractions of its siphon and other body parts aroused by shadows of predators, or orientation changes of the mantle triggered by increased light intensity (Land, 2003; Wilkens, 1986). Thousands of small eyes can be found particularly around the margin of *Tridacna* siphon (Wilkens, 1986). In front of the retina, the chamber contains “filler cells” (Land, 2003); Stasek (1966) calls this multicellular layer a lens, however, Wilkens (1986) adds that it is not suitable for focusing.

1.2. Complex Eyes

1.2.1. Eyes with Refractive Optics

Resolution and sensitivity of a pin-hole eye can be remarkably improved by adding a lens (Land & Nilsson, 2006). The arrangement of so-called camera-type eyes occurred several times – in vertebrates, molluscs, annelids etc. (Bloemendal, 1977; Purschke et al., 2006; Sivak, 1982). Some gastropod molluscs and annelids have “full mass” lenses of just one refractive index. As a result, blurring is reduced; however, a sharp image still cannot be formed. More advanced lenses are inhomogeneous as the refractive index decreases from the centre to the periphery. This causes reduction of the focal length and thus a sharper image is obtained. With the correct gradient, the lens can be devoid of spherical aberration (Land & Fernald, 1992). Spherical aberration – when the peripheral rays tend to be over-focused due to the spherical surface – is one of significant problems of spherical lenses; another important one is e.g. the chromatic aberration. Beside the index gradient, another way how to deal with spherical aberration is to flatten outer regions of the lens relative to its centre (Land, 1988).

1.2.1.1. Aquatic Animals

In aquatic animals, the refractive indices difference between water and a cornea is little. Therefore, the refractive power is in a lens so the lens has to be more curved. Hence the most lenses of aquatic animals have spherical appearance. To avoid spherical aberration, the refractive indices of such lenses are inhomogeneous (Björn, 2015; Land, 1988). Not only that this lens construction avoids the spherical aberration, moreover, it shortens the focal length, which is crucial for aquatic animals (Land, 1988). Since the refraction depends on the wavelength, the refractive power of lens may not be optimal for the whole light spectrum. The result of this phenomenon is chromatic aberration that manifests as “colour fringes” around the image since the whole spectrum is not focused at the same point (Björn, 2015). The cichlid fish *Haplochromis burtoni* and some other vertebrates avoid this phenomenon by having a multifocal lens with several concentric zones of various refractive indices. This arrangement improves spatial resolution of colour vision; however, it reduces the image contrast (Kröger et al., 1999).

1.2.1.2. Terrestrial Animals

In terrestrial animals, the main image-forming component of an eye is the interface between air and tissue because of the great difference in refractive indices between these two media. Therefore, a cornea is the most refractive eye part. Hence the main function of a lens (e.g. in terrestrial mammals) is not image forming, but accommodation to vary the focal length for better focus. For example, in a human eye, the major refractive part is the cornea. To reduce spherical aberration of the lens, there is a refractive index gradient; moreover, the lens is

flattened on the external regions (Land, 1988). Thanks to both these correcting mechanisms, the optical system of the human eye is near perfect on the axis resulting in high-acuity vision in the fovea – a part of retina with the highest density of photoreceptors (Curcio et al., 1990; Jonas et al., 1992; Land, 1988). The chromatic aberration is minimized by a pupil narrowing the light beams only to the lens centre. The fact that visual pigments in the human eye respond only in narrow ranges of light spectrum minimizes the aberration, as well as their distribution within the retina (e.g. yellow pigment in fovea cuts blur from blue light) (Björn, 2015; Bowmaker & Dartnall, 1980; Land, 1988).

1.2.1.3. Amphibious Animals

The problem of sharp vision is even bigger for amphibious animals. Various species living in both water and air, deal with it differently (Björn, 2015). For example, crocodiles can focus in air but not in water (Fleishman et al., 1988). Contrarily, penguins can see well in both environments thanks to a flat cornea and a powerful accommodative mechanism that compensates the loss of corneal refracting power in water (Howland & Sivak, 1984). Cornea of the flying fish *Cypselurus heterurus* has a shape of three-sided pyramid. This permits the animal to look through three different almost flat windows – up-forward by the anterior one, up-backward by the posterior one and down by the ventral face of the pyramid. This arrangement provides the fish with relatively good vision in both water and air (Baylor, 1967). Another fish species, the so-called four-eyed fish *Anableps anableps*, does not actually have four eyes. It has two of them, however, each of these eyes includes two corneas and two retinas but just one lens to form images from two different environments. *Anableps* usually swims just below the water surface with half of the eyes above the water line. Its special visual apparatus (shown in Figure 5) allows it to see simultaneously above and in water (Borwein & Hollenberg, 1973; Schwassmann & Kruger, 1965; Sivak, 1976; Swamynathan et al., 2003).

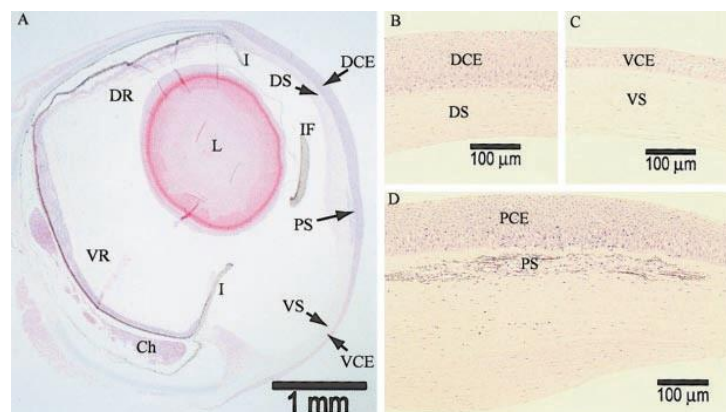


Figure 5 Light Microscopy of Eye of *Anableps*. A) Bright-field microscopy of 2 µm-thick methacrylate-embedded sections stained with hematoxylin and eosin. × 25. B) Dorsal cornea. × 200. C) Ventral cornea. × 200. D) Central cornea bisected by the water surface. × 200.

DCE, dorsal corneal epithelium; VCE, ventral corneal epithelium; PCE, pigmented corneal epithelium; PS, pigmented strip; I, iris; IF, iris flap; DS, dorsal corneal stroma; VS, ventral corneal stroma; DR, dorsal retina; VR, ventral retina; Ch, choroidal tissue; L, lens (figures and legend modified after Swamynathan et al., 2003).

1.2.2. Eyes with Reflective Optics

Refraction of lenses is not the only phenomenon applied in vision. In some types of eye, reflection of mirrors is utilised for several purposes. Many animals have evolved reflective tissues that can be found also on the surfaces of their bodies to camouflage or display, and also in the light-producing organs (Denton, 1970; Herring, 1994; Land, 1972). In general, the reflective tissues are used either for increasing reflectance (i.e. in eyes) or for colouration (“structural colours”) (Herring, 1994; Land, 1972). These so-called biological mirrors are made up of different kinds of material, such as guanine in fish scales, zinc salt of cysteine in cat eyes or riboflavin in bush baby tapeta (Land, 1972). The reflection can arise in two ways. The first one is a reflection of light rays at an interference of refractive indices; it is caused either by glancing angles of incidence light rays or by total internal reflection of the material of higher refractive index (Herring, 1994). The second way is a constructive interference from partially reflecting surfaces arranged in parallel layers (Herring, 1994; Parker & Martini, 2006). The reflection caused by interference is described more into detail in the following chapter (1.2.2.1).

1.2.2.1. Biological Multilayer Mirrors

A single crystal reflects only a small percentage of incident light, however, a row of even only ten crystals separated from each other by cytoplasm can reflect all light at the peak wavelength (Herring, 1994; Land, 1988). For complete constructive interference, the spacing of the layers has to be appropriate – for colours of the first order of interference maximum, the optical thickness of each layer should be equal to one quarter of the wavelength of incoming light (this optical thicknesses can be actually found e.g. in tapeta of the chondrichthyan fishes *Squalus acanthis* and *Scyliorhinus canicula*) and for the second-order colours, it is one third of the wavelength (Denton & Land, 1967; Herring, 1994). When the mirror thickness is adjusted to a particular wavelength, the mirror appears coloured, such as in case of the cuticle of the crab genus *Ovalipes* (Land, 1988; Parker et al., 1998). The observed colour changes with changing angle of the incident light rays (Parker & Martini, 2006).

The biological reflective structure can be achieved not only by multiple layers but also by a periodic texture of ribs or bars that acts as a diffraction grating, this arrangement can be found for example in crustaceans *Myodocopids* (Herring, 1994; Parker, 1995). The first natural diffraction gratings can be found in the fossil record from the Cambrian period. The evolution of animal reflectors is closely related to the evolution of vision (Parker, 2005).

1.2.2.2. Mirror Tapeta

Biological mirrors may work as the main image forming system in some eyes. This phenomenon is described in detail in the separate Chapter 2 devoted to the topic of mirror eyes. However, the reflecting layers might be also used to reflect light that has already passed through a retina to

provide photoreceptors with second opportunity to perceive a light signal (Land, 2000; Ollivier et al., 2004). As a result, the visual sensitivity is improved but the acuity may be impaired (Braekevelt, 1986; Ollivier et al., 2004). However, a special nonparallel arrangement of the reflecting surface can ensure that the light beams reflect back along their path and do not cause worsening of the image (Land, 1972). Since the reflected light passes back through the lens and the pupil, it is visible from the direction of the original illumination and the eye appears glowing (Denton, 1970; Land, 2000).

These reflecting layers, so-called tapeta, are usually present in animals adapted to environments with low intensity of light, such as nocturnal or deep sea species. The tapeta might be located within a retinal epithelium or in a choroid. Tapetum can be static or occlusible. The eye-shine of an eye with the occlusible tapetum varies, which might be caused by the migration of pigment melanin within the cells or by movement of the visual cells themselves, which is called a retinomotor movement (Ollivier et al., 2004). The function of the occlusible tapeta is probably reduction of eye-shine rather than modifying retinal sensitivity (Denton, 1970).

Tapeta might be found in eyes of many species, such as cats, cows, fishes, crocodiles, caimans, bats, lemurs or seals (Ollivier et al., 2004). Some of them are shown in Figure 6.

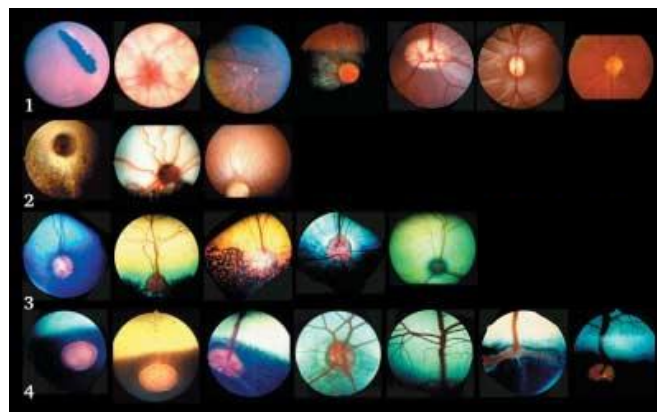


Figure 6 Ocular Fundus of Various Species Showing the Absence or the Presence of a Tapetum That Can Exhibit Various Colors. From right to left: lane 1 - absence of tapetum: bird, albinos rat, hooded rat, red kangaroo, pig, rhesus monkey, human. Lane 2 - retinal tapeta: alligator, possum, fruit bat. Lane 3 - Choroidal tapeta cellulosa: puppy, dog, cat, jaguar, leopard. Lane 4 - choroidal tapeta fibrosa: foal, horse, sheep, goat, cow, deer, mouflon (figure and legend modified after Ollivier et al., 2004).

1.2.2.3. Reflecting Cornea

Some animals, such as teleost fishes, possess iridescent corneas. These corneas contain multilayers of facets that reflect light. The iridescent layers compose of either whole cells or material derived from endoplasmic reticulum or connective tissue (Lythgoe, 1975). After a light exposure, a shift in reflected colour may appear as a consequence of osmotic changes due to altering ion pump activity (Herring, 1994). According to Bernard (1971), the wavelength-selective reflections may enhance contrast. However, Lythgoe (1975) suggests that it reduces intra-ocular flare or the iridescence might also serve to camouflage or display the eye, as well as to navigate.

1.2.3. Compound Eyes

The most numerous type of eye arrangement is a compound eye. There are two main sorts of compound eyes – apposition and superposition eyes – described by Exner (1989, as cited in Wolken, 1995*) and shown in Figure 7. The apposition eyes are common in diurnal species and create number of little images, whereas the superposition eyes construct a single image and may be found mostly within nocturnal species (Björn, 2015; Land & Nilsson, 2012). The compound eye consists of many tiny “eyes” called ommatidia on convex surface so the visual world is split into a lot of parts that are perceived simultaneously. Their small size compared with the light wavelength limits spatial resolution due to the diffraction (Barlow, 1952; Horridge, 1980; Land, 1988; Land & Nilsson, 2012). Contrary to the camera-type eye, the receptive fields can overlap so more light can be captured (Horridge, 1980).

The ommatidium compounds of an optical system (a corneal lens and a crystallin cone) and a photoreceptor system (a photosensitive rhabdom). The rhabdom consists of several photoreceptor cells with rhabdomeres – receptive organelles (Horridge, 1980; Land, 1988; Wolken, 1995).

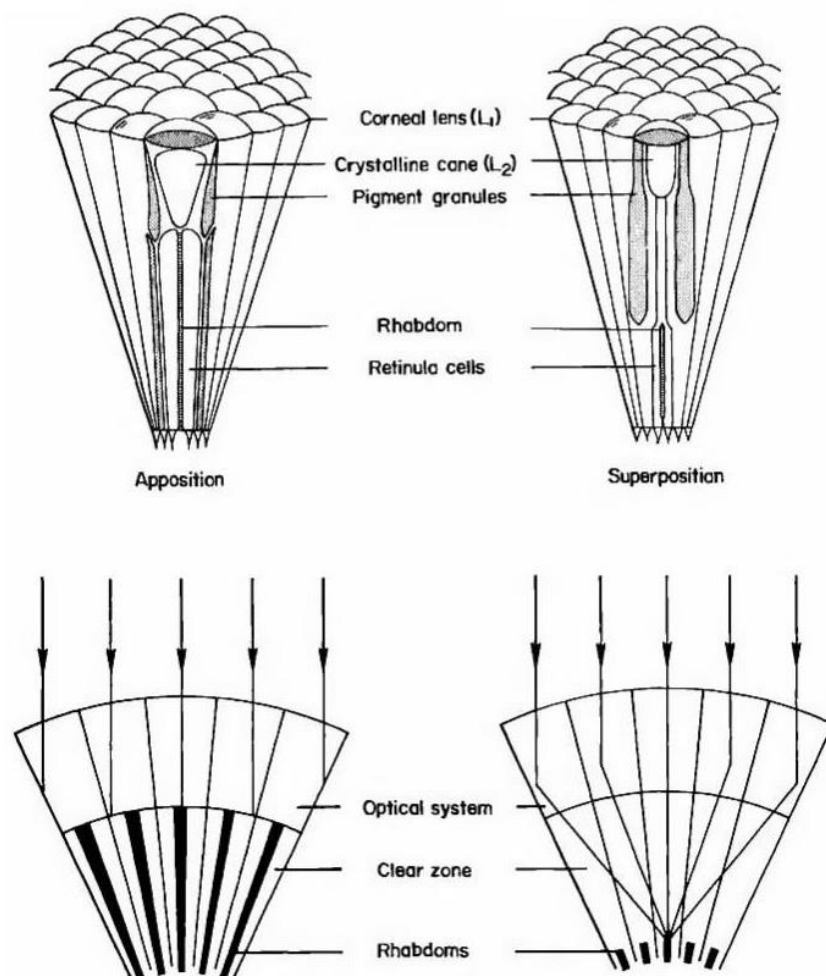


Figure 7 Compound Eye Structures, Eye Facets (Ommatidia), as Schematized for Apposition (left) and Superposition (right) Types and Their Optical Systems (figures and legend modified after Wolken, 1995).

1.2.3.1. Apposition Eyes

In apposition eyes, the photoreceptor lies right behind the optical system, as shown in Figure 7. The rhabdom is surrounded by pigment and it acts as a light-guide; therefore light cannot pass from one ommatidium to another (Wolken, 1995). For apposition eyes it is specific that every single ommatidium creates a small inverted picture. Since the fields of view of ommatidia appose (hence the name), all the tiny pictures together then create the overall erect image (Horridge, 1980; Land, 1988; Land & Nilsson, 2012). The apposition type of compound eye can be found in many diurnal insects, such as Hymenoptera (e.g. *Apis mellifera*), Orthoptera (e.g. *Locusta migratoria*) or Odonata (e.g. *Orthetrum caledonicum*) and decapod crustaceans (e.g. *Ocypode ceratophthalma*) (Horridge, 1978). A special type of these eyes (considered as a link between apposition and superposition eyes) – afocal apposition eyes can be found in some butterflies (Nilsson et al., 1984; Nilsson et al., 1988).

1.2.3.2. Superposition Eyes

In superposition eyes, there is a gap between the crystallin cones and the photoreceptors called clear zone, as shown in Figure 7 (Land & Nilsson, 2012). The lens refracts light beams parallel to those entering the eye. Within the crystallin cone, there is a refractive index gradient (similar to the one in a spherical lens as mentioned above) – the highest in the axis, the lowest in the edges – that binds light rays to a single focus. A rod with such a gradient is called lens cylinder and it can be found even in some apposition eyes (Land, 1988). In superposition eyes, the retina is a solid sheet and rhabdoms can gain light rays from more optical systems of different ommatidia. Single erect image is created by superposition of light rays (hence the name) and lies relatively deep in the eye (Land, 1988; Land & Nilsson, 2012; Wolken, 1995). The superposition of light rays increases the light intensity of the picture, which is why the superposition eyes can be mostly found in nocturnal insects, such as Lepidoptera (e.g. *Ephestia kühniella*), Neuroptera (e.g. *Drepanopteryx phalaenoides*) or Coleoptera (e.g. *Melolontha vulgaris*) and deep-water crustaceans (e.g. *Gennadas* sp.) (Kunze, 1972; Land, 1988; Nilsson, 1990; Wolken, 1995). Several superposition eyes (of e.g. some shrimps) use rather reflective than refractive optics (Land, 1988). These eyes are more discussed in Chapter 2. Another special type of compound eye – parabolic superposition eye was found for example in the crab *Portunus* (Nilsson, 1988).

1.2.3.3. Light and Dark Adaptation of Compound Eyes

There are several possibilities of light and dark adaptation of compound eyes. The most effective one is a migration of pigment between ommatidia. In light, the pigment is distributed in the whole gap between ommatidia to reduce the light influx, while in darkness, it stays close to the basal membrane of the eye. This phenomenon affects light screening and light sensitivity (Höglund & Struwe, 1970; Land & Nilsson, 2012; Meyer-Rochow, 1974).

2. Mirror Eyes

The majority of image forming systems in animal eyes are based on refractive optics. However, there are several eye types that use biological mirrors as main image forming devices. Such eyes are thus called mirror eyes (Land, 2000). The first mirror eyes were described in molluscs (in scallops) by Land in 1965. Later on, mirror eyes have been found also in crustaceans (Vogt, 1975). Recently, mirror eyes have further been reported from vertebrates – in barreleyes, or also called spook fish (Partridge et al., 2014; Wagner et al., 2009). All these three main types of mirror eyes are schematically shown in Figure 8.

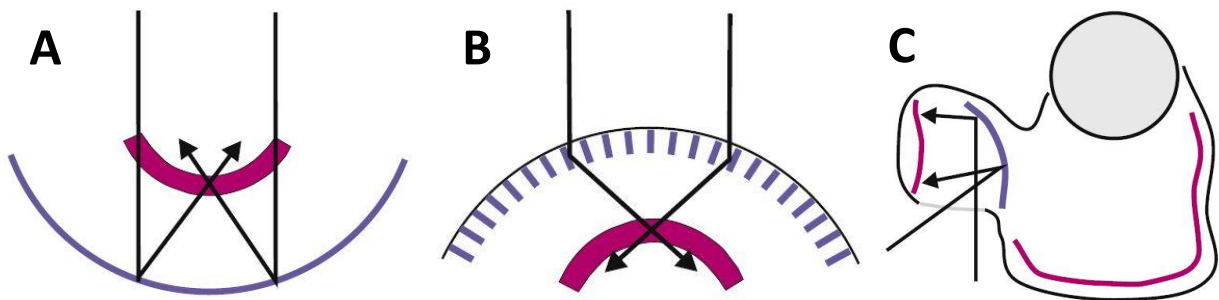


Figure 8 Mirror Eyes. In all panels, mirrors are shown in blue and retinæ in red. (A) Concave mirror optical system of a scallop. (B) Optical system of a decapod crustacean, in which each element of the compound eye is a square mirror box. (C) Double eye of *Dolichopteryx longipes*, with the lens eye pointing upwards, and the mirror eye pointing downwards (figure and legend modified after Land, 2009).

2.1. Molluscs

Mirror eyes have been found in two bivalve molluscs – scallops and cockles (Land, 2000). While eyes of the scallops have been studied by many scientists for more than a century (Speiser & Wilkens, 2016), only little is known about the eyes of cockles (Barber & Land, 1967).

2.1.1. Scallops

Pecten is a genus of scallops – bivalve shells. *Pecten* possesses tens of small eyes along the edge of the mantle. Each eye is single-chambered and contains a cornea, a lens, a two-layered retina, an argentea and a pigment layer, as shown in Figure 9 (Barber et al., 1967; Land, 2000). The generalised eye of *Pecten* only is described in this chapter, however, similar eyes can be found in almost all members of Pectinoidea (Speiser & Wilkens, 2016). In some species, the eyes may morphologically and physiologically slightly vary, often due to the environment they live in (Speiser & Johnsen, 2008; Speiser & Wilkens, 2016). Some morphological differences among various species of scallops are shown in Figure 10.

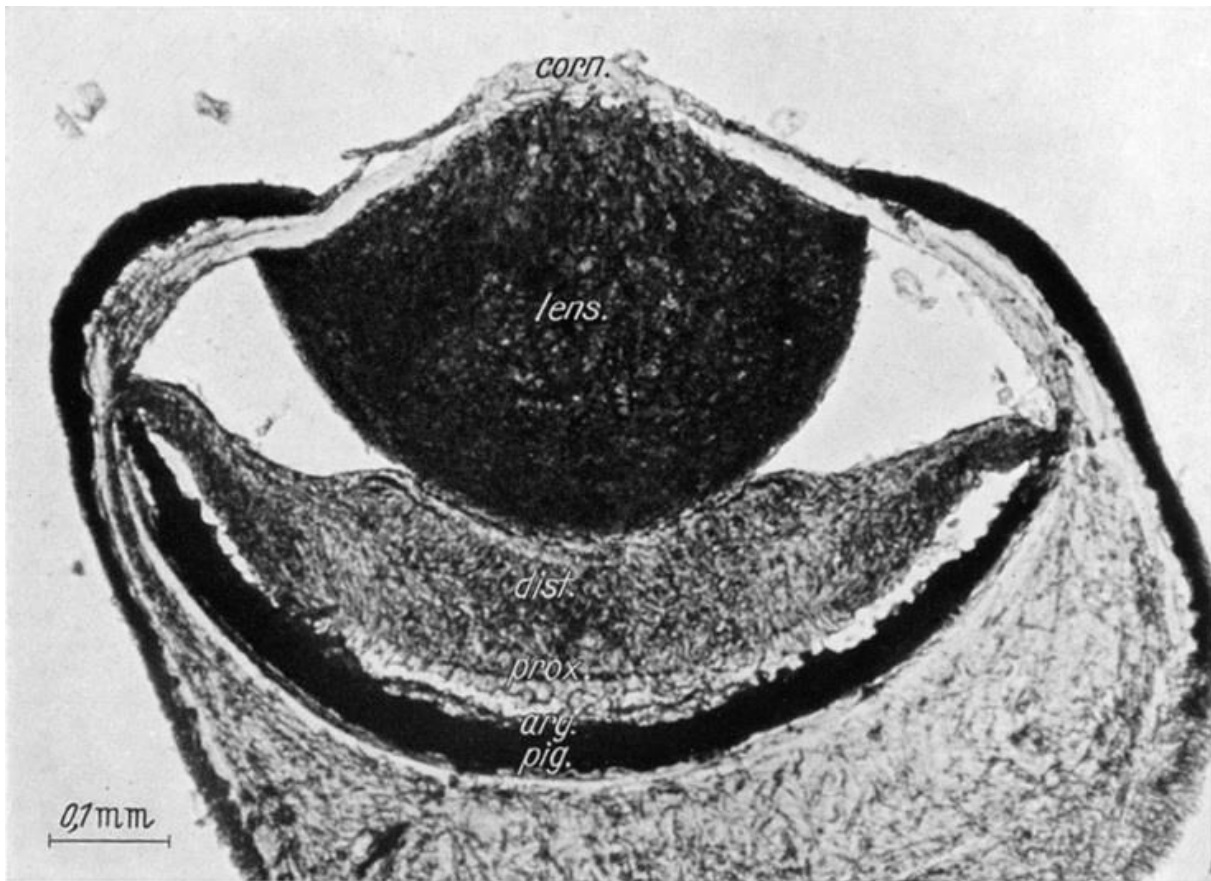


Figure 9 Light Micrograph of a Frozen, Unstained Sagittal Section of the Eye of *Pecten*. corn, cornea; lens; dist, distal retina; prox, proximal retina; arg, argentea; pig, pigment layer (figure and legend modified after Barber et al., 1967).

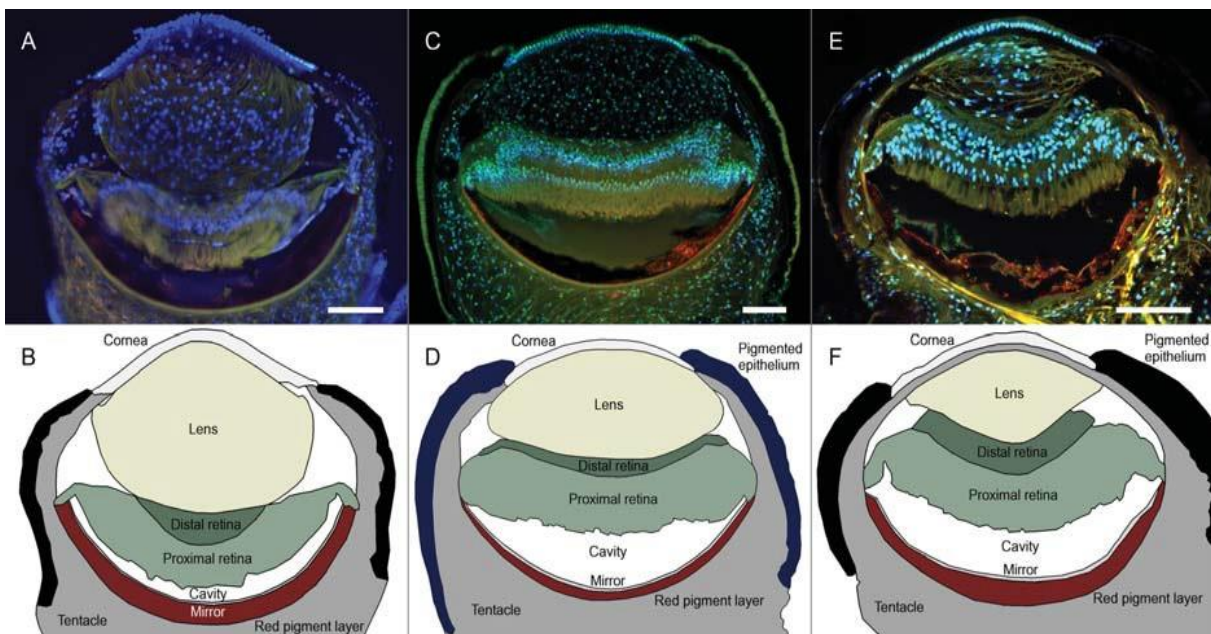


Figure 10 Mantle Eye Sections from the Swimming Scallops *Placopecten magellanicus* (A), *Argopecten irradians* (C) and the Sessile Scallop *Spondylus americanus* (E). (A) a (C) are imaged under a 10× confocal objective, (E) is imaged under a 20× objective. Eyes were stained with Hoescht dye, causing cell nuclei to appear blue, and alpha-tubulin, causing microtubules to appear green. The pigment layer underneath the mirror appears red both in the images and in vivo. The diagrams (B, D, and F) correspond to the confocal images above and are labeled accordingly. Scale bar = 100 μm (figure and legend modified after Speiser & Johnsen, 2008).

Light enters the eye through the single-layered cornea with microvilli that might also have secretory function (Barber et al., 1967; Speiser & Wilkens, 2016). Between the cornea and the lens, there is a thin layer of connective tissue (Speiser & Wilkens, 2016). The lens is a big, jelly-like structure with a low homogeneous refractive index (Barber et al., 1967; Land, 2000). The irregularly arranged lens cells contain only few organelles, their cytoplasm is granular. The lens lies on the 2 μm thick basement membrane. The retina consisting of two separate parts – distal and proximal – is situated below the basement membrane. The distal retina is composed of cells with many cilia and a few microvilli. The cilia create flat receptive plates towards the lens. Axons of distal retinal cells pass along the basal membrane and form an optic nerve. In contrast, the proximal retina is composed of cells with more microvilli than cilia; furthermore, the microvilli receptors face the opposite side of the eye than the ciliary ones in the distal retina (Barber et al., 1967). Axons of proximal retinal cells arise distally, aim to the edges of the retina and subsequently create the second branch of the optic nerve (Barber et al., 1967; Hartline, 1938). The optic nerves then join the circumpallial nerves (Speiser & Wilkens, 2016). Subsequently, the retinal axons project to the lateral (optic) lobes of the parietovisceral ganglion which is the biggest ganglion of the scallop (Spagnolia & Wilkens, 1983; Wilkens & Ache, 1977). Below the proximal retina, there is a spherical single-layered tapetum called argentea for its silvery appearance. It consists of many crystal layers; hence, it works as a biological mirror (Barber et al., 1967; Land, 2000). Finally, there is a pigment layer containing many granules below the argentea (Barber et al., 1967).

The image in the eye of *Pecten* is not formed by refraction at the lens because the lens would create an image outside the eye. The image is created on the retina thanks to the fact that light is reflected by the spherical argentea. Though the *Pecten* mirror can excellently concentrate light on the retina, it greatly suffers from spherical aberration; hence, the resolution of the image produced only by the argentea would be poor. By virtue of its shape and homogenous refractive index, the lens might serve as a corrector of the spherical aberration of the argentea. However, high resolution is probably possible only in the centre of the retina (Land, 1965). Cells of the distal retina tend to be sensitive to longer wavelengths of light than the proximal retina cells. This phenomenon could serve as a correction of self-screening and chromatic aberration (Speiser et al., 2011). Since light passes through the retina twice – firstly unfocused, secondly focused by the mirror, the image is low in contrast. Moreover, *Pecten* cannot focus more distant objects (Colicchia et al., 2009).

The argentea – which is shown in Figure 11 – reflects best the blue-green part of the light spectrum. It consists of tens of layers of guanine crystals less than 100 nm thick, probably loosely distributed in cytoplasm; the layers of cytoplasm between the crystal layers are slightly thicker, about 100 nm. Optical thicknesses of both crystals and cytoplasm are approximately one

quarter of the blue-green light wavelength. Such a structure has theoretically almost 100% reflectivity so it can work as a very efficient biological mirror (Land, 1966a).

As already mentioned, the *Pecten* retina consists of two parts – the distal one and the proximal one, each forming a separate branch of the optic nerve. The ciliary cells of the distal retina (shown in Figure 12) exhibit the “off” response – nerve impulses occur after decrease of illumination (overall or partially). In contrast, the microvilli cells of the proximal retina (shown in Figure 13) exhibit the “on” response – nerve impulses occur after increase of illumination (as well as during permanent illumination in some species) (Gorman & McReynolds, 1969; Hartline, 1938; Land, 1966b). The “off” and “on” responses are independent of each other and they are triggered by light (Hartline, 1938; Land, 1966b). Both of them are connected with a membrane conductance increase (McReynolds & Gorman, 1970a). Nonetheless, the “off” response is related to hyperpolarization when illuminated and depolarisation when shaded afterwards. The “on” response is a consequence of depolarisation during illumination (McReynolds & Gorman, 1970a; McReynolds & Gorman, 1970b; Speiser & Wilkens, 2016). However, there was a third membrane response found in the *Pecten* eye. In the proximal part of retina with large representation of glial cells, there was a biphasic response recorded – the resting potential was large, the resistance was low, the responses to light were slowly rising and prolonged, and also summation of responses occurred. Probably, it was a response of glial cells (McReynolds & Gorman, 1970b).

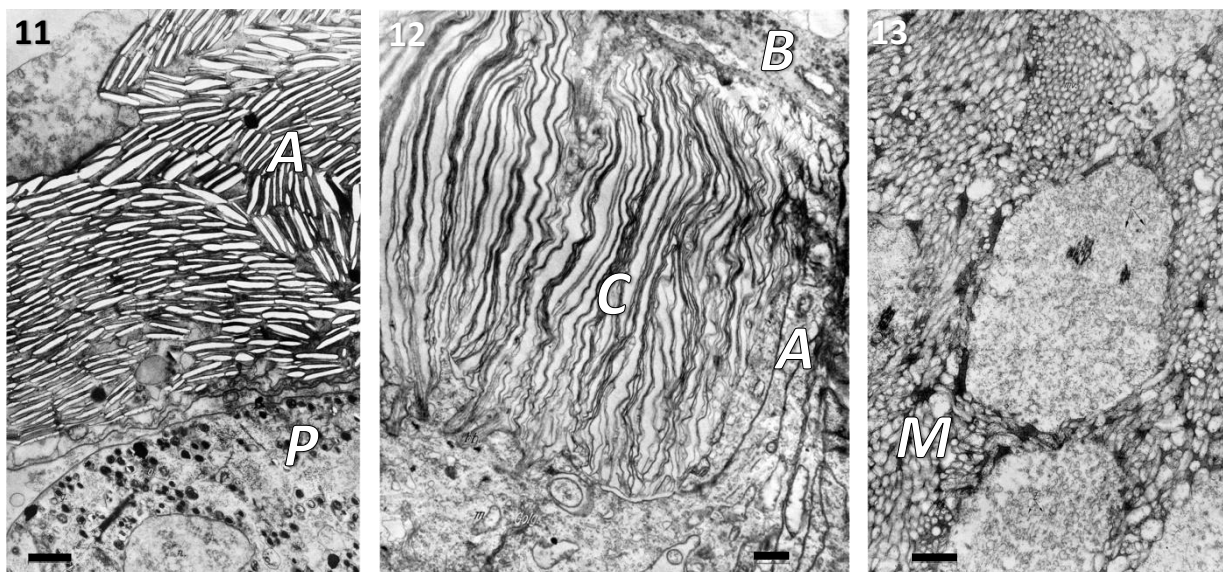


Figure 11 Sagittal Section of the Argentea of *Pecten*. It is showing the holes left after the reflecting crystals were dissolved out in electron microscopical preparation. Below the argentea (A), there is the pigment cell layer (P). Fixed osmium, Millonig's phosphate buffered, stained lead citrate. Scale bar = 1 μ m.

Figure 12 Sagittal Section of the Distal Layer of the Retina of *Pecten*. It is showing the distal basement membrane (B) and the receptive array of the distal cells composed of ciliary lamellae (C). The cells bear lateral axons (A). Fixed osmium, Millonig's phosphate buffered, stained lead citrate. Scale bar = 1 μ m.

Figure 13 Transversal Section across the Proximal Cells of the Retina of *Pecten*. It is showing the microvilli (M) of the proximal cells. Fixed osmium, veronal acetate buffered, stained lead citrate. Scale bar = 1 μ m (figures and legend modified after Barber et al., 1967).

Phototransduction in the distal retina cells is mediated by G_o-protein cascade resulting in increase of cGMP and therefore opening of potassium channels so K⁺ ions flow outwards which leads to the hyperpolarisation of the cells (Gomez & Nasi, 1994; Gorman & McReynolds, 1974; Kojima et al., 1997; Shimatani & Katagiri, 1995; Speiser & Wilkens, 2016). The depolarisation after shading is caused by closure of potassium channels and calcium influx. However, the inactivation of Ca²⁺ channels is removed by hyperpolarisation when illuminated. Therefore light causes both excitatory and inhibitory response. Nevertheless, the inhibition exceeds excitation so the cells hyperpolarise while illuminated (Cornwall & Gorman, 1979; Cornwall & Gorman, 1983; Speiser & Wilkens, 2016). The proximal retina cells depolarise due to the influx of Na⁺ ions caused by opening of ion channels as a consequence of the phototransductional G_q-protein mediated cascade (Kojima et al., 1997; Speiser & Wilkens, 2016).

Only the distal retina lies in the plane of the image created by the argentea. The distal retina responds to changes in the environment, such as a movement of an oncoming predator, resulting in the shadow reflex – closing the shell when darkened. The information about overall intensity of illumination provided by the proximal retina might be important for a choice of habitat (Land, 1966b; Speiser & Wilkens, 2016). Moreover, the visual information is important for feeding and swimming of scallops too (Morton, 2000).

2.1.2. Cockles

The cockle *Cardium edule* is a small bivalve mollusc. It possesses around 100 eyes on tentacles located around the bases of siphons. A reflecting tissue creates an eye cup that encloses 12-20 ciliary receptor cells giving only off responses (in decrease of illumination) (Barber & Land, 1967; Barber & Wright, 1969a). Some of the cilia of the receptor cells create arrays similar to the ciliary plates in the eye of *Pecten* (Barber & Wright, 1969a). The axons of the *Cardium* receptor cells leave the eye at the edge of the reflector cup and join the external pallial nerve (Barber & Land, 1967; Barber & Wright, 1969a). On the opposite side of the eye, the epithelial cells contain pigment granules. The pigment epithelium probably serves as a filter and shields the reflector (Barber & Wright, 1969a). The reflecting tissue is created by approximately 20–30 layers of parallel-sided crystal plates separated by cytoplasm. This structure works as a biological mirror that forms an image on the receptor cells (Barber & Land, 1967; Barber & Wright, 1969a). Because of the low number of receptor cells, *Cardium* is probably capable only of simple shadow detection important for a shadow response (Barber & Wright, 1969a).

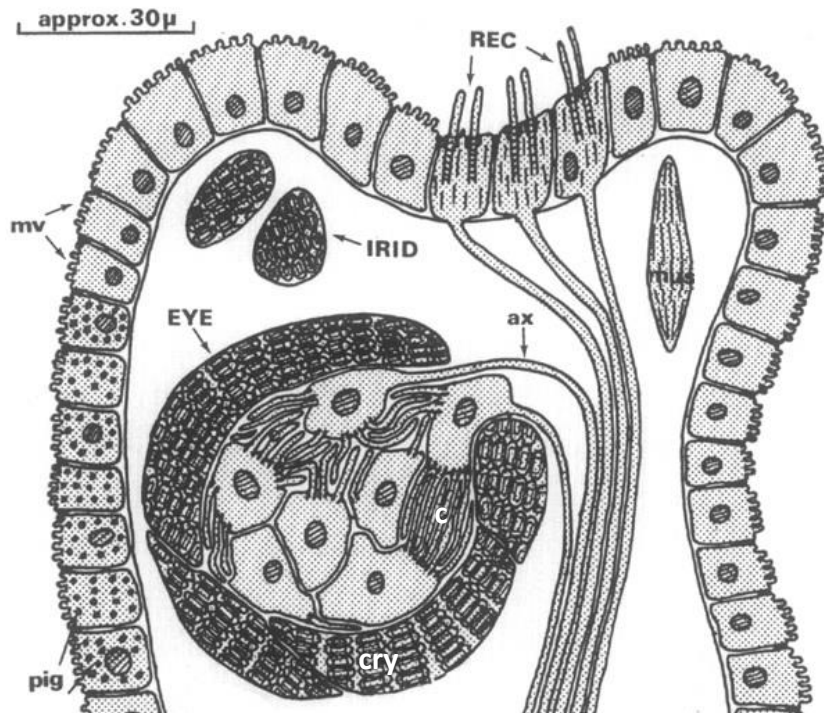


Figure 14 Diagram of Sagittal Section of Optic Tentacle of *Cardium*. The reflector cup consists of cells containing layers of crystals (cry). The receptor cells bearing cilia (c) are present inside the reflector cup. These cells bear axons (ax). Other receptor cells bearing cilia (REC) are present at the apex of the tentacle. Muscle fibers (mus) and iridophores (IRID) are present in the tentacle. The cells of the outer epithelium of the tentacle bear microvilli (mv). In the region behind the eye cells of the outer epithelium contain pigment granules (pig) (figure and legend modified after Barber & Wright, 1969a).

2.2. Crustaceans

For some time, it was not known how the decapod crustaceans see since the optical features of their eyes did not correspond with the refractive formation of images (Björn, 2015; Land & Nilsson, 2012). In 1975, Vogt described the crayfish eye as a reflective superposition eye. Right after that, Land (1976) described another decapod – shrimp having the same type of eye. Later on, it has turned out that several crustacean species, e.g. the copepod *Sapphirina* or the ostracod *Notodromas*, possess even other types of mirror eyes (Land, 2000; Land & Nilsson, 2012).

In the reflective superposition eyes, the ommatidia cones are coated with reflective tissues. Since the mirrors are arranged into a square pattern, the light beams of any angle of incidence may be utilised and redirected on the retina (Cronin, 1986). However, it is important that the mirror boxes are of the right size and depth so the light beams do not reflect too many times (Land & Nilsson, 2012).

The proteins used in the reflective tissues of crustaceans are mainly pteridines, such as isoxanthopterin or xanthopterin (except copepods and probably ostracods) and secondarily purines (e.g. xanthine, hypoxanthine and guanine) (Zyznar & Nicol, 1971).

2.2.1. Decapods

Though decapods possess superposition eyes, they differ from those of insects. While in insects facets are shaped as hexagons, decapods have square facets (Wolken, 1995). Moreover, the

refractive indices are usually high and possessing a gradient in insects, but they are quite low and roughly homogeneous in decapods (Land & Nilsson, 2012). Vogt (1975) found out that the crayfish eye uses reflective optics rather than refraction since the crystallin cones and multi-layered tissue, which encloses them, both together form orthogonal reflectors. Such arrangement can be found also in other long-bodied decapod crustaceans, e.g. prawns and lobsters, however, not in hermit and true crabs (Land & Nilsson, 2012). In this thesis, I will focus in detail only on the first two discoveries of the superposition reflective eyes – the crayfish *Astacus* and the shrimp *Oplophorus*.

The compound eye of the crayfish *Astacus* consists of thousands of ommatidia. Each ommatidium compounds of a corneal facet, a crystallin cone (divided into two parts – distal and proximal) surrounded by pigment cells, a rhabdom consisting of 8 retinular cells, a tapetum and a basement membrane (Krebs, 1972; Vogt, 1980). The corneal facet has a squared shape and homogenous refractive index (Vogt, 1980). It works as a weak lens to pre-focus light (Land & Nilsson, 2012). The distal part of the crystallin cone is shaped as a regular four-sided pyramid where the sides form approximately right angles (Vogt, 1977; Vogt, 1980). The refractive index is homogeneous in the distal part of the cone. However, it decreases axially onwards the rhabdom in the proximal tail of the cone (the clear zone). The sides of the distal part of the cone work as biological mirrors since they are made of few (3–4) ordered parallel layers of purine crystals (Vogt, 1977; Vogt, 1980). Though the number of the crystal layers is low, the reflectance is high due to the great angles of incidence (Vogt, 1977). Each of the crystal layers is about 200–300 nm thick, separated from the others by more than 100 nm thick layer of cytoplasm (Vogt, 1980). Thanks to the special orthogonal arrangement, this system works for any incident light beam; hence, the ray reflects once or twice in the cone. The combination of the multi-layered reflective tissue of the distal part of the cone and the refractive index gradient in the proximal part of the cone allows the superposition image formation further in the eye – in the rhabdom (Vogt, 1977). Image created in the crayfish eye is bright with good spatial resolution (Vogt, 1980). The rhabdom extends in the direction from the cone to the basement membrane (Krebs, 1972). The retinular cells in the rhabdom are specially arranged so they can determine even the polarization of light (Muller, 1973). The axons of the eight retinular cells of one ommatidium join the axons rising from other ommatidia. The cells of the tapetum contain a lot of pigment granules and vacuoles. The reflection from the tapetum back to the rhabdom is probably caused by the total reflection of light on the gaseous vacuoles. The basement membrane is not important only for the retina stability but also for nutrition of the retinular cells (Krebs, 1972).

The eyes of other crayfish species may significantly vary from the eyes of *Astacus*. For example, the reflecting superposition eyes of the crayfish *Cherax destructor* possess corneal facet lenses for better light focus (Bryceson, 1981).

The shrimp *Oplophorus spinosus* possesses almost spherical superposition eyes. The cones material has too low refractive index to be able to form an image by refraction. However, the cone sides are internally covered by a layer of reflecting material; therefore, they work as biological mirrors. The incoming light reflects at one of the sides of each cone. Finally, the image is formed due to the thin-film interference (Land, 1976). The optical and anatomical structure of the eye of *Oplophorus spinosus* is shown in Figure 15.

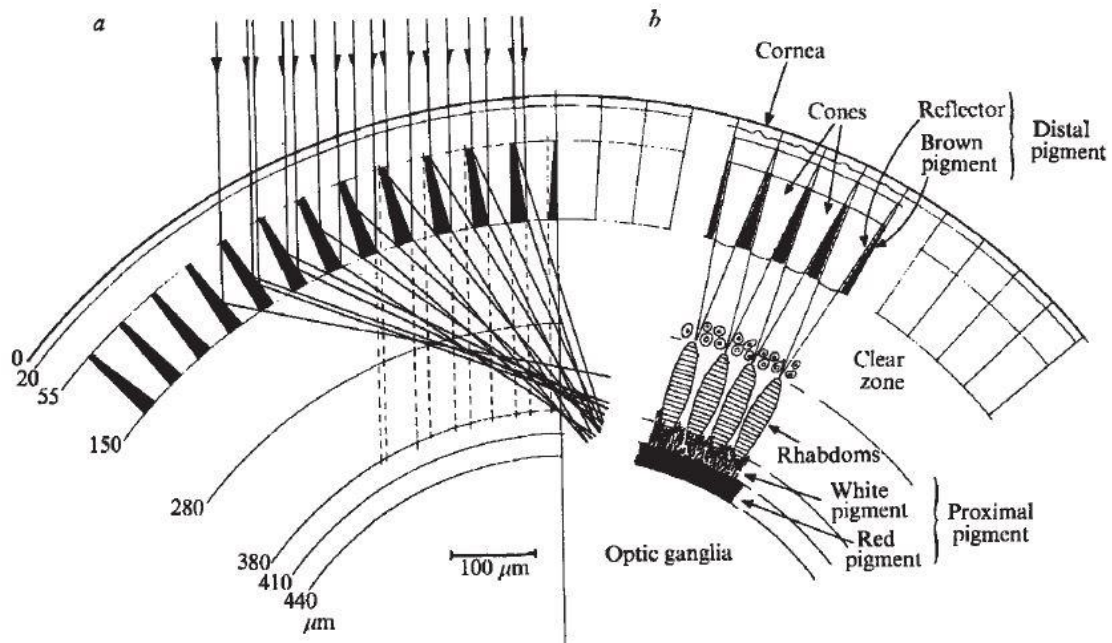


Figure 15 Optical (a) and Anatomical (b) Structure of Part of the Eye of the Shrimp *Oplophorus*. In (a) it is assumed that the only optical components in the eye are the reflector-lined faces of the cones. Solid lines show how reflected light is brought to a focus; dashed lines indicate pencils of rays that pass through directly. The numerals on the left show the depth of each layer from the surface. (b) shows the parts of the eye as visible in a hemisected eye seen through a dissecting microscope (figure and legend modified after Land, 1976).

2.2.2. Amphipods, Copepods, Ostracods

There are many other crustacean species that possess biological mirrors in their eyes. However, it is not clear whether these eyes should be called mirror eyes since the reflectors do not create images in these eyes (neither other optical system does). However, they serve as light collectors; moreover, they might provide the photoreceptors with rough information about the direction of light. Simple eyes with such mirrors can be found e.g. in the amphipod *Scypholanceola*, the ostracod *Gigantocypris* or the ostracod *Vargula*. Nauplius mirror eyes can be found in the copepod *Sapphirina* and the ostracod *Notodromas* (Herring, 1994; Land & Nilsson, 2012).

The nauplius eye occupies a great part of the head of *Sapphirina* (Elofsson, 1966). The eye consists of three cups (a ventral cup and two lateral cups) connected together by connective tissue that also forms a capsule around the eye (Elofsson, 1966; Elofsson, 1969). The ventral cup is small directed ventrally, the lateral cups are large; however, they are not connected to the ventral cup (Elofsson, 1966). In the dorsal side of the ventral cup, there are two pigment cells with red pigment granules and two tapetal cells with crystals. The flat square double platelet

crystals are arranged in parallel layers situated below the rhabdoms. The *Sapphirina* tapetum is likened to the argentea of *Pecten* due to its morphology; therefore, it might have the same function. There are two other cells similar to the tapetal cells but lacking the crystals on the opposite side of the ventral cup. Moreover, there are two groups of retinula cells. The rhabdom of one of them heads anteriorly, the rhabdom of the second group points posteriorly. In each lateral cup, there are two lenses, two groups of retinula cells, two pigment layers (red and black), a tapetal cell and four more cells situated towards the tapetum (Elofsson, 1969). The larger lens forms and image onto the smaller lens attached to the retina (Land, 2012). The tapetal cell extends between the retinula cells, the crystal platelets are found only near the rhabdoms similar to the ventral cup. In a small area of the inner pigment layer, there can be crystal platelets found too (Elofsson, 1969). Interestingly, the rear parts of the eyes can move to the sides (Land, 2012).

The nauplius eye of *Notodromas* consists of three cups – a ventral cup and two dorsolateral cups. However, these cups are not divided as in *Sapphirina* but they are connected by the pigment cells. The pigment cells are arranged into a shape of letter Y, as shown in Figure 16. The cups are situated at the end of each arm (Andersson & Nilsson, 1981; Turner, 1896). Each cup consists of two tapetal cells, sensory cells, a valve lens and connective tissue. Furthermore, each lateral cup possesses a cuticular lens (Andersson & Nilsson, 1981; Claus, 1891). The connective tissue and the basal laminae enclose the whole eye (Andersson & Nilsson, 1981). The pigment cells connecting the cups contain red-brown pigment concentrated to the cell edges (Andersson & Nilsson, 1981; Elofsson, 1966). The tapetal cells consist of parallel layers of crystal platelets. There are about 25–35 layers in the ventral cup and approximately 15–20 layers in the lateral cups. While the nuclei of the tapetal cells of the ventral cup are elongated, they are spherical in the lateral cups. There are 9 retinular cells in the ventral cup and 18 retinular cells in each lateral cup. Each of the retinular cells laying on the tapetum bears an axon. The axons leave the cups in bundles and enter the protocerebral neuropile. Each of the lenses is formed by a single cell. The lenses appeared to be homogenous in the refractive indices. The refractive indices of the cuticular lenses are high compared to the low refractive indices of the valve lenses. Since the lenses alone would create images behind the cups, the tapeta are necessary for the image formation on the retinular cells. The cuticular lenses work as an effective prefocusing system compared to the valve lenses with low refractive indices that contribute on the light focusing only little. *Notodromas* might possess stereoscopic vision due to the overlap of the visual fields of the cups. However, the contrast and resolution are poor due to the fact that light passes through the retinal cells twice (firstly unfocused and then focused by the tapetum); moreover, the rhabdoms do not lie in the image plane. However, the neuropile might compensate the visual restriction on the neuronal level (Andersson & Nilsson, 1981).

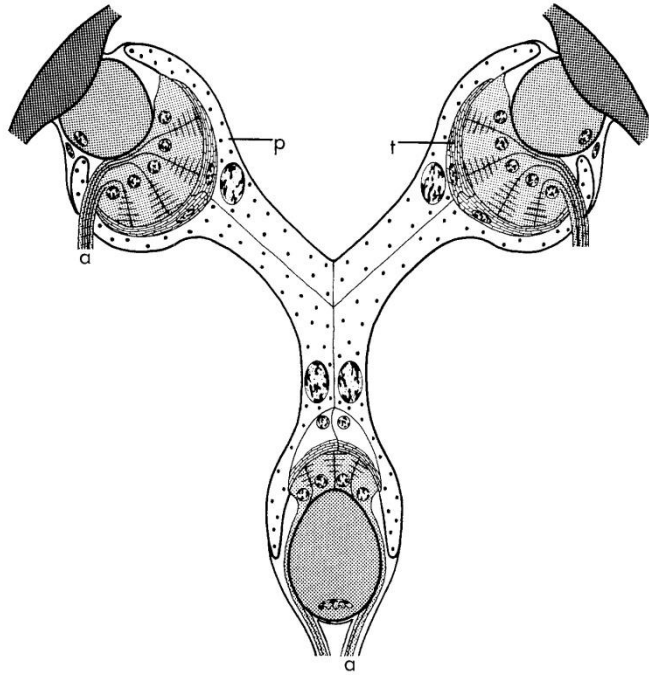


Figure 16 Schematic Drawing of a Frontal-Sectioned Nauplius Eye of *Notodromas*.
a, axons; p, pigment cell; t, tapetal cell; coarsely stippled, cuticular (valve) lenses; fine stippled, lens and reticular cells (figure and legend adapted from Andersson & Nilsson, 1981).

2.3. Fishes

In 2009, *Dolichopteryx longipes* was described by Wagner et al. as the first vertebrate possessing mirror eyes. In 2014, Partridge et al. described another fish, *Rhynchohyalus natalensis*, with reflective optics that belongs to the same family of fish – Opisthoproctidae (also known as barreleyes or spook fish) as *Dolichopteryx longipes*. Although the mirror eyes (diverticula) of these two species are similar, they vary in two important attributes – the origin of the reflective tissue and the orientation of their reflective plates (Partridge et al., 2014).

2.3.1. *Dolichopteryx longipes*, the Brownsnout spookfish

Dolichopteryx longipes is a cylindrical elongated fish living in the mesopelagic zones of warm-water areas of the northern Atlantic and the northern Pacific ocean (Gregory & Conrad, 1936; Grey, 1952; Land & Nilsson, 2012; Parin et al., 2009). It has two eyes, each divided into two parts separated by a septum – a bigger upwards oriented tubular eye and a smaller lateral diverticulum, as shown in Figure 17. The eye appears silvery thanks to a tapetum – argentea on the internal part of a capsule that is made of connective tissue that surrounds both eye parts together. Because of the choroid containing melanin, the diverticulum looks black since its dorsal part lacks the argentea. The upper part of the eye works as a proper lens tubular eye processing the visual world dorsally; however, the lateral part of the eye forms images of the lateroventral visual world based on the reflective optics (Wagner et al., 2009).

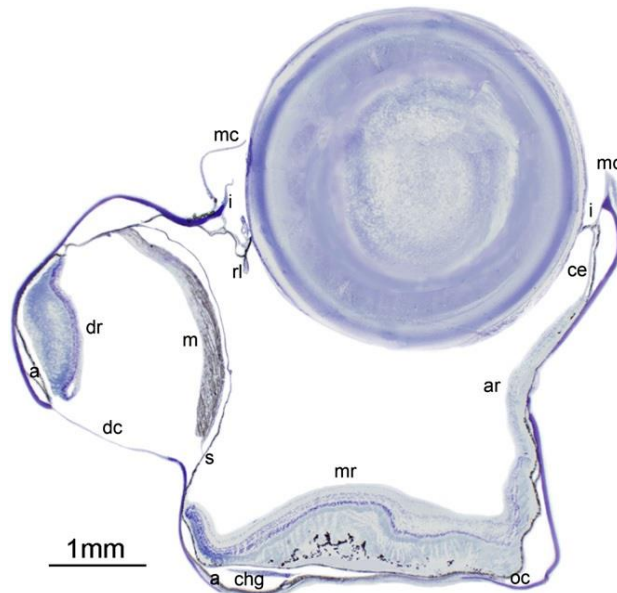


Figure 17 Transverse Section of the Entire Right Eye of *Dolichopteryx longipes*. It is showing both a main, upwardly directed tubular portion and a lateroventrally directed diverticulum. The section was taken 522 mm from the rostral edge of the eye. a, argentea; ar, accessory retina; ce, ciliary epithelium; chg, choroid gland; dc, diverticular cornea; dr, diverticular retina; i, iris; m, mirror; mc, main cornea (partially removed for facilitating the impregnation of tissue with resin); mr, main retina; oc, outer coats of the eye, consisting of sclera, argentea, and choroid; rl, retractor lentis muscle (ventral part); s, septum between the main tubular eye and the diverticulum (figure and legend adapted from Wagner et al., 2009).

In the diverticulum, the retina lies on the lateral, caudal and rostral surfaces. The retina is thick and composed of layers of photoreceptor cells in the centre; however, it contains thin single-cell layer in the edges. The retina of the diverticulum is continuously connected with the retina of the tubular eye. The reflective layer (a biological mirror) lies on the medial surface of the diverticulum – in the septum dividing the eye parts. The mirror is approximately 200 μm thick and it is surprisingly derived from the retina and not from the argentea. It consists of organized small plates of high refractive index probably made of guanine. The plates are not oriented parallel to the surface of the septum, instead their angles gradually change as their position from the geometric centre increases. This arrangement together with the fact that the mirror is parabolic and off-axis provide the eye with a well-focused image high in brightness and contrast over most of the retina. However, when the light beams are close to the vertical, only a part of the mirror is utilized so the image is less bright at the dorsal part of the retina (Wagner et al., 2009).

To accommodate the eye for closer objects, the mirror would have to be moved away from the retina. Since the *retractor lentis* – a muscle of the tubular part of the eye – is attached to the septum, there might be a possibility of accommodation of the *Dolichopteryx longipes* diverticulum (Wagner et al., 2009).

Whereas the tubular part of the eye probably serves to capture dark objects against the residual sunlight, the diverticulum is supposed to detect primarily bioluminescent flashes coming from the deeper water layers, i.e. from the ventral side of the fish (Wagner et al., 2009).

2.3.2. *Rhynchohyalus natalensis*, the Glasshead barreleye

Rhynchohyalus natalensis is a mesopelagic, probably circumtropical, fish species of the Opisthoproctidae family (similar to *Dolichopteryx longipes*) (Hartel et al., 2008; Partridge et al., 2014). Each of the eyes of *Rhynchohyalus natalensis* consists of two parts separated by a septum – a dorsal tubular eye and a ventro-lateral diverticulum (as shown in Figure 18) dividing the visual space in similar way as in *Dolichopteryx longipes*. Also in *Rhynchohyalus natalensis*, the inner surface of the scleral capsule of the eye is covered by a choroidal argentea so the eyes appear silvery. The cornea lies ventrally on the lateral part of the diverticulum and it can probably receive light even from the contralateral side. It is made of connective tissue with the epithelial outer layer (Partridge et al., 2014).

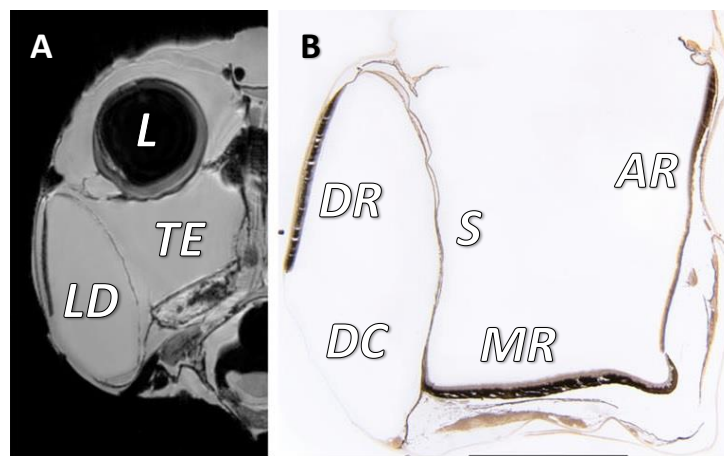


Figure 18 Gross Morphology of the Eye of *Rhynchohyalus natalensis*. (A) MRI section of the right half of the head showing the tubular eye (TE) including the lens (L) and the lensless ventro-lateral diverticulum (LD); (B) 25 mm thick resin-embedded histological section of the eye with the lens removed. Scale bar = 10 mm.

DR, diverticular retina; DC, diverticular cornea; S, septum with mirror on the lateral side; MR, main retina of tubular eye; AR, accessory retina of tubular eye (figure and legend modified after Partridge et al., 2014).

The tubular part of the eye has a four-layered retina and a thinner accessory retina that is reduced to a simple ciliary epithelium on the surface of the septum. The retina of the diverticulum is similar to the tubular eye retina and lies on the lateral wall, as shown in Figure 18. Below the retina, there is a choroid with the argentea and a cartilaginous sclera. On the opposite side of the eye – on the septum, there is a lateral choroid and a reflective tissue laying internally – a biological mirror. The mirror of *Rhynchohyalus natalensis* is derived from the lateral argentea (in contrast, the mirror of *Dolichopteryx longipes* is derived from the retinal tissue). It contains few (3-4) layers of probably guanine crystals orientated parallel to the basal membrane of the septum separated by cytoplasm. The crystals vary in their thickness that is significantly bigger than the ideal quarter of the wavelength (Partridge et al., 2014). Therefore the mirror probably works as “chaotic” reflector, similarly to the scales of fish, such as *Trichiurus lepturus* or *Lepidopus caudatus* (McKenzie et al., 1995; Partridge et al., 2014). Hence the diverticulum can form an image by reflection (though the reflectance is approximately only 20–30%), with probably good preservation of spatial information (Partridge et al., 2014).

3. Vision in the Deep Sea

Seawater covers 71% of the Earth surface with an average depth of 3800 m. That makes the sea the largest habitat involving 75% of the biosphere (Angel, 1997). Great variability of various biotic and abiotic factors generates huge ecological diversity and therefore influences animal adaptations (Angel, 1997). One of the most important factors are changes in light conditions since vision is an important sense in habitats of low food and low frequency of mates (Warrant & Locket, 2004).

The penetration of the sunbeams (as well as the light from the moon and the stars) into the water column is affected by many variables, such as wind on the surface or water reflectance (Björn, 2015). Light is greatly absorbed by water so its intensity and polarisation decreases with increasing depth (Warrant & Locket, 2004). Therefore it reaches maximally the depth of approximately 1 km, there has been no detection of photons below this point (Angel, 1997; Björn, 2015). Light penetrance further depends on other aspects, such as a concentration and a distribution of plankton or mineral particles in water (Björn, 2015). Moreover, different wavelengths are absorbed and scattered at different depth levels so the spectral composition of light changes significantly with depth (Björn, 2015; Warrant & Locket, 2004). In general, the edges of the light spectrum are absorbed more than the middle part of the light spectrum. The long-wavelength orange-red light is the most absorbed; short-wavelength ultraviolet part of the spectrum is absorbed a little bit less. In contrast, the blue-green part of the spectrum penetrates the deepest (Angel, 1997; Warrant & Locket, 2004).

However, the sun, the moon and the stars are not the only light sources in the sea. Some organisms, such as bacteria, algae, fishes etc., are able to produce light by themselves. This ability is called bioluminescence. The emission of photons is caused by enzymatic exergonic reactions of oxygen and luciferins (Wilson & Hastings, 1998). Some of the organisms that are not capable of producing light on their own, accommodate bacteria in their light organs, like for example many of the ceratioid anglerfishes known for possessing a bioluminescent lure reminding of a lantern (Helfman et al., 2009). Furthermore, some of the light-producing organs use the reflection of biological mirrors (Herring, 2000). Since the sunbeams penetrate maximally to the depth of 1 km, the point bioluminescent flashes are the only light source in waters deeper than 1000 m (Warrant & Locket, 2004).

The sea environments may be classified in many ways. The basic sorting is into the benthic (in or on the seabed) and the pelagic (the open sea) zone, both of them may be further subdivided, as shown in Figure 19. Moreover, the absence or presence of sunlight defines aphotic (darkness) or photic (light) zone, respectively (Vernberg & Vernberg, 2013). The changes in the light spectrum and intensity together with other features determine different

zone profiles (Angel, 1997). Since the marine environments differ, various selective pressures affect the adaptations of organisms and specially of their sensory systems (Warrant & Locket, 2004).

Vision is important for the deep-sea animals as much as for the terrestrial ones. It allows them to navigate in space, find feeding resources and mates, or avoid danger. Nonetheless, as the nature of light passing through water changes rapidly, it gets dimmer and composed of narrower part of the light spectrum with increasing depth. Due to this fact, the demand on efficient optical system is high. Therefore, features, such as great sensitivity, high contrast, good spatial acuity and long visual range, are required. However, there is a great trade-off between these properties necessary since one of them usually comes at the expense of another one (Warrant & Locket, 2004).

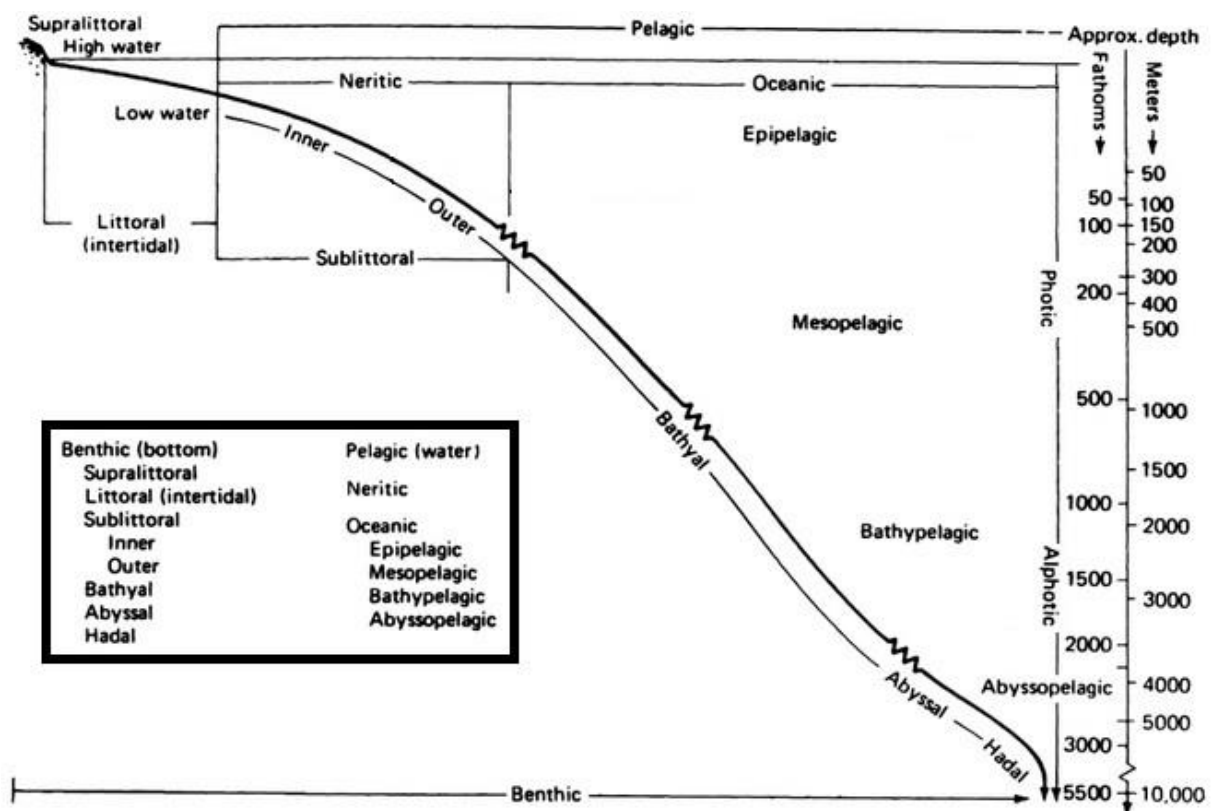


Figure 19 Classification of Marine Environments (figure and legend modified after Iledgpath & Ladd, 1957).

Animals living in the bright marine environments, such as in the epipelagic zone (to the depth of 200 m), encounter similar visual needs as those on land. However, the situation changes in the deeper zones when the light intensity declines and bioluminescent point flashes are becoming more important to detect (Warrant, 2000; Warrant & Locket, 2004).

In the mesopelagic zone (approximately 200 – 1000 m undersea), both light sources meet; hence the diversity of visual system adaptations of mesopelagic animals is very broad since they might be customized to one or both of them (Warrant & Locket, 2004). The light-gathering power of the eyes may be improved by possessing larger pupils (or facets in

compound eyes) and lenses, as well as by bigger size of the eyes themselves (Salvanes & Kristofersen, 2001; Warrant, 2000). Therefore many mesopelagic animals, such as the fish, Eastern Pacific roughy (*Hoplostethus pacificus*), or the Giant squid (*Architeuthis dux*), possess big eyes compared to the rest of their bodies (Kotlyar, 2010; Warrant & Locket, 2004). To further support the light perception, many mesopelagic animals, e.g. the copepod crustacean *Macrocylops albidus*, possess reflective tapeta to provide the receptors with a second opportunity of light detection (Fahrenbach, 1964; Warrant & Locket, 2004). Moreover, the receptive fields of ganglion cells are generally larger and the brain structures specialised on vision are proportionally bigger than in the shallow-water species (Wagner, 2001; Warrant, 2000). To improve spatial resolution, some mesopelagic fishes have evolved tubular eyes with large spherical lenses (Salvanes & Kristofersen, 2001). The tubular eyes are orientated in different directions due to the hunting methods of the fish – for example the eyes of the telescopefish (*Gigantura chuni*) are orientated frontally, but the eyes of the pearleye (*Scopelarchus michaelsarsi*) point dorsally (Warrant & Locket, 2004). Similarly, the invertebrate eyes are often pointing dorsally to capture as much of daylight as possible (Warrant & Locket, 2004). The photoreceptors of mesopelagic organisms are often arranged in many layers – rods multibanks. The multibanks may work as a spectral filter and therefore improve sensitivity of the eye; however, the exact mechanism of the multibank retina function remains unclear in many cases (Denton & Locket, 1989; Warrant & Locket, 2004). Furthermore, the photoreceptors are mostly sensitive to the blue-green part of the spectrum since these are the most common light wavelengths in this part of the ocean (Salvanes & Kristofersen, 2001; Warrant & Locket, 2004). Moreover, photoreceptors of some species are packed into groups isolated by reflective crystals (such as guanine) creating “a macroreceptor” that has wider and more sensitive receptive field than a single photoreceptor would have (Warrant & Locket, 2004). Finally, some predators can even detect light polarisation or filter certain wavelengths to break the camouflage of pray, therefore they can see transparent organisms as well as those using bioluminescent counter-illumination (Warrant & Locket, 2004).

The bathypelagic zone (bellow 1000 m undersea) is a cold and dark environment with extremely low amount of food and mates, hence the energy cost is very important for organisms to survive. Therefore they move slowly, their skeletons and muscles are weak and their respiration rates are very low (Warrant & Locket, 2004). Since sunlight does not penetrate into such depth, bathypelagic organisms often compensate the lack of visual stimuli by improving other sensory systems for perceiving e.g. chemical information (Kotrschal et al., 1998). Due to this fact and also by reason that the eyes are energy-intensive organs, eyes of bathypelagic species tend to be small and sometimes even reduced, such as in the amphipod *Scypholanceola*. However, in other species the eyes might be very sophisticated. Since bioluminescent flashes are

the only and vital source of light, the bathypelagic species have to be able to detect it and localise it. Therefore, the visual system must meet requirements of high sensitivity, good spatial resolution and depth discrimination (Warrant & Locket, 2004). Some of them are achieved by the manners already mentioned in previous paragraph – e.g. the teleost fish *Bajacalifornia drakei* possesses large eyes with many rods multibanks in fovea (Locket, 1985). In general, bathypelagic organisms have large pupils but the eyes are small since large eyes would be energetically very expensive; moreover, they would detect flashes from insignificant distances (Warrant & Locket, 2004). Nevertheless, this is not the case for some crustaceans – for example the largest known isopod *Bathynomus giganteus* possesses big compound eyes consisting of approximately 3500 ommatidia (Chamberlain et al., 1986).

Some of the animals living at the boundary of two light zones have evolved special visual systems to obtain the maximum of both light sources – extended space light from brighter region above and the bioluminescent flashes from the darker area below. The most extreme example of adaptation to such environment are the aforementioned spookfish (*Dolichopteryx longipes*) and barreleye (*Rhynchohyalus natalensis*) possessing eyes divided into two parts, dorsally pointing tubular eye giving images of high resolution, and ventro-laterally oriented diverticulum for sensitive perception of bioluminescent flashes (Partridge et al., 2014; Wagner et al., 2009).

Importantly, not all the organisms live at the same sea depth for the whole life. Therefore the requirements for an appropriate optical system are even more complex in some cases (Richards, 2005). Most of the deep sea fish larvae grow in the shallow epipelagic region rich in nutrients, and only later in their development, they transform and sink or drift to the deeper zones of the sea. For example, the larvae of the telescopefish (*Gigantura indica*) live in the epipelagic zone, juveniles in the mesopelagic area and adults in the bathypelagic region (Richards, 2005). Moreover, many organisms regularly vertically migrate in the water column. For example, the patchwork lanternfish (*Notoscopelus resplendens*), spends the daylight hours in the mesopelagic depths of 100–300 m but it migrates up to the surface (the epipelagic zone) at night (Hulley, 2015; Warrant & Locket, 2004).

In contrast to the pelagic habitat, the benthic area (at the sea-floor) is just two-dimensional and generally rich in nutrients. The size of the eyes of benthic organisms depends on the illumination in the same manner as in the pelagic region; the eyes of benthic crustaceans tend to be large. The objects of visual interest, such as predators are located on the horizon – interface between water and bottom. Therefore, the eyes of some benthic fishes possess so-called “visual streaks” that are elongated strips of ganglion cells by virtue of better visual perception on the horizontal line (Warrant & Locket, 2004).

4. Biomimetics of the Mirror Eyes

Nature has always been inspirational for people. Chinese tried to make artificial silk more than 3000 years ago, Leonardo da Vinci designed flying machines based on his studies of flying birds, George de Mestral invented Velcro according to the burdock seeds hooked in his dog's fur (Bhushan, 2009; Vincent et al., 2006). Terms "bionics" or "biomimetics" refer to technological application of the concepts known from nature, both describing the same thing. The term bionics was used for the first time by Jack Steele in 1960 for the scientific field that uses knowledge about natural systems and copy or imitate them (Vincent, 2001). The term biomimetics (bios = life, mimesis = imitate) meaning transfer of designs, methods and processes from biology to technology was coined by Otto Schmitt in 1950s (Bar-Cohen, 2005; Vincent et al., 2006).

The biomimetics is an interdisciplinary field whose innovations are used in many various fields, such as engineering, electronics, nanotechnology, robotics, artificial intelligence, biosynthesis, bioengineering etc. (Bar-Cohen, 2005). There have been various successful achievements of biomimetics, like for example self-cleaning surfaces, antireflective surfaces, camouflage principles, designs of ships and aircrafts, building designs, microstructures and nanomaterials, biomaterials, artificial textiles, artificial tissues and organs, implants, self-healing materials, biosensors and many more (Bar-Cohen, 2006; Bhushan, 2009; Vincent et al., 2006).

The reflective superposition eyes of decapods described earlier served as an inspiration for innovation in the field of astrophysics – the lobster-eye X-ray telescopes. While the decapod eyes work in the visible spectrum, the technical applications of the lobster-eye telescope work in the field of X-ray imaging at energies from 0.1 to 10 keV. For the X-ray application, the "cones" have to be much longer than in the decapod eyes. Such mirror channels distributed over a spherical surface reflect rays at very small angles of incidence called grazing angles and bring them to focus (Angel, 1979). The image of a point source gained from this kind of device shows a single peak (created by rays reflected from both the horizontal and the vertical walls) accompanied with a cruciform structure (created by rays reflected either from the horizontal or from the vertical walls) and a background (Irving et al., 2003). An advantage of such arrangement compared to a concave spherical mirror is that the field of view may be made as large as needed by covering more of the sphere with the square channels. Therefore, the lobster-eye X-ray telescopes may be used as all-sky monitors. Another advantage is that it works at wide range of grazing angles, and thus it is effective even at low energies with a large collection area in comparison to other X-ray optics (Angel, 1979; Irving et al., 2003; Peele et al., 1996). Recently, numerous lobster-eye X-ray arrangements have also been designed, developed and tested in the Czech Republic. For instance, this lobster-eye optics is used in the first Czech technological nanosatellite VZLUSAT-1 that will be launched in 2016 (Pina et al., 2014; Pina et al., 2015).

5. Discussion

Extreme habitats with diverse selective pressures may trigger the emergence of various adaptations in organisms. For example, light conditions in the deep sea affect the arrangements of visual systems (Björn, 2015; Warrant & Locket, 2004). One of the most remarkable adaptations to the deep sea environment is utilization of mirrors as the main focusing devices, instead of lenses (Land, 2000). The mirror eyes are quite rare and can be found only within several species of molluscs, crustaceans and fishes as summarized within this thesis. Table 1 shows the most important cases of the mirror eyes supplemented by their optical parameters.

species	group	type of mirror eye	f-number	FOV
<i>Pecten maximus</i>	molluscs	single-chambered	0.6	90°-100°
<i>Cardium edule</i>	molluscs	cup	unknown	unknown
<i>Astacus leptodactylus</i>	crustaceans	compound	0.38	**33°
<i>Oplophorus spinosus</i>	crustaceans	compound	unknown	unknown
<i>Sapphirina angusta</i>	crustaceans	nauplius	unknown	unknown
<i>Notodromas monachus</i>	crustaceans	nauplius	unknown	*100° 150°
<i>Dolichopteryx longipes</i>	fishes	diverticulum	1.17	48°
<i>Rhynchohyalus natalensis</i>	fishes	diverticulum	unknown	40°

Table 1 Comparison of Mirror Eyes Described in the Thesis.

f-number, focal ratio; FOV, field of view of an eye or (**) a single facet of a compound eye, the information about FOV of the whole compound eye was not available. * Left number refers to a lateral eye and right number refers to a ventral eye. Establishing of this table was limited by the lack of available literature (Andersson & Nilsson, 1981; Land, 1965; Land, 1976; Partridge et al., 2014; Speiser & Johnsen, 2008; Vogt, 1980; Wagner et al., 2009).

The focal ratio, so-called *f*-number, is a ratio of the focal length of the eye to the diameter of the pupil aperture (f/A). It describes the light-gathering ability of the eye well. The lower the *f*-number is, the brighter the image is (Land, 1965; Warrant & Locket, 2004). The *f*-number of a typical vertebrate camera-type eye is approximately 1.25, such as in the tubular part of the eye of the fish *Dolichopteryx longipes* (Wagner et al., 2009). The lowest *f*-number among fishes is about 0.8, while the *f*-number of human eyes varies from 2.5 in the dim light to 8.5 in the bright light (Land, 1965; Colicchia et al., 2009). As seen in table 1, the mirror eyes exhibit generally very low *f*-numbers; therefore, they serve as powerful light-collectors. Interestingly, the *f*-number of the biological mirror of the spookfish (*Dolichopteryx longipes*) itself is only 0.69, however, the *f*-number of the whole eye system is higher (1.17) because of the off-axis geometry of the mirror (Wagner et al., 2009). Extremely low *f*-number can be obtained in some crustacean eyes, as shown in table 1. Probably the lowest *f*-number among known animals, only 0.25, is obtained in the parabolic reflecting eyes of the bathypelagic ostracod *Gigantocypris mülleri* (Land, 2000; Warrant & Locket, 2004). It is obvious that the mirror eyes serve as very good light-gathering devices, and, thus, they facilitate higher sensitivity to a dim light, which is crucial for the life in the deep sea.

The field of view (FOV) is the number of degrees of visual angle over which an image is formed on the retina and it reflects the visual needs of the organism that correspond with its habitat and ecological preferences (Speiser & Johnsen, 2008). Though a single eye of *Pecten maximus* can see about 90°-100°, all the eyes together cover the field of approximately 300° (Land, 1965). In the compound eyes of crustaceans, a single facet covers only a small part of the visual field; however, if the facets cover a part of a sphere, the field of view of the whole eye expands significantly. This is a reason why their biomimetic application, the lobster-eye X-ray telescopes, exhibit a large field of view and thus can be used as all-sky monitors (Irving et al., 2003). The current state of knowledge of other optical parameters, such as optical resolution, is very poor. In the available literature, the majority of them are not specified.

All mirror eyes possess reflective tissues made of layers of material with alternating high and low refractive indices (Land, 2000). The crystals of the multilayer biological mirrors are usually made of pteridines or purines (Zyznar & Nicol, 1971). However, the position of the mirror differs and thus the eye optics varies. The reflective tissue is located behind the retina in *Pecten*, *Sapphirina* and *Notodromas*, it forms a cup enclosing the photoreceptors in *Cardium*, it creates the cone sides in *Astacus* and *Oplophorus*, and it is located on the lateral part of a septum in *Dolichopteryx* and *Rhynchohyalus* (Andersson & Nilsson, 1981; Barber et al., 1967; Barber & Wright, 1969a; Elofsson, 1969; Land, 1976; Partridge et al., 2014; Vogt, 1977; Wagner et al., 2009). Moreover, the mirrors are developmentally derived from different tissues, for example the mirror of *Dolichopteryx* develops from a tapetum within the retinal pigment epithelium but the mirror of *Rhynchohyalus* is derived from the choroidal argentea (Partridge et al., 2014). To accommodate the mirror eye for closer objects, the mirror has to be moved away from the retina. Since the mirror is firmly attached to the eye structure in the most cases, the organisms possessing such eyes cannot focus at different distances. However, there is a muscle attached to the septum carrying the mirror of *Dolichopteryx* that could possibly move the mirror and thus allow the basic accommodation of the eye (Wagner et al., 2009).

Beside the mirror, some of these eyes also possess lenses, for example *Pecten*, *Sapphirina* and *Notodromas*. These lenses probably serve for prefocusing light and correcting aberrations (Andersson & Nilsson, 1981; Elofsson, 1969; Land, 1965). Pigment cells serving as a shield can be found in almost all described eyes, for example in *Pecten*, *Sapphirina* or *Notodromas* (Andersson & Nilsson, 1981; Barber et al., 1967; Elofsson, 1969). In decapod crustaceans, they play a special role in the light and dark adaptation (Meyer-Rochow, 1974).

Since the light conditions in the space are in some cases similar to those in the deep sea, the optical needs of deep sea organisms and astronomers might be similar. Therefore, some principles of the mirror eyes might be utilised as biomimetic application in astronomical optical technology, as demonstrated in case of the lobster-eye X-ray telescopes (Angel, 1979).

Conclusion

The mirror eye is an eye type unique for using reflection of biological mirrors rather than refraction of lenses or corneas for image forming. This eye type is quite rare in the animal kingdom and it can be found only in several species of molluscs, crustaceans and fishes living in the dim or deep water. The mirror eyes were described for the first time in 1960s. Since that time, several other types of mirror eyes have been reported in invertebrates. Furthermore, in the last decade, the mirror eyes have been described in two fish species, which is the only known case of such eye type found in vertebrates.

Multi-layer biological mirrors are greatly used by organisms for several purposes. They can be often found on the body surfaces to display or camouflage; furthermore, they are part of many animal eyes. However, not all eyes containing the reflective tissue are considered as mirror eyes. The reflective tissue is commonly present in iridescent corneas of some fishes, or it creates an internal reflective layer, so-called tapetum, in many animal species. Such tapetum reflects light that has already passed through retina to provide the photoreceptors with second opportunity to perceive the light signal. In this case, the mirror is not used for image forming but just for increasing the light detection.

In many cases, it has been hard for me to distinguish if the reflecting tissue is used for image forming or not. Many crustaceans, for example, possess reflecting tissues in their simple eyes. However, their eyes appear to be constructed to detect the presence of light, rather than create an exact image of the object. For example, the ostracod *Gigantocypris* possesses enormous light-gathering reflector eyes that are extremely sensitive but their resolving power is very poor. In this thesis, I call the mirror eyes only such eyes, which demonstrably create an image by reflection. Therefore, some organisms using reflection for light perceiving but not image formation in common sense are not described into detail or mentioned at all.

This thesis represents the most comprehensive review about the mirror eyes including comparison of invertebrate and vertebrate mirror eyes, which has never been compared before. The current knowledge about most of the mirror eye types remains largely incomplete and future research is necessary to fully understand this rare and fascinating structure employed in vision. Though several types of mirror eyes have been described, the majority of them were reported by examination of a single specimen due to the logistical difficulties in obtaining deep sea samples. The physical (optical) parameters were rarely measured in live organisms; most of them come from the ray tracing of the eye models instead. However, there are very few such results so far. Therefore, the information about the mirror eyes is very limited and in many cases even unavailable. For better understanding, more detailed anatomical examination is needed (e.g. of the ultrastructure of multilayer reflectors) as well as molecular and genetic analyses

together with advanced mathematical modelling of the ocular performance and investigating the image created in live specimens.

In future, there is an enormous potential of further studies, especially of biomimetic application of some principles of the mirror eyes, such as light and dark adaptation in the superposition eyes of crustaceans, detection of polarisation of light, or tilting of mirror plates in the recently described eyes of the spookfish (*Dolichopteryx longipes*). The biomimetic application of mirror eyes has also been a topic of my ongoing internship at the Czech Academy of Sciences during my bachelor studies, which contributed to the creation of this thesis. The main goals of my internship have been understanding the way the mirror eyes work and finding out whether the mirror eye optics could be used in advanced optical devices, for example in astronomy.

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