

Review

The exceptional diversity of visual adaptations in deep-sea teleost fishes

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ABSTRACT

The deep-sea is the largest and one of the dimmest habitats on earth. In this extreme environment, every photon counts and may make the difference between life and death for its inhabitants. Two sources of light are present in the deep-sea; downwelling light, that becomes dimmer and spectrally narrower with increasing depth until completely disappearing at around 1000 m, and bioluminescence, the light emitted by animals themselves. Despite these relatively dark and inhospitable conditions, many teleost fish have made the deep-sea their home, relying heavily on vision to survive. Their visual systems have had to adapt, sometimes in astonishing and bizarre ways. This review examines some aspects of the visual system of deep-sea teleosts and highlights the exceptional diversity in both optical and retinal specialisations. We also reveal how widespread several of these adaptations are across the deep-sea teleost phylogeny. Finally, the significance of some recent findings as well as the surprising diversity in visual adaptations is discussed.

1. Introduction

While the majority of teleost fishes inhabit well-lit shallow waters, some have found their way into the deep-sea, an extreme environment where low temperature, high pressure, and a lack of light make life seemingly difficult [1]. In this, the largest habitat on earth, most organisms possess eyes, or at least some form of photoreceptor, evidence to the fact that light still plays a role. Zonation in the ocean may be defined by the amount of daylight present, with the deep-sea starting at around 200 m where downwelling light becomes insufficient to allow photosynthesis [2]. From 200–1000 m, in the mesopelagic or twilight zone, residual daylight is present but is increasingly attenuated with depth. Below 1000 m, in the bathypelagic zone, light from the sun no longer penetrates and the only source of light is bioluminescence, the light emitted by the deep-sea inhabitants themselves [2]. Light in the ocean not only changes in intensity with depth but also in spectral composition. Whereas shallow waters are spectrally rich, with wavelengths ranging from 300 to 800 nm (i.e., ultraviolet to red), short- and long-wavelengths are rapidly attenuated through scatter and absorption at deeper depths until only blue-green wavelengths (~480 nm) prevail [2]. The majority of bioluminescent emissions in the deep are also found in the blue-green centre of the spectrum, although as detailed later, some depart from this range. The intensity, duration and frequency of bioluminescent emissions also varies from species to species [3]. Even though the deep-sea is one of the dimmest habitats on earth, many of its teleost inhabitants heavily rely on vision for prey, predator,

or mate detection, to communicate, camouflage, or for navigation, including to stay within a particular depth range [4,5]. In this dimming to dark world with intermittent and in general point-source illumination, visual systems show adaptations that in many cases are unique amongst vertebrates.

Variations in eye design are shaped by a combination of environmental, behavioural (i.e. ecology) and evolutionary (i.e. phylogeny) forces [6]. Diurnal shallow-water teleosts that inhabit bright and often colourful environments have evolved visual systems that prioritise acuity and colour vision with, aside from the crepuscular species, less concern for sensitivity [7]. In contrast, teleosts that use their visual systems in dim-light environments, either due to living in deeper or murky habitats, or due to being active at night, possess visual specialisations that enhance sensitivity, often at the cost of acuity [8].

Deep-sea fish vision is adapted to see two different types of visual scenes based on the difference in light source available; extended (downwelling light) and point-like (bioluminescence emissions). Depending on how deep they occur, some species will be subjected to a single type of light (i.e. bioluminescence in the bathypelagic zone) while others may experience both types (i.e. in the mesopelagic zone) [9]. Deep-sea visual specialisations are also subjected to species specific ecologies. For instance, several mesopelagic species perform diel vertical migrations in order to feed, escape predation and breed [10]. Consequently, their visual systems are often more general, allowing the visualisation of different types of light signals, compared to the ones found in species confined to a specific part of the deep-sea. Another

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notable characteristic of life in the deep ocean is that there is relatively little of it, compared to surface waters, meaning that meals and mating opportunities are few and far between [1]. The result is a slow, metabolically depressed existence for many deep-sea creatures but one with remarkable compensatory adaptations, both visual and otherwise, to ensure that when a meal or mate does come along, it is capitalised upon. Finally, while bioluminescence is used for many different purposes such as counterillumination, communication, attraction or repulsion [11] not all species rely on it in the same way or to the same degree. This results in eye designs that are tailored to a particular signal or a range of signals.

Here we review some of the diversity of visual adaptations known in deep-sea fishes, starting with the most common ones that are shared with other teleosts from different dim-light environments, and moving to more extreme adaptations, most of which are unique to the deep-sea environment. The occurrence of some of these specialisations is also aligned to the latest deep-sea teleost phylogeny to illustrate how widespread these adaptations are and suggest when they evolved. Lastly, we discuss the significance of some recent findings and propose a number of future avenues of research in the field.

2. Generalist visual adaptations to dim light conditions

a) Increased pupil aperture

One of the simplest ways to enhance the sensitivity of an eye at lower light intensities is to increase the pupil aperture allowing more light to enter the eye at any one time. This is achieved in two ways, 1) by increasing the overall size of the eye and 2) by increasing the size of the pupil itself with, for example, the help of an aphakic gap between the lens and the iris.

A bigger eye generally yields a larger lens and a larger pupil, all of these allowing more photons to reach the retina and therefore enhancing sensitivity at lower light intensities. As a result, many teleosts that rely heavily on vision and inhabit dim light environments, have evolved large eyes [12–14]. While a large eye seems to be a common trait in mesopelagic fishes to view the increasingly dim extended scene created by the downwelling light, the trend shifts to much smaller eyes with relatively larger pupils in bathypelagic species. In that case, having large eyes might be unnecessary given that at that depth, residual daylight no longer penetrates and only point-like bioluminescent flashes are present and would appear sufficiently bright against a completely dark background to be detected by smaller eyes [15]. Despite these general trends, eye size in deep-sea teleosts can vary greatly, even within the same family (e.g. lanternfishes [16]), with some species having much smaller eyes than others at similar depths [16] or even degenerated eyes [17] (Table S1), suggesting they rely more on other sensory systems.

Increased pupil aperture is also achieved with the presence of aphakic gaps, areas where the lens does not meet the margins of the pupil and light may strike the retina without travelling through the lens first. These gaps can be classified into two categories: 1) crescent-shaped, a gap located in a specific part of the pupil and present in shallow-water (diurnal and nocturnal) as well as deep-sea representatives, and 2) circumlental, a gap all around the pupil and only found in deep-sea teleosts [18,19] (Fig. 1D, E). In the deep-sea, most crescent-shaped aphakic gaps are rostral or ventral and are often associated with an area of high acuity in the temporal retina that receives increased illumination through the gap [1,20,21]. Depending on their size, circumlental aphakic gaps may either increase the sensitivity of the entire eye (large gaps) or increase the maximum size of the centrally illuminated retina to facilitate the detection of weak luminous signals in the lateral field of view (small gap) [19]. While these gaps enhance sensitivity by increasing the amount of light entering the eye, it comes with the loss of spatial resolution in those areas of the visual field where the light reaching the retina is not refracted by the lens [22]. However,

in an environment like the deep-sea where any gain in photons may dramatically increase your chance of survival, the benefit of having an aphakic gap seems to outweigh the potential loss in spatial resolution.

b) Tapetum lucidum

Once the light enters the eye, photon capture by the photoreceptors may be enhanced by the presence of a tapetum lucidum. The tapetum lucidum is a reflective layer positioned at the back of the retina, sclerad to the photoreceptors, that reflects any unabsorbed light back onto the photoreceptors, providing a second opportunity for photon absorption [23]. Although reflection may confer the disadvantage of an unfocused image and reduced resolution due to light scatter, this is of little concern compared to the gain in sensitivity, which may be equivalent to doubling the length of the photoreceptor outer segment [22]. Some deep-sea teleosts even circumnavigate this issue by having tapeta for individual photoreceptors [1,24]. Tapeta are common across many teleost families, particularly in fish that experience dimmer light environments, such as nocturnal shallow-water and deep-sea fishes as well as some freshwater fishes inhabiting turbid waters [25,26]. In deep-sea fishes tapeta are present in at least 19 families spanning several orders (Fig. 2, Table S1). Two types of tapetum lucidum are found based on their location: 1) retinal pigment epithelium (RPE) tapetum, found in most teleost fishes, and 2) choroidal tapetum, found in some shallow nocturnal teleosts (e.g. the bigeyes from the genus *Priacanthus*) as well as a few deep-sea teleosts (e.g. Myctophiformes) [20,23,26–28].

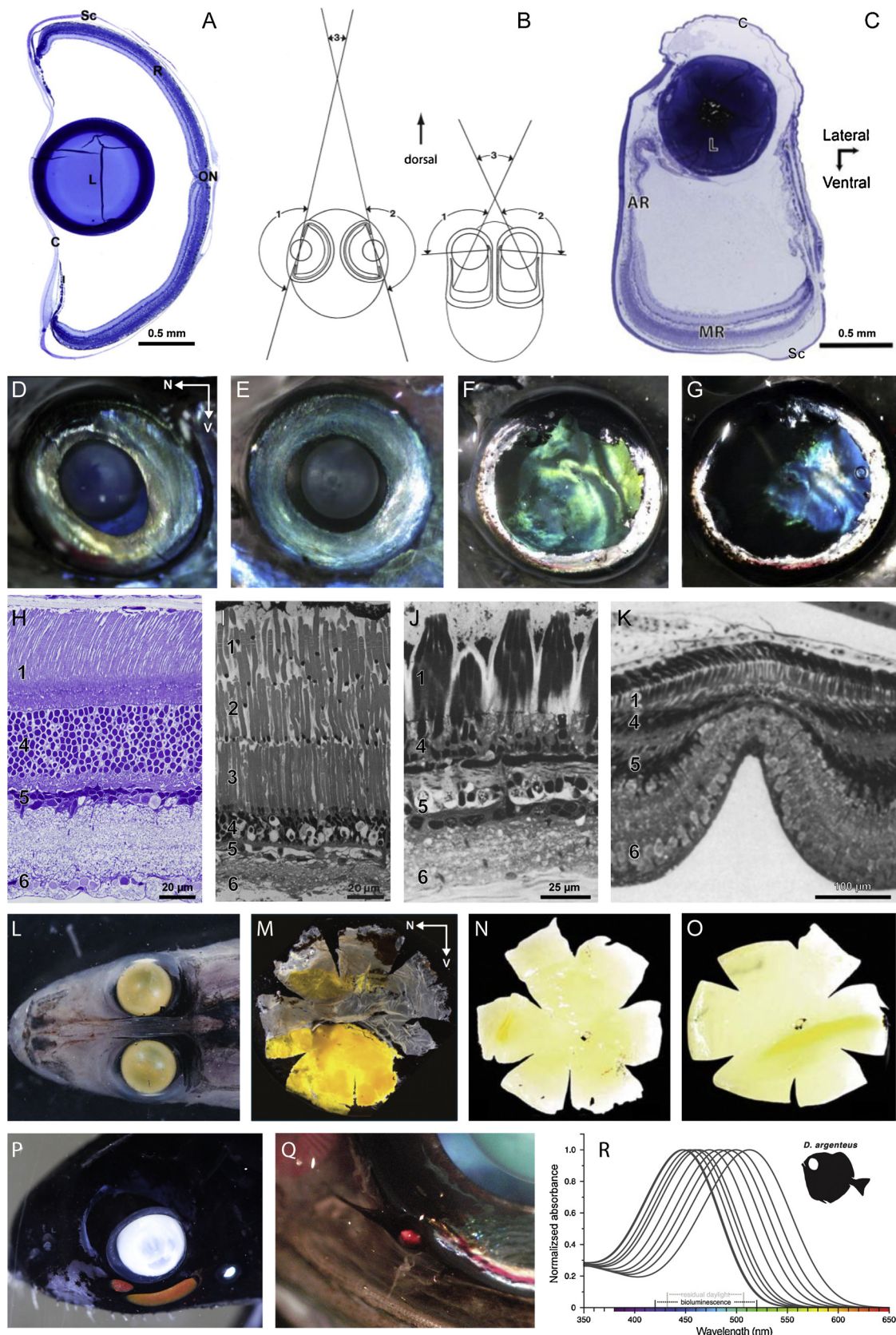
Depending on the type of tapetum lucidum, its reflective material, structure and arrangement, the spectra of the reflected light may vary and usually matches the corresponding light environment. As such, the tapeta of deep-sea teleosts normally reflect shorter blue-green wavelengths of light which predominate at greater depths, while the tapeta of shallower nocturnal species reflect across more of the spectrum, often appearing silvery or golden in colour [27,29]. Moreover, variations in tapeta distribution and spectral reflectance also exist. For example, in lanternfishes the tapetum may be localised in a specific area (e.g. *Bolinichthys longipes*) [20], can reflect light of different wavelengths in different parts of the retina to match the spectral distribution of the downwelling light (e.g. *Notoscopelus resplendens*) [30], or can even be sexually dimorphic (e.g. *Diaphus danae*, Fig. 1F, G) [20].

c) Photoreceptor adaptations

Several adaptations to increase visual sensitivity are found at the photoreceptor level. Since rods are the photoreceptors specialised for dim-light vision, nocturnal organisms, including teleosts, tend to have a rod-dominated retina [31]. In the absence of daylight in their environment, most deep-sea fishes have pushed this adaptation to its extreme by possessing a pure-rod retina (Fig. 1H–J). While cone photoreceptors are quite rare in the deep-sea, they are still found in 15 families from across the deep-sea teleost phylogeny (Fig. 2, Table S1). However, even in those species that possess cones, the retina is usually still rod-dominated and only one deep-sea species, the hammerjaw *Omosudis lowii*, has so far been described to possess a cone-dominated retina [32].

As well as adding more rods, photon absorption is optimised by increasing the length of the rod outer segment, the light-sensitive part of the photoreceptor. Consequently, many deep-sea fish rod outer segments are more than double in length compared to those found in their diurnal shallow-water counterparts [1,21].

Finally, photoreceptor sensitivity can be maximised by tuning the absorption spectrum of the visual pigment to the ambient light [33]. While the rod photoreceptors of most shallow-water fishes have a mean peak spectral sensitivity (λ_{max}) of ~500 nm, rods in deep-sea species have an absorbance centring around 480 nm λ_{max} [30,34,35], which matches both downwelling light and most bioluminescent emissions [2,3]. In a few extreme cases, spectral sensitivity has expanded or



(caption on next page)

Fig. 1. Examples of visual adaptations found in deep-sea teleosts. (A-C) The two main eye designs showing the shape and position of the eyes in the head: transverse section through the typical-shaped eye of *Ceratoscopelus warmingii*, placed laterally in the head (A), transverse section through the tube-shaped eye of *Opisthoproctus grimaldii*, placed dorsally in the head (C), schematic of both eye designs and their fields of view (B). Sc = sclera, R = retina, MR = main retina, AR = accessory retina, C = cornea, L = lens, ON = optic nerve, 1 and 2 = monocular field of view of each eye, 3 = binocular field of view. (D-E) The two main types of aphakic gaps in lanternfishes: crescent shaped (ventral) (D) and circumlental (E). (F-G) Example of tapetum lucidum variation in distribution and reflectance in *Diaphus danae* female (F) and male (G). (H-K) Examples of retinal adaptations: one bank of long and fine photoreceptors in *Diogenichthys laternatus* (H), multibank retina in *Notacanthus chemnitzii* (I), rod bundles in the main retina of *Scopelarchus guentheri* (J), fovea in *Scopelosaurus lepidus* (K). 1-3 = number of photoreceptor banks, 4 = outer nuclear layer, 5 = inner nuclear layer, 6 = ganglion cell layer. (L-O) Examples of short-wavelength-absorbing yellow filters: yellow lenses in *Scopelarchus analis* (L), yellow retinal pigmentation in *Diretmus argenteus* (M), *Myctophum nitidulum* male (N) and female (O). (P-Q) Red luminescent organs in species able to view far-red bioluminescence: in *Pachystomias microdon* (P) and the lanternfish *Bolinichthys distofax* (Q). (R) Spectral sensitivities of the 14 RH1 visual pigments expressed in the retina of *D. argenteus*. White arrows indicate the orientation of the eyes or retinal wholemounts, N = nasal, V = ventral. Images modified and reproduced with permission from the following sources: [20](A, D-H) [22]; (B) [101]; (C) [44]; (I) [1]; (J) [49]; (K) [30]; (L) [78]; (M, R) [73]; (N-O); Images courtesy of Wen-Sung Chung (P) and Fanny de Busserolles (Q).

diverged from the classical ~ 480 nm λ_{\max} and these cases will be discussed later.

d) Increased neural summation

Collecting light over a wide visual angle optimises photon capture at the cost of visual resolution. Since the limit to spatial vision in vertebrates is defined by the density of ganglion cells, increasing the number of photoreceptors that converges onto a single ganglion cell widens the receptive field for each visual channel, therefore increasing sensitivity [21,22]. In deep-sea fishes, neural summation (i.e. the photoreceptor to ganglion cell ratio) is increased compared to nocturnal shallow-water fishes, and even more so when compared to diurnal shallow-water fishes [8,36,37]. As a result, deep-sea fish retinas often have dense, well-developed photoreceptor and outer nuclear layers, but sparse inner and ganglion cell layers (Fig. 1H-K).

In mesopelagic fishes, depending on the light source being downwelling light (an extended source) or bioluminescence (a point-like source), high summation is achieved in two different ways: 1) by packing more and thinner photoreceptors or 2) by pooling several photoreceptors together. To be able to see point-like sources of light and efficiently distinguish them from the background space-light, thinner photoreceptors are advantageous in detecting the signal without being contaminated by the background space-light [38]. This is commonly seen in lanternfish species that rely heavily on bioluminescence and have rods as thin as 0.9 μm , resulting in the highest density of rods ever recorded in vertebrates (e.g. > 2 million rods/ mm^2 in *Symbolophorus evermanni*) [39]. Interestingly, the evolutionary thinning of rods is physically constrained to approximately the levels observed in the deep-sea; any thinner and light would mainly be forced outside the perimeter of the photoreceptor and may be lost [40]. On the other hand, to be able to see extended light sources, wider receptors are advantageous [38]. Some species have achieved this by grouping multiple rod and/or cone photoreceptors into cup-like bundles or “macroreceptors” that are each surrounded by reflective structures (i.e. essentially a mini-tapetum) and perform as a single functional unit [41] (Fig. 1J). For example, in the pearleye *Scopelarchus guentheri*, grouping photoreceptors into bundles of 23 widens the receptive field over seven times compared to a single rod, resulting in an increase in sensitivity to downwelling light of around 50 times [42,43]. Although the potential boost in sensitivity using grouped photoreceptors is quite substantial, these structures are rarely found in deep-sea fishes and occur in only seven families, six of which are within the order Aulopiformes (Fig. 2, Table S1).

e) Improved spatial resolution

While increased sensitivity is the main goal in deep-sea fishes, high visual resolution appears to be important too. Studies of the distribution of ganglion cells across the retina of deep-sea species revealed that, in common with their shallow-water counterparts, deep-sea fish retinas have regions with high cell densities that provide higher acuity in a

specific part of the visual field [44,45]. Two main types of topographic specialisations exist in teleosts: areas that have concentric increases in cell densities and streaks that are defined by an elongated increase in cell density across a retinal meridian. Contrary to shallow water species that possess either type of retinal specialisation [46,47], deep-sea teleosts only seem to possess areas [44,45]. These areas can be found in different parts of the retina and therefore, most likely serve different ecological purposes. Some species possess an area in the ventral or ventro-temporal part of the retina, often elongated (but not as much as a streak), providing higher acuity in the visual field above and in front of the fish where silhouettes may be detected against the lighter background of the downwelling light (e.g. several species of lanternfish and hatchetfish, the eel *Synaphobranchus kaupi*, the pearleye *Scopelarchus michaelsarsi*). Others have an area in the temporal part of the retina providing higher acuity directly in front of the fish to look for prey (e.g. several lanternfish species, the spiderfish *Bathypterois dubius*), as well as an area in the nasal area to look for predators (*B. dubius*). Finally, some have a large area in the central part of their retina providing higher acuity in a sizeable part of their monocular field of view, suggesting a more generalist approach (e.g. lanternfish from the genus *Lampanyctus*, the bigscale *Poromitra capito* and the arrowtail *Melanonus zugmayeri*).

Another specialisation providing higher visual acuity is a fovea. A fovea is a depression in the retinal tissue forming a pit that in teleosts is always associated with a higher density of both photoreceptors and ganglion cells [48] (Fig. 1K). The shape of the foveal pit follows two main designs: deep (convexiculate) foveae and shallow (concaviculate) foveae. Both designs have been observed in teleost fishes. In deep-sea fishes, shallow foveae have been reported in species from the Bathylagidae family while deep foveae have been observed in the families Notosudidae, Platytrichtidae, and particularly in the family Alepocephalidae (Table S1) [48]. The composition of foveae in deep-sea teleosts is somewhat variable with some composed entirely of cones (e.g. blackfin wryfish *Scopelosaurus lepidus*) [49] and others purely of rods (e.g. legless searid *Platytrichtes apus*) [50]. Most deep-sea fish foveae are found in the periphery of the temporal retina which perceives the visual field in front of the fish mediating binocular vision [51]. In addition to increasing resolution, foveae in deep-sea teleosts may also enhance depth perception as well as providing a method to detect point-like bioluminescent flashes and break bioluminescent camouflage [22,52].

f) Trade-off between visual sensitivity and temporal resolution

Contrarily to most shallow water teleosts and with the exception of polar species, many deep-sea fishes face a compromise between visual sensitivity and temporal resolution (i.e. the speed of vision) due in part to the extremely low water temperature of the deep-sea ($\sim 4^\circ\text{C}$) [1]. In fact, while low temperatures may improve absolute light sensitivity by reducing the chance of spontaneous activation of the rhodopsin molecules at very low light intensities, also referred to as “dark” noise [53,54], they may also reduce retinal response and therefore the speed

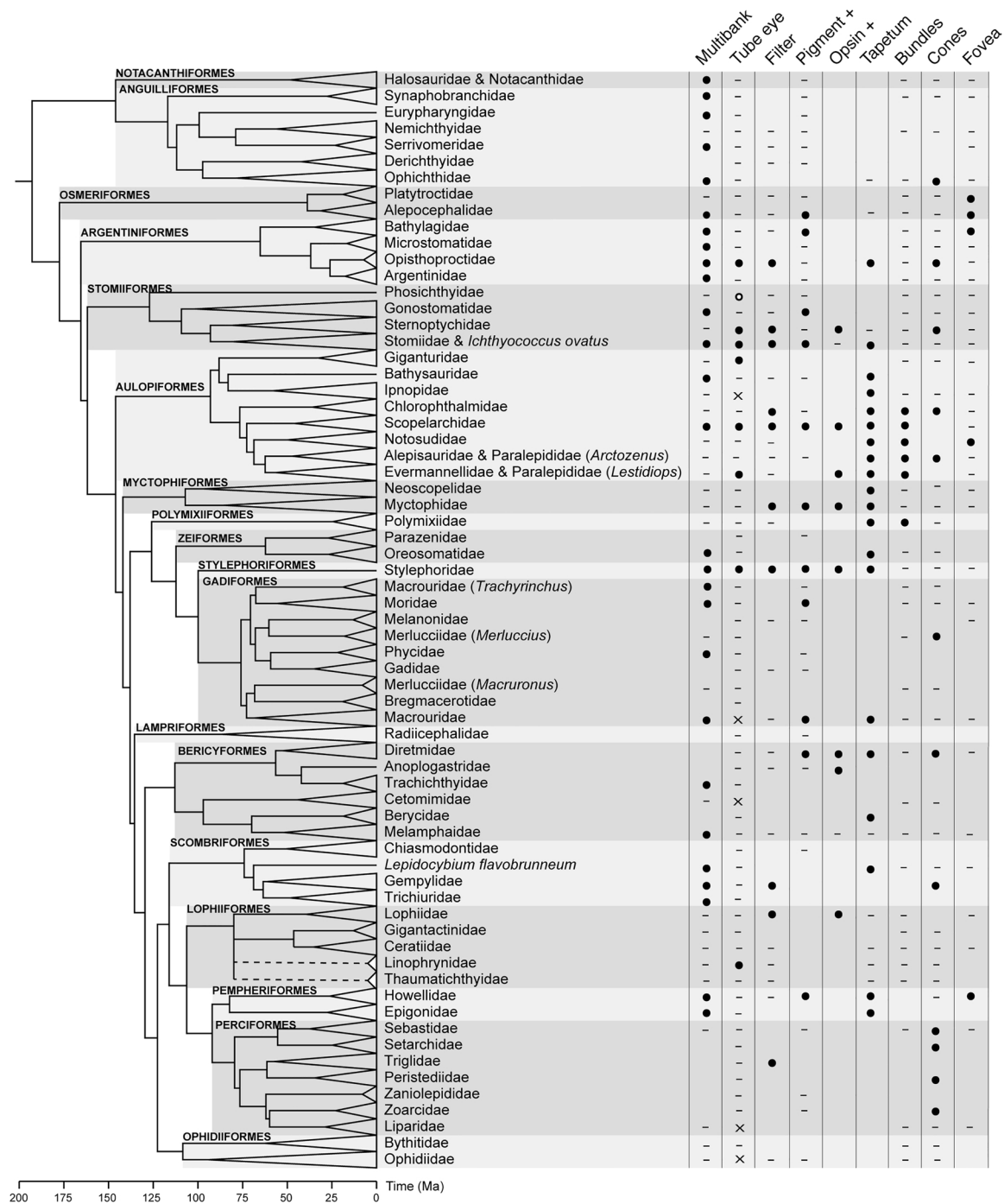


Fig. 2. Deep-sea teleost phylogeny showing the occurrence of various visual adaptations at the family level. Depicted are multibank retina, tubular eyes, short-wavelength filters, multiple visual pigments (pigment +), multiple opsins (opsin +), tapetum lucidum, rod bundles, cone photoreceptors, fovea. The phylogeny is based on The Fish Tree of Life accessed on the 25/01/2020 [114]. Different orders are shaded in grey. A plain black circle indicates that the specialisation is present and a dash that the specialisation was absent in at least one representative of the family. Empty cells indicate that the specialisation has not been studied for that family yet. An unfilled circle indicates slightly tubular and a cross degenerated eyes, respectively. For details within each families and associated references, refer to Table S1.

of vision [55–57]. As a result, most deep-sea fishes probably have a low temporal resolution, a disadvantage for detecting fast moving prey and/or predators. Even those species migrating toward the surface at night are likely to have slow vision, although slightly improved by warmer temperatures, because of the limited amount of light present [57]. The swordfish *Xiphias gladius*, has evolved a unique strategy to counteract this issue. This powerful visual predator maintains high visual acuity by warming its eyes and brain several degrees above ambient temperatures. Consequently, swordfishes are able to improve their temporal

resolution up to ten times compared to other fishes at similar depths, which enables them to catch fast-moving prey [56]. However, this strategy may only be beneficial to certain depths, after which light intensities become so low that a reduction in dark noise as a result of low temperatures would be more advantageous than maintaining high temporal resolution [38,56].

It is worth mentioning that the extreme pressure experienced by deep-sea fishes may also impact their visual capabilities (e.g. [58]). However, further studies are needed to understand the impact of these

extreme conditions on the visual ecology of deep-sea fishes.

3. Extreme deep-sea visual adaptations

a) Tubular eyes

Most teleosts possess more or less spherical eyes placed laterally (on the side of the head), however, at least 20 deep-sea fish genera from eight families belonging mainly to the Argentiniformes and Aulopiformes have evolved tubular eyes (Fig. 2, Table S1). Tubular eyes are asymmetrical and roughly cylindrical in shape and allow maximisation of the pupil diameter while maintaining focal length in order to enhance sensitivity and resolution [59]. This atypical eye shape may therefore be an evolutionary solution to the anatomical and metabolic limitations of increasing eye size while still improving sensitivity [60]. At the bottom of the tubular eye lies the main retina, which is well developed and receives focused light. On the side, against the medial wall, lies an accessory retina that is less developed and does not receive focused light due to its proximity to the lens but may be sufficient for movement detection [1] (Fig. 1C).

Tubular eyes are normally directed upward to view a large, dorsal binocular field encompassing downwelling daylight against which other organisms may form a silhouette [61] or try to camouflage themselves using counterillumination. However, due to the immobility of most tubular eyes, the fish's visual field becomes severely limited, making it vulnerable to predation and at a disadvantage for viewing bioluminescent signals in other parts of the visual field. To remedy this problem and extend their field of view laterally and ventrally, some species have evolved additional specialisations. These include retinal diverticula, lens pads, optical folds and eye rotation. Retinal diverticula are protrusions originating from the eye's lateral wall, located opposite of the accessory retina in most cases, that are lined with retinal tissue. They have several degrees of complexity, ranging from a simple retina receiving unfocused light (*Opisthoproctus*, *Gigantura*, *Winteria*, and *Macropinna* [62]) to more complex "secondary eyes" able to view focused light using reflective optics (*Dolichopteryx* [63] and *Rhynchohyalus* [61]). It should be noted that small retinal diverticula have also been reported on the same side as the accessory retina, near the optic nerve in *Scopelarchus* [42,62] and *Benthallbella* [62], potentially receiving light from the head, mouth or underneath the animal instead of through the eye [42]. Lens pads (found in *Scopelarchus* and *Benthallbella* [62,64]) and optical folds (found in *Evermanella* and *Coccorella* [1,65]), although from different origin, are similar in structure and function. They are lamellate structures adjacent to the eye that direct light from the ventrolateral field of view onto the dorsal accessory retina. Extension of the field of view of tubular-eyed species is also achieved by rotation of the eyes in the head. So far this adaptation has been observed in two species of Opisthoproctidae, *Macropinna microstoma* [66] and in *Winteria telescopa* (unpublished, personal observation), most likely allowing the animal to detect prey against downwelling light when eyes are in the dorsal position and to see the targeted prey in front of the mouth when eyes are in the rostral position. It should be noted that the position of the tubular eyes of another species, *Stylephorus chordatus*, also changes, but in that case, change in direction is either associated with body position – *S. chordatus* and other elongated deep-sea fishes often swim vertically in the water column, not horizontally – or the opening and closing of the mouth as a side effect of its extreme modification [1,67]. This latter mechanical requirement does not provide any visual advantage, while vertical positioning in the water column might allow both visualisation of prey against downwelling light and minimise the body silhouette of a long slender fish.

b) Red vision

Most deep-sea fishes emit and see bioluminescent signals in the blue-green range of the visible spectrum (450–500 nm). However, a

few species have evolved the ability to emit and see far-red bioluminescence (> 700 nm). So far, three genera of dragonfish (family Stomiidae) have been found to do so: *Aristostomias*, *Pachystomias* and *Malacosteus*. In all three genera, in addition to producing blue bioluminescence through their body photophores and postorbital organ, far-red bioluminescence is emitted by their suborbital (*Aristostomias* and *Malacosteus*) and preorbital (*Pachystomias*) organs [68,69] (Fig. 1P). These dragonfishes have become somewhat sensitive to their own far-red bioluminescence by possessing multiple visual pigments tuned to longer wavelengths. *Aristostomias* and *Pachystomias* both possess at least three long-wavelength-shifted visual pigments (~ 515, 550 and 590 nm λ_{max}) [70,71] supposedly based on two rod opsin proteins (one of which is longwave-shifted) bonded to an A1 or A2 chromophore, although the presence of two rod opsin genes remains to be confirmed at the molecular level. *Malacosteus*, on the other hand achieves far-red vision using a different method. While species possesses two long-wavelength-shifted visual pigments (~ 520 and 540 nm) based on a single opsin gene [72] associated with an A1 and A2 chromophore, far-red sensitivity (~ 670 nm) is achieved via the addition of a long-wavelength-absorbing, chlorophyll-derived, photosensitising pigment in its outer segment [72]. Although the visual sensitivity to far-red bioluminescence in the three genera does not perfectly match the wavelength of their own far-red bioluminescence (~ 590–670 nm vs 700 nm), it appears to be a good enough compromise to illuminate and see potential prey and/or communicate without being detected by others [72].

A few species of lanternfish (family Myctophidae) may also be able to perceive red bioluminescence by having an additional visual pigment that is tuned to longer wavelengths (~ 520–530 nm in *Myctophum* species [35,73] and ~ 550 nm in *Bolinichthys longipes* [74]) and may be combined with a chlorophyll-derived photosensitiser similar to *Malacosteus* (~ 670 nm in *Bolinichthys longipes* [74]). Since lanternfishes were not known to emit any red bioluminescence, it was suggested that their long-wavelength-sensitivity had evolved in response to the red-emitting light of their stomiid predators [74]. While this might still be the case, we report here, for the first time, an orbital red photophore in a specimen of *Bolinichthys distofax*, captured in the Indian Ocean in 2017 on board of the RV Sonne. The red photophore is situated in the ventral part of the eye, also called a Vn photophore (Fig. 1Q, Figure S1). The emission spectra, spectral reflectance and histology of this red photophore still needs to be investigated in detail to confirm that it is indeed emitting red bioluminescence. Nevertheless, the discovery of this red photophore in *B. distofax* suggests that lanternfishes also use red bioluminescence for communication and/or species recognition. On the other hand, the extremely small size of this photophore makes illumination of potential prey unlikely.

c) Short-wavelength-absorbing filters

The light entering the eye may be modified by different ocular filters before reaching the visual pigment inside the photoreceptors. These ocular filters are very common amongst both vertebrates and invertebrates, especially in species inhabiting high light intensity environments [75,76]. Such filters often function to remove shorter wavelengths of light before they reach the photoreceptors and most obviously appear very light to dark yellow. In shallow water teleosts these filters are mainly found in the cornea, lens and very occasionally the retina, most-likely protecting the eye from damaging short-wavelength radiation such as ultraviolet (UV) radiation, while increasing image quality [76]. Given the apparent necessity to maximise photon capture in the low-light deep-sea, it is perhaps surprising, to find that yellow filters are also found in some deep-sea teleost lenses [30,77], and retinas [73,78]. In the deep sea, cutting out shorter wavelengths might be useful to increase the hue discrimination between bioluminescent signals as well as to break the camouflage of species that use ventral blue bioluminescence as counterillumination in order to hide

silhouetting against the remaining downwelling blue light [79]. While downwelling light and most bioluminescent emissions have similar peak spectra around 480 nm, bioluminescent signals tend to extend into longer wavelengths. By cutting out shorter wavelengths, yellow filters therefore decrease the background illumination, potentially accentuating bioluminescent signals.

So far, 21 species of deep-sea teleosts from ten families spanning the phylogeny have been identified to possess short-wavelength-absorbing pigments in their lenses (Fig. 2, Table S1). Out of these 21 species, five have been described to have notably visible yellow lenses. Retinal yellow filters have only been observed so far in few species of lanternfishes from the sub-family Myctophinae [73] and in the silver spinyfin *Diretmus argenteus* [78,80]. While yellow filters in lenses and retinas most likely have the same purpose, lanternfishes and *D. argenteus* have taken the specialisation a step further by restricting the yellow pigmentation to specific parts of the retina as opposed to the whole lens (Fig. 1L–O). In these species, instead of cutting out shorter wavelengths for the entire eye, segregated/localised yellow filters enhance bioluminescence signals only for specific parts of their visual field. Interestingly, these segregated retinal yellow filters have also been found to be species-specific and sexually dimorphic in few species of lanternfish in the sub-family Myctophinae. Since these species are also sexually dimorphic in their luminous organs, the yellow pigmentation in the lanternfish retina could therefore be used in sexual communication [73].

d) Rod opsin (*RH1*) duplication

Five different visual opsin classes (four cone opsins and one rod opsin), those most likely to have been present in a common vertebrate ancestor, can be found in extant vertebrates [34]. In teleosts in particular, cone opsin diversification seems to be common with gene duplications and losses occurring many times over across the fish phylogeny [78,81]. The evolutionary history of rod opsins (*RH1*), on the other hand, is far less complex with most teleosts having a single, or at most two, *RH1* copies within their genomes [78]. Since green wavelengths dominate dim-light environments, having multiple copies of *RH1* seems evolutionary obsolete. An exception to this can be found in the deep sea, where *RH1* genes proliferated independently in at least three different deep-sea fish lineages: the tube-eyes (Stylephoriformes; six *RH1*s), the lanternfishes (Myctophiformes; five *RH1*s), and the spinyfins (Beryciformes/Trachichthyiformes; 18–38 *RH1*s) [78]. In the most extreme case, *D. argenteus* has 38 *RH1* copies in its genome, which together with two cone opsins, makes it the vertebrate with the highest number of visual opsins known to date.

Whenever rod opsins expanded in the deep-sea, they experienced strong positive selection with amino acid changes occurring in almost all of the *RH1* spectral tuning sites known from across vertebrates. Consequently, the spectral sensitivities of these visual pigments are predicted to have shifted away from the classical 480 nm λ_{\max} most likely covering a broader range of light (e.g. 444–519 nm λ_{\max} in *D. argenteus*) that spans both the residual daylight and the bioluminescent wavelengths emitted by deep-sea organisms [78]. While this may be a remarkable example of convergent evolution, the reasons as to why these fishes expended their *RH1* repertoires remain elusive. In their recent paper, Musilova et al. [78] propose five non-mutually exclusive explanations that either provide some kind of colour discrimination or increased sensitivity: 1) allow “classic” colour vision; 2) provide unconventional colour vision where different spectral sensitivities are hardwired to a specific behaviour; 3) increase the sensitivity of the entire retina; 4) increase the sensitivity across the light spectrum; 5) optimise sensitivity and/or contrast in specific parts of the visual field or at different stages of development.

e) Multibank retinas

A multibank retina differs from the duplex retina (with one layer of rods and one layer of cones) in that it has multiple banks of rods stacked into layers. This peculiar retinal organisation seems to be restricted to teleost fishes with the only exception being the nocturnal oilbird *Steatornis caripensis* [82]. In teleost fishes, it occurs mainly in deep-sea fishes, although it has also been reported in few shallow and freshwater species: some elopomorph species [83–86], the torrent fish *Cheimarrichthys fosteri* [87], the bastard halibut *Paralichthys olivaceus* [88] and in holocentrids (squirrelfish and soldierfish, [89]). In deep-sea teleosts, it has been reported in over 70 species from 28 families and covers most orders with deep-sea representatives (Fig. 2, Table S1), making this one of the most common deep-sea fish specialisations.

Most species possess a multibank retina that is well-ordered with uniform rod outer segment lengths in each bank [90] and between two and six banks in total (Fig. 1, Table S1). However, a few species diverge from this classical organisation with some species having ‘in depth’ or staggered rods as opposed to clearly defined banks and others having a varying number of banks in different regions of the retina (Table S1). An extreme example of this variability exists in the bigeye smooth-head *Bajacalifornia megalops*, which possesses 28 banks of rods in its fovea, summing to a prodigious 750 μm thickness, but only has 2–3 banks elsewhere [91]. In several species, the number of banks also varies during ontogeny with banks added as the fish increases in size, either continuously or until the maximal number of banks is reached [92,93]. Despite having been first described over 60 years ago, the function, structural variation and ontogenetic development of teleost multibank retinas remain largely unknown and unresolved. Possible functions will be discussed later.

f) Photoreceptor transmutation

A common paradigm in vertebrate vision is the duplex retina with photoreceptors either classified as rods or cones. In some cases, however, rods and cones are not as distinct as previously thought and intermediate forms of photoreceptors sharing characteristics of both cell types at a morphological, electrophysiological and/or molecular level have been identified. These intermediate forms, also called transmuted photoreceptors, were first discovered in squamate reptiles [94] and were subsequently observed in lampreys [95], skates [96] and amphibians [97]. Recently, photoreceptor transmutation was reported for the first time in a teleost fish, the deep-sea pearlside [98].

In pearlshades, *Maurollicus* spp. (Stomiiformes, Sternoptychidae), photoreceptors are all rod-like morphologically. However, only 1% of these photoreceptors are in fact true rods with 99 % of photoreceptors being transmuted cones or rod-like cones; an intermediate variant with a rod morphology but expressing a cone opsin (*RH2*) and cone phototransduction cascade. The function of this peculiar visual system is most likely to increase the sensitivity of the pearlside to the mesopic light conditions of its preferred environment. Compared to other deep-sea fishes, pearlshades behave atypically in that they are mainly active at dusk and dawn at the ocean’s surface, where the ambient light is blue-wavelength shifted (~ 450 nm) and much more intense than that usually found in the deep-sea (i.e. downwelling light in the mesopelagic zone ~ 480 nm). At these mesopic light intensities (0.2 cd m^{-2} to 127 cd m^{-2}) both rods and cones are usually functional, albeit not at their optimum. By possessing a single transmuted photoreceptor combining the properties of both photoreceptor types, pearlshades may have found a metabolically and optically effective way to optimise visual performance; the rod morphology most likely allowing for a greater photon catch, while the cone pigment and phototransduction cascade may be more appropriately suited for the light intensities and wavelengths found during twilight conditions [98].

4. Challenges and future directions

a) Can deep-sea fishes see in colour?

Most teleosts use between two and four differently tuned cone photoreceptors during photopic conditions while during scotopic conditions, the majority of teleosts rely on a single rod photoreceptor for vision [33]. Consequently, most diurnal teleosts are likely to see in colour, while nocturnal fishes are generally thought to be colour blind. An exception to this rule might be found in the deep-sea where both the presence of multibank retinas and differently tuned rod photoreceptors have been speculated to enable colour vision in some species [78,90].

Two cases in particular are strong candidates for colour vision in the deep-sea. The first one is found in lanternfishes where several species have been shown to have rod photoreceptors with different spectral sensitivities, multiple rod opsin genes, and to exhibit sexual dimorphism in their bioluminescent organs and visual systems [73,78]. The second case is found in *D. argenteus*, which as an adult, expresses 14 out of the 38 *RH1* genes found in its genome, theoretically conferring a wide range of spectral sensitivities [78] (Fig. 1R). The internal arrangement of the photoreceptor array is also complex, consisting of a multibank retina with different numbers of banks between different areas of the retina. The banks themselves differ in thickness due to variation in outer segment length including an astonishing 525 μm for the ultra-long rods in the ventral area, the longest known for any vertebrate species [99]. Cones are also present in the ventral part of the retina and expresses both the blue and green-cone opsins, *SWS2* and *RH2*, respectively [78,100]. Together with the yellow pigment also isolated to the ventral photoreceptors, this may extend even further the range of spectral sensitivities found in *D. argenteus*. While a colour vision system seems to make sense in species relying heavily on bioluminescence signals for a range of different tasks like lanternfishes [37], it is quite surprising in a non-bioluminescent species like the spinyfin. However, and as pointed out previously, other reasons besides colour vision might exist for expressing so many rod opsins [90].

A number of steps can be taken to try and determine whether deep-sea fishes can see colour and how common this might be. First, a thorough survey of *RH1* expansions at the genomic and transcriptomic level across all deep-sea fish lineages is needed. Although relatively rare, out of the nearly 200 deep-sea species studied to date, 26 have been described to possess at least two photoreceptors with different spectral sensitivities (Table S1). Out of these, only five species have been studied at the molecular level so far and found to express two or more rod opsin genes (Table S1) leaving a number of top candidates still to survey. Other steps to be taken include the mapping of gene and/or protein expression at the retinal level; the modelling of colour vision taking known physiological and environmental (light) parameters into consideration; and, electrophysiological responses of the eye, the photoreceptors, and higher-order neurons to different wavelengths of light. Ultimately, however, the only way to prove colour vision exists in the deep-sea is by using behavioural experiments, something that remains expensive and difficult.

b) Transmutation: occurrence, function and origin

The discovery of photoreceptor transmutation in a deep-sea teleost fish has opened several avenues for future research and raises multiple questions regarding its occurrence, function and evolution in teleost fishes. Firstly, the discovery of rod-like cones in a previously described pure rod retina calls into question our ability to properly discriminate photoreceptor types. Most studies on vertebrate vision and nearly all studies looking at deep-sea fishes have generally relied on the use of morphology alone to identify photoreceptor types. In the case of the pearlsides, it is obvious that morphological observations alone were insufficient to distinguish the two visual cell types. Photoreceptor transmutation may therefore be more common than originally thought and more thorough and complete studies combining molecular and morphological analyses are needed to identify its occurrence. Several deep-sea fish species are of particular interest including those that have been identified with several visual pigments based on physiological

measurements of photoreceptor sensitivities (26 species from 11 families and 9 orders, Table S1) and/or species with several morphologically distinct photoreceptor types. For the latter, sabertooth (*Evermannella* spp.), hatchetfish (*Argyrolepechus* spp.), and the hammerjaw (*Omosudis lowii*), are all ideal candidates for photoreceptor transmutation. In *Evermannella balbo*, two rod-like photoreceptor types have been identified based on differences in morphology [65], but this species expresses a single *RH1* and a *RH2* cone opsin within its retina (unpublished data). In *Argyrolepechus affinis* and *A. sladani*, three photoreceptor types have been identified: two rod-like and one cone-like [101] even though a single visual pigment has been found [102,103]. In *O. lowii*, an almost pure-cone retina has been described, an oddity in the deep-sea. The question remains whether these photoreceptors are really cones or whether they are in fact transmuted rod photoreceptors.

Secondly, the likelihood of additional cases of photoreceptor transmutation in deep-sea teleosts raises the question of their functionality. Unlike in pearlsides, all other deep-sea fishes in which transmutation is likely are mesopelagic/bathypelagic species where rod photoreceptors are the most suited cell types for vision, making the use of transmuted photoreceptors to optimise visual sensitivity unlikely. In other vertebrates, photoreceptor transmutation is a mean to regain vision under certain light conditions after an evolutionary loss of the original photoreceptor type. For example, extant nocturnal geckos have transmuted rod-like cones which they use to see in dim-light. However, an evolutionary compensation/regain is unlikely in deep-sea fishes as all species appear to possess both photoreceptor types at some stage during their development [104,105]. In view of the discovery of *RH1* duplications and the associated potential for colour vision, transmutation in deep-sea fishes may therefore provide an additional way to see colours. Considering that opsin gene duplication and functional diversification is a rather slow and at least partially stochastic process [106], some species of deep-sea fish may instead have co-adapted their pre-existing cone cells to form rod-like photoreceptors potentially allowing colour discrimination in dim-light conditions.

Finally, transmutation in pearlsides and novel data on opsin gene expression during ontogeny in deep-sea fishes raise some additional questions about the evolution and development of transmuted photoreceptors as well as the deep-sea fish retina in general. Since the pearlside study was done on adult fish only, it remains unclear how a cone opsin evolved to be expressed in a rod-like cell. Two evolutionary scenarios are possible, one where the morphology of the cell changes and another where it is the visual pigment machinery that is replaced. While de Busserolles et al. [88] present some arguments for the former scenario, only a detailed ontogenetic study of the pearlside retina will elucidate this question. Unfortunately, very little data is available on the development of the teleost retina and even less so on deep-sea fish larvae. From what is understood, vertebrates (including teleosts) seem to start their lives with a cone-dominated retina with rods added later during development [107]. However, whether this is also true for deep-sea fishes with pure rod retinas as adults remains to be fully investigated. A study by Bozzano et al. [104] indicates that lanternfish larvae start with a rod-dominated retina, with cones completely disappearing in older larval stages, although their study only included morphological data. However, a recent study investigating the opsin repertoire of few deep-sea species at the larval and adult stage showed that several species may indeed start with a pure cone retina, at least at the molecular level [105]. In some cases, a complete or near-complete switch in opsin expression going from pure *RH2* in larvae to pure *RH1* in adults was found, suggesting a transition from a pure cone retina to a pure rod retina during ontogeny. This begs the question whether the cone cells in those species are eliminated and replaced by rods or whether they are transmuted during development. Future investigations of the visual system of deep-sea fish larvae that focus both on the molecular and morphological levels are needed to answer these questions.

c) The enigma of the multibank retina

Although multibank retinas are very common in deep-sea fishes their function remains a mystery. There seem to be a number of hypotheses that have stood the test of time: [1] multibank retinas enhance sensitivity [2], they allow for colour vision in dim light and [3] they serve the renewal or regeneration of rods. The sensitivity hypothesis was put forward on the assumption that several layers of rods stacked on top of one another would increase the path length for photon absorption, similar to an increase in rod outer segment length [22], while also increasing rod density and therefore summation [43,44]. The colour vision hypothesis was proposed by Denton & Locket [90] who suggested that the different banks could act as spectral filters, changing the light chromatically as it passes through the different rod layers and therefore providing each bank with a different spectral sensitivity. This would allow species with a single visual pigment to make some sort of rod-based colour discrimination while enhancing hue discrimination in species with two visual pigments. While the theory at the photoreceptor level is sound, it also requires that the neural circuits underlying the photoreceptors are able to compare inputs from the various visual channels (i.e. the different banks) in order for colour vision to be possible. This is yet to be investigated.

Interestingly, the first two hypotheses were challenged by an ERG study conducted in conger eels which suggested that only the most vitread bank of rods is functionally active [108]. This led to the theory that the additional banks may form a reserve that can replace photoreceptors upon bleaching of the most vitread rods. However, this theory has its own caveats: 1) the bleaching rates of rhodopsin in deep-sea teleosts exposed to bioluminescence are negligible, largely negating the need for extensive regeneration [2], 2) rod outer segment renewal occurs in all banks suggesting that all rods are metabolically functional [109], 3) in several species banks may be added at the vitread side during growth, shifting the older and supposedly less functional layers toward the back of the eye [1], 4) if not all banks are active then the length of the theoretical light path would be greatly reduced therefore reducing sensitivity.

While further investigations about the function of the multibank retina in deep-sea fishes is made difficult due to the challenge in accessing and working with such species, it is surprising that more attention has not been given to this specialisation in shallower representatives. The recent discovery of a multibank retina in an entire family of nocturnal coral reef fishes, the Holocentridae (squirrelfish and soldierfish) [89] may hold the key to unravelling the function of this adaptation. Holocentrids offer an ideal model to study the function of multibank retinas in deep-sea fishes for the following reasons: 1) they have a well-developed multibank retina ranging from 6 to 17 banks, 2) their ancestors inhabited intermediate depths [110] and some modern species live as deep as 600 m [111], 3) their visual systems share several other adaptations with deep-sea fishes [89,110], and 4) they are easily accessible and can be kept in aquaria, therefore allowing the use of physiological and behavioural methods that are near impossible in deep-sea fishes.

d) Visual sexual dimorphism.

Sexual dimorphism in the visual system of a non-primate vertebrate was described for the first time in lanternfishes [20,73]. In two species of the genus *Myctophum*, the dimorphism is found at the retinal level in the form of a yellow pigmentation (described previously), and in one species of *Diaphus* the dimorphism appears in the location and reflectance of the tapetum lucidum. In all cases, both males and females possess the adaptation but in different areas of the retina and both types of specialisation are able to modify the spectrum and/or amount of light received by the photoreceptors in this specific area. Since these three visually dimorphic species are also sexually dimorphic in their luminous organs, a function in sexual communication is very likely. Given

that many other deep-sea species are also sexually dimorphic in luminous organs [112] this raises the question of how common visual sexual dimorphism is within deep-sea teleosts. Future studies should therefore put more emphasis on these sexually dimorphic bioluminescent species by looking for differences in the visual system between male and females at any level, morphological, physiological, molecular and if possible, behavioural.

e) Evolution of deep-sea visual systems

Even though the deep-sea represents a relatively simple visual environment, especially in the pelagic realm where no physical structures are present, an extraordinary wealth of visual adaptations have emerged. Within this array of specialisations, many have the same purpose but achieve it in different manners and at varying levels. Great examples of this are the multitude of ways to maximise photon capture (e.g. large eyes, aphakic gaps, tapetum lucidum, increased rod length, multibank retina, bundled photoreceptors) or to tune the visual system to specific wavelengths or signals (e.g. yellow filters, photosensitising pigment, visual pigment tuning, *RH1* duplication, multibank retina). This surprising diversity or “visual arms-race” is likely the result of strong selection for the most efficient visual system in order to survive in this extreme environment [37], although this remains to be investigated in a phylogenetic comparative manner.

While phylogenetic inertia, ecology and the light environment are all likely contributing to the evolution of deep-sea fish visual systems [37], the specific forces that drove the occurrence of one adaptation over another are not well understood. Some headway was made using lanternfishes as a model. Results show that within this family some adaptations are strongly constrained by phylogeny (e.g. eye size [16]), while others are influenced by the depth range of a species at night (e.g. photoreceptor size [21]). However, data for this kind of analysis is still very limited, especially since ecological information is missing for many deep-sea taxa.

Plotting several visual specialisations against the phylogeny (Fig. 2) reveals some interesting patterns. Firstly, some adaptations appear more common than others. For example, multibank retinas are one of the most widespread deep-sea visual adaptation, while other specialisations such as bundled photoreceptors and red vision are only present in one or two orders. How common a particular specialisation is may thus imply its success or advantage compared to others. The fact that multibank retinas have been found in many different families and orders including the most ancestrally derived lineages, but also some shallow water representatives, suggests that this is a very successful adaptation that has been maintained within teleost fishes for a long time. The expansion of *RH1* genes, on the other hand, seems a rather rare event that is likely to have evolved independently in several lineages [78], and therefore might only be useful to very specialised taxa. Secondly, few families/orders stand out by having a lot more adaptations than others, with the most specialisations found in the Scopelarchidae, a family within the Aulopiformes. Others, like the Ophidiiformes, have none or very few visual specialisations suggesting that these may rely more heavily on other sensory organs. However, since many species still remain to be investigated this current picture is far from complete.

Overall, from what we know, deep-sea teleosts have evolved some astonishing visual adaptations to overcome the limitations imposed by their extremely dim environment. However, a lot more secrets are left to be discovered in the most remote part of our world. Specifically, the high inter- and intraspecific variability in visual adaptations seen in deep-sea teleosts reinforces the idea that all vertebrate visual systems are unique and adapted to specifically meet each species visual demands [113]. As such, more in-depth comparisons between species, in addition to comprehensive analyses combining several methods, are needed to further our understanding of deep-sea fish vision and the interplay of phylogenetic and ecological constraints on the evolution of

vertebrate dim-light vision in general.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.semcd.2020.05.027>.

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