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A complex system of ligaments and a muscle keep the crystalline lens in place in the eyes of bony fishes (teleosts)

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ABSTRACT

The suspension of the crystalline lens in the eye was studied in 11 species of teleost (bony fish) from 10 families and 7 orders by light and electron microscopy. In all species there were 4–5 ligaments in about the equatorial plane of the eye, in which also the tendon of the retractor lentis muscle attaches to the lens. In two cichlid species two additional ligaments were found running from the mid-posterior surface of the lens to the optic nerve head, where they attach to the falciform process. Lens suspension in teleosts is more complex than previously described and well-suited to firmly keep the heavy spherical lens in position for well-focused vision.

1. Introduction

In aquatic vertebrates like teleosts the cornea is optically inactive since it borders on both sides to fluids of similar refractive indices as its own and the refractive power of the eye resides exclusively in the typically spherical lens. Most fish lenses have short focal lengths relative to the diameter of the aperture, i.e., their *f*-numbers are small (Fernald & Wright, 1983; 1985a; Kröger, Campbell, Munger, & Fernald, 1994; Matthiessen, 1880; 1882; 1886; 1893; Sroczyński, 1975a; 1975b; 1977; 1978; 1979; Walls, 1942). This maximizes the light gathering abilities of fish eyes (Land & Nilsson, 2002).

Another effect of a small *f*-number is short depth of focus, such that even slight defocus leads to considerable blur. This complicates color vision since animal lenses have longitudinal chromatic aberration (e.g. Kröger & Campbell, 1996; Mandelman & Sivak, 1983; Palmer & Sivak, 1981; Sivak & Bobier, 1978). Long wavelengths are focused at a longer distance from the lens than short wavelengths. Fishes and many other vertebrates compensate for this problem with multifocal lenses (Karpestam, Gustafsson, Shashar, Katzir, & Kröger, 2007; Kröger, Campbell, Fernald, & Wagner, 1999; Malmström & Kröger, 2006). These lenses have several focal lengths in monochromatic light. In polychromatic light each of these focal lengths focuses a different spectral range on the retina, such that a well-focused color image is created.

Because of short depth of focus, it is essential that the lens is firmly held in place in the eye to exactly maintain the correct distance between the lens and the retina. It was therefore questionable that the classical descriptions of lens suspension in fish eyes are complete. According to those descriptions, summarized by Walls (1942, pp. 577, 583) and Duke-Elder (1958, pp. 293, 301, 302), the lens is suspended by a *suspensory ligament* on the dorsal side and the tendon of a muscle in the campanula of Haller on the ventral side. Both the ligament and the tendon are attached to the lens in about the equatorial plane. In the majority of species, the action of the muscle moves the lens in a temporal direction and slightly posteriorly (Beer, 1894) to adjust focus for the temporal region of the retina, where many fishes have highest cell densities and thus maximum spatial resolution (Collin & Pettigrew, 1989; Fernald, 1983). Some species even have a fovea in this region (Duke-Elder, 1958, pp. 309–310; Walls, 1942, p. 304). The muscle was named *musculus retractor lentis* by Beer (Beer, 1894), and in contrast to the mammalian mode of accommodation, the teleost eye is adjusted for near vision in the relaxed state (Beer, 1894).

The spherical crystalline lens of a typical teleost eye is a relatively heavy structure. It cannot be held in place by the iris, because the pupil is so large, often with some aphakic space on the nasal side of the lens, that the iris does not usually cover any significant part of the lens and a large proportion of the lens protrudes through the pupil into the anterior chamber (Beer, 1894; Fernald & Wright, 1985b). This is also true in bright light since light flux to the photoreceptors is regulated by mechanisms located in the retina and the pigment epithelium instead of pupil constriction (Burnside & Nagle, 1983; Douglas, 1982).

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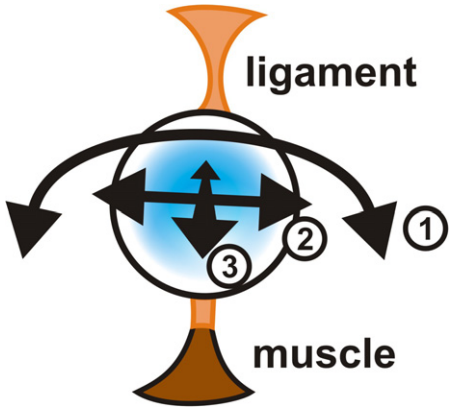

Fig. 1. Schematic illustration of the classical description of the suspension of the crystalline lens in fish eyes. Several modes of lens movement would be possible if the lens were only held by the dorsal elastic ligament and the ventral tendon of the retractor muscle. The lens could rotate between the points of attachment (1) and make translational movements at right angles to the line between the points of attachment (2 and 3). Combinations of these modes would also be possible.

Suspension of the lens at only two points would allow for various unwanted movements of the lens during rapid movements of the animal. Firstly, the lens could rotate around the axis between the suspension points (Fig. 1). Although fish lenses usually are optically rotationally symmetric, the crucian carp (*Carassius carassius*)—and may be other species—has a pronounced anterior–posterior asymmetry in the optical properties of the lens (Malkki & Kröger, 2005). Slightly flattened lenses have also been described (Matthiessen, 1886). In such cases, rotation of the lens would change the properties of the retinal image. Secondly, the lens might move translationally (Fig. 1). Movements of this kind would lead to blur and movements of the image in various parts of the retina, depending on the axis of movement. Combinations of these modes of movement are, of course, also possible and likely in agile animals such as most bony fishes.

The inconsistency between the need for high stability in lens position and the apparently simple and poor suspension of the lens was the motivation to re-investigate the morphology of fish eyes with modern methods. Furthermore, occasional observations made in fresh fish eyes used in earlier studies had hinted at a more complex suspensory system of the lens.

2. Materials and methods

The eyes of 11 species of bony fish from 7 orders and 10 families were investigated. The species were selected to cover a wide range of lifestyles and teleost families (Table 1). The animals were obtained alive from either local fishermen or Simontorps Säteri (Brentarp, Sweden), a local distributor of live animals. The fish were sacrificed by rapid decapitation and pithing. The procedures were in accordance with Swedish animal welfare legislation and the study was approved by governmental bodies.

2.1. Light microscopy

The eyes were fixed at room temperature in freshly prepared fixative (1% paraformaldehyde, 2.5% glutaraldehyde, and 3% sucrose in 0.07 M sodium phosphate buffer, pH 7.3) and kept in a refrigerator at 4 °C for at least two nights. Specimens were washed 4 times in 0.1 M sodium phosphate buffer (pH 7.3) and embedded in 0.23% chicken egg albumin, 0.5% gelatine, and 0.04% glutaraldehyde in phosphate-buffered saline (PBS), or in 3% agar solution (35 °C). The embedded specimens were covered with PBS and stored in a refrigerator. The cornea and iris were removed under a dissection microscope (Stemi SV 6, Zeiss, Oberkochen, Germany) and pictures were taken with a digital camera (DSC-F707, Sony, Tokyo, Japan). Some eye preparations were stained with 5% thymidine blue in PBS overnight at 4 °C.

2.2. Transmission electron microscopy

The eyes were opened immediately after excision and the tissue of interest was carefully cut out and put on a lysine-coated microscope slide. The slides were put in freshly prepared fixative (same as for light microscopy) at room temperature and kept in a refrigerator overnight. Specimens were washed 4 times (20 min) in 0.1 M sodium phosphate buffer (pH 7.3), and post-fixated (2% osmium tetroxide in 0.06 M phosphate buffer) for about 90 min at 4 °C. Thereafter the specimens were washed 3 times (20 min) in demineralised water and stained overnight (5% uranyl acetate in 70% ethanol) at 4 °C. The next day the specimens were dehydrated (10 min 70% ethanol, 2 × 10 min 96% ethanol, 2 × 10 min 100% ethanol) and embedded (2 × 5 min 100% acetone, 25 min acetone–Epon 3:1, 40 min acetone–Epon 1:1, 55 min acetone–Epon 1:3, and 100% Epon overnight in an evacuated desiccator). Epon blocks were mounted and trimmed with razor blades. Semi-thin sections (1 μm) were made with a glass knife and stained with thymidine blue to control the location of the tissue in the trimmed block. Finally, ultra-thin sections (50 nm) were made with a diamond knife, stained with lead citrate, and viewed with a JEM-1230 transmission electron microscope (JEOL, Tokyo, Japan).

2.3. Scanning electron microscopy

The eyes were opened immediately after excision to ensure that the fixative quickly penetrated the tissues inside the eyes. Thereafter the eyes were placed in freshly prepared fixative at room temperature (1% paraformaldehyde, 2.5% glutaraldehyde, and 3% sucrose in 0.07 M sodium phosphate buffer, pH 7.3) and kept in a refrigerator overnight.

The next day the specimens were washed 4 times (20 min) in 0.1 M sodium phosphate buffer (pH 7.3) and each eyeball was cut in two parts along its equator with a fine pair of scissors. The tissues were dehydrated (10 min 70% ethanol, 2 × 10 min 96% ethanol, 2 × 10 min 100% ethanol) and critical point dried. The dried tissues were carefully glued to metal sockets, coated with platinum or gold in a pit coater and viewed with a JSM-5600LV scanning electron microscope (JEOL, Tokyo, Japan).

3. Results

In all species studied, lens suspension was more complex than previously described. The eyes of at least two fishes were studied per species and noteworthy individual variability was not observed

Table 1
The species studied, their general lifestyles, and the water types in which they occur naturally

Species	Common name	Family, order	Lifestyle	Water type	Observed ligaments (for numbering see Fig. 2)					
					4	5	6	7	8	9,10
Aequidens pulcher	Blue acara	Cichlidae, Perciformes	Bentho-pelagic	Freshwater	X	X	X	X	X	X
Astatotilapia burtoni	(No name)	Cichlidae, Perciformes	Bentho-pelagic	Freshwater	X	X	X	X	X	X
Scardinius erythrophthalmus	Rudd	Cyprinidae, Cypriniformes	Bentho-pelagic	Freshwater, brackish	X	X	X	X	X	—
Salmo salar	Atlantic salmon	Salmonidae, Salmoniformes	Bentho-pelagic	Freshwater, brackish, marine	X	X	X	X	X	—
Platichthys flesus	Flounder	Pleuronectidae, Pleuronectiformes	Demersal	Freshwater, brackish, marine	X	X	X	X	—	—
Clupea harengus harengus	Atlantic herring	Clupeidae, Clupeiformes	Bentho-pelagic	Brackish, marine	X	X	X	X	—	—
Myoxocephalus scorpius	Dhorthorn sculpin	Cottidae, Scorpaeniformes	Demersal	Brackish, marine	X	X	X	X	—	—
Eutrigla gurnardus	Grey gurnard	Triglidae, Scorpaeniformes	Demersal	Brackish, marine	X	X	X	X	X	—
Gadus morhua	Atlantic cod	Gadidae, Gadiformes	Bentho-pelagic	Brackish, marine	X	X	X	X	X	—
Zoarces viviparus	Viviparous blenny	Zoarcidae, Perciformes	Demersal	Brackish, marine	X	X	X	X	(X)	—
Centrolabrus exoletus	Rock cook	Labridae, Perciformes	Reef-associated	Marine	X	X	X	X	(X)	—

The information was obtained from fishbase.org (2007/5), except for the genus name of *Astatotilapia burtoni*, where we followed Greenwood (1981). X: structure is present; (X): structure is present, but weakly developed; —: structure appears to be absent.

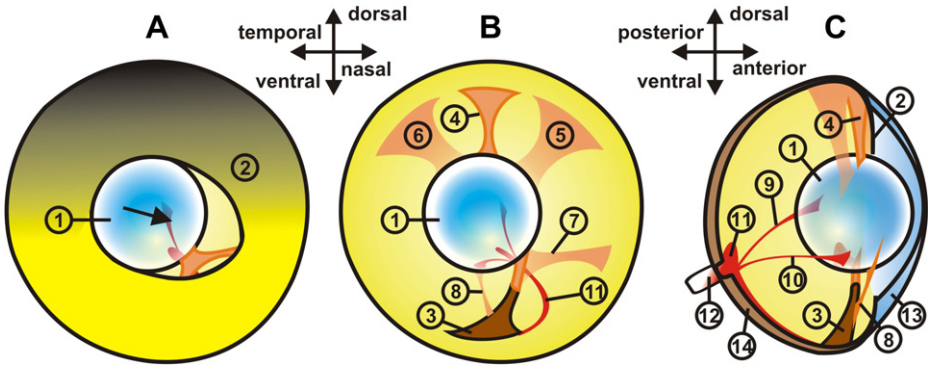

Fig. 2. Schematic illustration of the suspensory apparatus of the lens (accommodated) in the right eye of a teleost in axial views (A and B) and temporal view (C). The drawings are based on photographs taken on the eyes of *Aequidens pulcher*. (A) The large aphakic space naso-ventrally to the lens is present in many teleost species and is usually oriented more nasally than in *A. pulcher*. The arrow indicates the direction of lens movement when the retractor lentis muscle relaxes. Note that the pigmented muscle is not in the way for light that enters the eye from a naso-ventral direction and is focused on the dorso-temporal region of the retina, where the animals have highest spatial resolution. (1) lens; (2) iris; (3) retractor lentis muscle in the campanula of Haller; (4) central suspensory ligament; (5) nasal suspensory ligament; (6) temporal suspensory ligament; (7) frontal ligament; (8) accessory ligament; (9) dorsal posterior ligament; (10) ventral posterior ligament; (11) retinal embryonic fissure with falciform process; (12) optic nerve; (13) cornea.

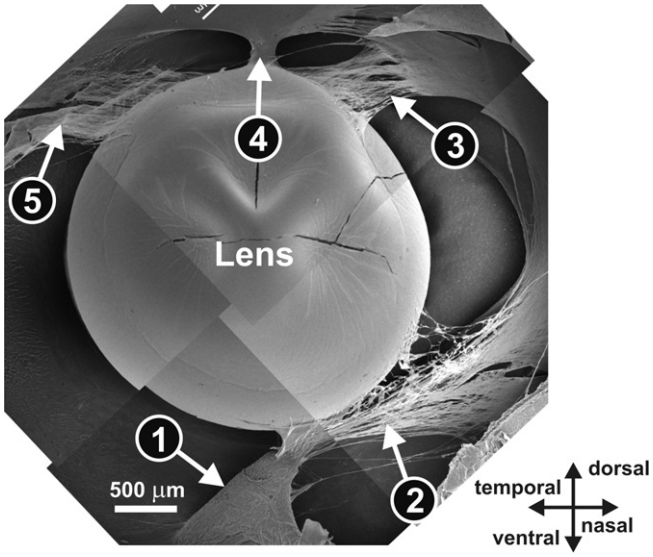

Fig. 3. Composite scanning electron micrograph of lens suspension in the shorthorn sculpin (*Myoxocephalus scorpius*) seen from the posterior chamber. (1) Retractor lentis muscle; (2) frontal ligament; (3) nasal suspensory ligament; (4) central suspensory ligament; (5) temporal suspensory ligament. Note that the central ligament is the most solid one of the suspensory ligaments. An accessory ligament is absent in this species.

in any species. In the following, numbers in brackets refer to the numbering of structures in Fig. 2, in which the findings in all species investigated are schematically illustrated.

Several ligaments attach to the lens in about the equatorial plane. On each side of the previously described *central suspensory ligament* (4), there is an additional ligament [the *nasal* (5) and *temporal* (6) *suspensory ligaments*], which in some species splits up into separated threads (Fig. 3). From the point of attachment to the lens of the retractor muscle's tendon, there is a band-like *frontal ligament* (7) attaching to a nasal (frontal) part of the ciliary region. This ligament may be, depending on the species, so thin that it generates interference colors in light microscopy (Fig. 4A). From the pigmented body of the retractor muscle, a thin *accessory ligament* (8) may extend to the lens at a wide angle to the tendon of the muscle (Fig. 4). This ligament consists only of a few filaments or is lacking completely in some species (Table 1).

In the cichlid fishes studied (*Aequidens pulcher* and *Astatotilapia burtoni*), two thin, thread-like ligaments were observed [the *dorsal* (9) and *ventral* (10) *posterior ligaments*] which run from the mid-posterior part of the lens to the region of the optical disc, where they attach to the falciform process (11) (Fig. 5A and B). The structures were identified as ligaments by transmission electron microscopy, which revealed layered structures of low contrast and devoid of cellular components (Fig. 5C). The posterior ligaments attach to the lens with a fan-like structure (Fig. 5A). They could be confirmed beyond doubt only in cichlids. In some of the species studied, the structures attached to the lens were markedly polarized towards the nasal (frontal) side (Fig. 6).

4. Discussion

The suspensory apparatus of the crystalline lens in the typical teleost eye was found to be more complex than previously described (reviewed by Walls, 1942, and Duke-Elder, 1958). Five ligaments in about the equatorial plane effectively prevent rotation and unwanted lateral displacements of the lens. In cichlids, two posterior ligaments prevent the lens from moving anteriorly through the large pupil. Posterior displacement of the lens is counter-acted by the gelatinous vitreous body. These supportive structures keep the lens firmly in place, such that unwanted movements in any direction that could lead to image blur and/or movements are prevented. Because of the short depth of focus of powerful fish lenses, it is particularly important that they are well stabilized within the eyes.

The newly described ligaments are all considerably thinner than the previously described central suspensory ligament, which may be the reason why they had escaped the attention of earlier workers. The presence and shapes of the ligaments could be documented best by scanning electron microscopy that has become available after the classical studies had been performed. The posterior ligaments are particularly thin and difficult to detect. Their existence could be confirmed only in cichlids, but they may also be present in other teleost families.

During accommodation, the lens moves along the long axis of the pupil (Fernald & Wright, 1985b) and slightly inwards (posteriorly) (Beer, 1894) to adjust focus for the temporal region of the retina, where cell densities and thus spatial resolution are highest (Collin & Pettigrew, 1989; Fernald, 1983). This movement is accomplished by the contraction of a muscle that is located outside the path light is taking to the temporal retina, such that optimal

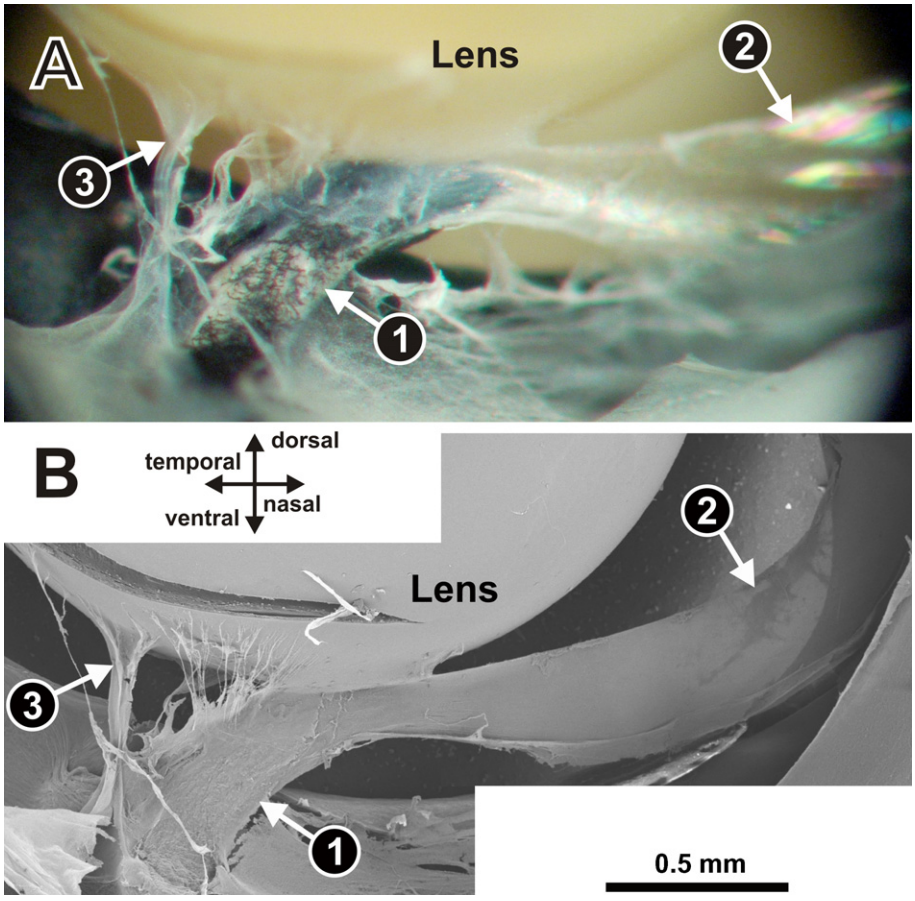

Fig. 4. Light (A) and scanning electron (B) micrographs of the area of attachment between the tendon of the retractor lentis muscle and the lens. The micrographs are from the same eye of an Atlantic salmon (*Salmo salar*) and have the same magnification. (1) Tendon of the retractor lentis muscle; (2) frontal ligament; (3) accessory ligament. Note that the frontal ligament is so thin that it generates interference colors in the light microscope. The accessory ligament (3) is well-developed in salmon.

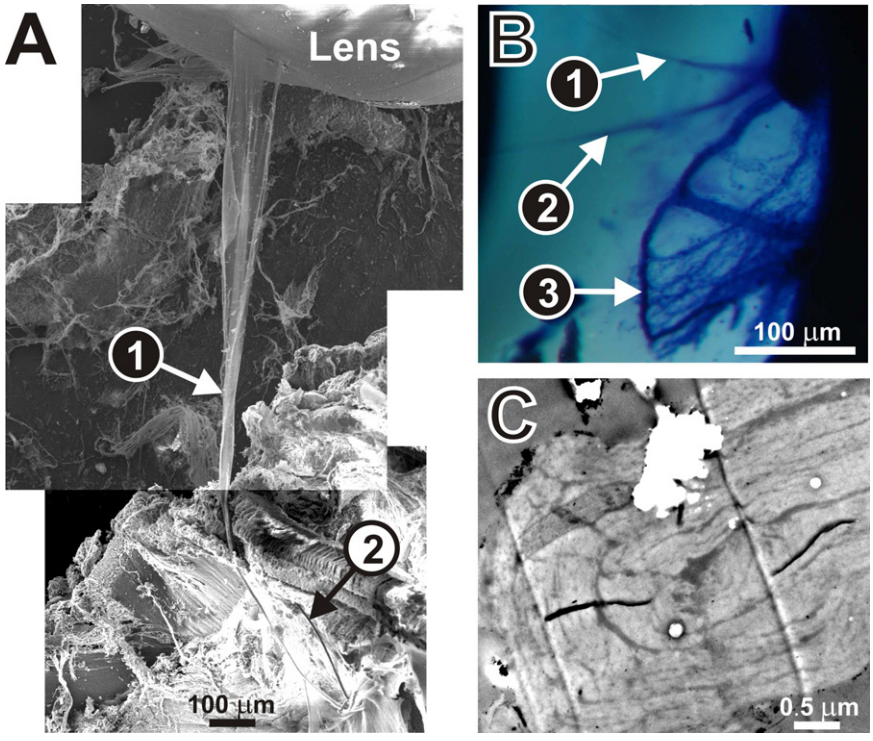

Fig. 5. Scanning electron (A), light (B), and transmission electron (C) micrographs of details of the posterior ligaments in *A. pulcher* eyes. (A) One of the very thin posterior ligaments is intact (1) while the other one is broken (2). Note the fan-like insertion at the lens. (B) The attachment of the dorsal (1) and ventral (2) posterior ligaments to the falciform process (3). (C) Section of a part of a posterior ligament. Contrast had to be maximized to visualize the layered structure of the ligament.

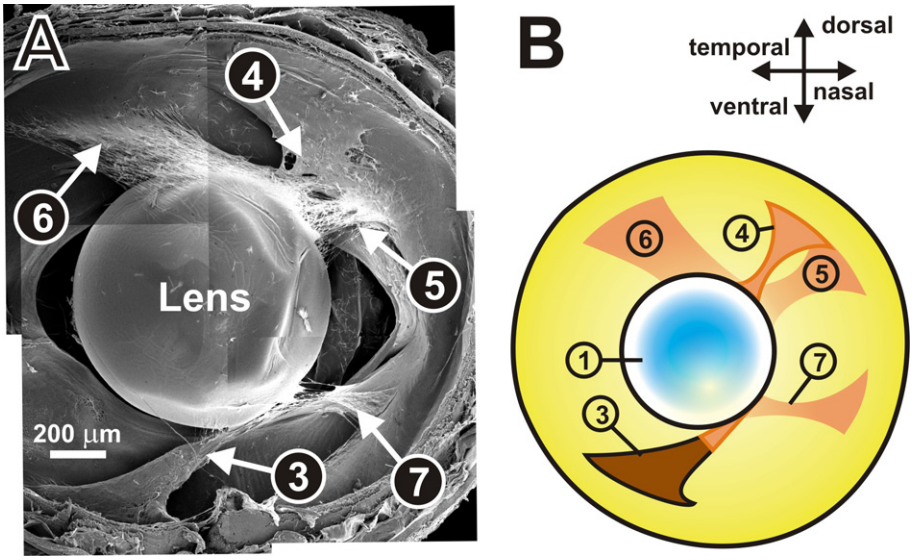

Fig. 6. Composite scanning electron micrograph (A; left eye, seen from posterior) and schematic sketch (B; right eye, seen from anterior) of lens suspension in the viviparous blenny (*Zoarces viviparus*). This species has a profound nasal polarization of the suspensory apparatus of the lens. For easier comparison, the structures are numbered as in Fig. 2. (1) Lens; (3) retractor lentis muscle in the campanula of Haller; (4) central suspensory ligament; (5) nasal suspensory ligament; (6) temporal suspensory ligament; (7) frontal ligament.

imaging conditions are achieved. The off-axis position of the retractor muscle (Fig. 2) may be the reason for the rather complicated system of ligaments. Because the elastic properties of the ligaments are unknown, creating a mechanical model of accommodation in teleosts was beyond the scope of this study.

The pattern of the ligaments and muscle shown in Fig. 2 was recognized in all species investigated, albeit with some variability in the shapes, sizes, and angles of the structures (Fig. 6). The current sample of species is still too small to draw any conclusions concerning how this variability may be correlated with the ecologies and/or phylogenies of the species studied. One can conclude, however, that there is a typically teleostean pattern. It would be interesting to know when during evolution of vertebrates this pattern has arisen. The lens is suspended by an equatorial membrane in lampreys (agnatha) (Gustafsson, Collin, & Kröger, 2008). Elasmobranchs have another type of lens suspension with a *musculus protractor lentis* (Walls, 1942, pp. 565, 567). Lens suspension in chondrosteans appears to be similar to the classical description of lens suspension in teleosts, i.e., with a single dorsal suspensory ligament and a ventral structure that may be homologous to the campanula of Haller in teleosts or the ventral papilla in elasmobranchs (Duke-Elder, 1958, p. 317; Walls, 1942, p. 571) or may even be an independent "invention", since it does not seem to follow the embryonic developmental pattern of either the campanula or the papilla (Walls, 1942, p. 571). Among the holosteans, *Lepisosteus* has a dorsal suspensory ligament and a small ventral retractor muscle (Munk, 1968; Walls, 1942, p. 575), while *Amia* has two dorsal ligaments; a posterior one similar to the teleostean central suspensory ligament and an anterior one that extends from the annular ligament to the lens in the anterior chamber of the eye (Jokl, 1927; Munk, 1968). The retractor muscle is well-developed in *Amia* (Walls, 1942, p. 575). The available descriptions, however, do not provide any information concerning the additional ligaments that have been observed in teleost eyes in this study, such that further studies are necessary for valid comparisons.

5. Conclusions

The classical descriptions of lens suspension in teleost eyes are incomplete. Instead of just one suspensory ligament, there is a complex system of ligaments that prevent unwanted lateral and rotational movements of the lens. In cichlids and may be other families, there are in addition two posterior ligaments that prevent axial movements of the lens in the anterior direction. The suspensory apparatuses of teleost lenses seem to be well-suited to firmly keep the lens in place, which is a precondition for stable and well-focused vision.

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