Observations on the shape of the lens in the eye of the silver lamprey, *Ichthyomyzon unicuspis*

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The shape of the lens in the eye of the silver lamprey, *Ichthyomyzon unicuspis* was examined in live, frozen, and fixed material. Contrary to other reports, the lens was found to be nonspherical with a cone-shaped posterior. The egg-shaped lens, which contains horizontal sutures on both the anterior and posterior surfaces, is also asymmetric in the nasotemporal axis. Its equatorial diameter exceeds its axial diameter (thickness) and the radius of curvature of the lens in the dorsoventral axis is greater than the radius of curvature in the anterioposterior axis. The lens is surrounded by a thick basement membrane with the anterior lens surface covered by a single layer of cuboidal epithelial cells. Juxtaposed to the lens capsule is a dense layer of lens fibres, which stain more darkly and surround an ill-defined lens nucleus. The shape of the lens is discussed in relation to that in aquatic gnathostomes and compared with the putative multifocal lenses of some mesopelagic teleosts. It is also hypothesized that the previously reported active focussing ability of the lamprey eye may have been misinterpreted, owing to failure to take into account the nonspherical lens shape, and may reflect measurements taken of the eye and lens at different angles.

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La forme du cristallin chez la lamproie *Icthyomyzon unicuspis* a fait l'objet d'une étude; des cristallins vivants, surgelés ou fixés ont été utilisés. Contrairement aux résultats d'autres études, il semble que le cristallin de la lamproie ne soit pas sphérique et comporte une partie postérieure conique. Ce cristallin en forme d'oeuf, qui contient des sutures horizontales sur la surface antérieure et sur la surface postérieure, est également asymétrique dans l'axe nasotemporal. Son diamètre à l'équateur est plus grand que son diamètre axial (épaisseur) et le rayon de courbure du cristallin dans l'axe dorsoventral est plus grand que le rayon de courbure dans l'axe antéropostérieur. Le cristallin est entouré d'une membrane basale épaisse et sa surface antérieure est recouverte d'une couche unique de cellules épithéliales cuboïdes. Apposée à la capsule se trouve une couche dense de fibres qui se colorent plus fortement et qui entourent le noyau indistinct du cristallin. La forme du cristallin est comparée à celle des gnathostomes aquatiques ainsi qu'aux cristallins présumés multifocaux de certains téléostéens mésopélagiques. Il est possible que les chercheurs qui ont conclu à la capacité de focalisation active chez la lamproie aient fait des erreurs d'interprétation, puiqu'ils n'ont pas tenu compte de la forme non sphérique du cristallin, et leurs conclusions reflètent peut-être des mesures de l'oeil et du cristallin à des angles différents.

[Traduit par la rédaction]

Introduction

The lamprey lens has been described as circular (Duke-Elder 1958), globular (Kleerekoper 1972), and perfectly spherical (Walls 1942), as in most bony fish, by Franz (1932), and Dickson and Graves (1981). However, it is thought by Capraro (1934), Prince (1956), and Nicol (1989) to be flattened, but few other details are discussed in these studies. It has been thought for many years that a spherical lens is the most effective means of focussing light on the retina in an aquatic environment, since the cornea plays little or no part in the refraction of light (Walls 1942; Duke-Elder 1958; Pumphrey 1961). This is mostly true for teleosts, where the focal length is proportional to the lens radius multiplied by a constant, 2.55 (Matthiessen's ratio). However, this ratio is not absolute, since Matthiessen (1880) recorded a range of values from 2.40:1 to 2.82:1. Furthermore, absolute values of focal length are difficult to calculate, since it may vary slightly with wavelength (chromatic aberration), position of the incident light beam on the lens (spherical aberration), and variations in the gradient of the lens refractive index (Sivak 1990). Therefore, it is important to take these factors into account when calculating the focal length for a given species.

In the lamprey eye there is no suspensory ligament or zonule of Zinn. The pupil of the lamprey does not constrict or dilate and the shape or position of the lens cannot be altered directly within the eye (Rovainen 1982). The lens is pressed against the iris by the vitreous, and this supports it and holds it in position (Kleerekoper 1972). Dynamic accommodation of the lens is thought to occur by contraction of an extraocular corneal muscle, which inserts on the spectacle by a tendon that causes the cornea to flatten. As the lens and cornea are in contact, the lens is pressed inwards towards the retina and the eye becomes more hyperopic. Accommodation in the opposite direction is thought to be due to extraocular muscle contractions (Franz 1932). In *Petromyzon fluviatilis*, Franz (1932) also recorded a refractive change of over 100 dioptres elicited by a combination of both positive and negative accommodation and bending of the head in a horizontal direction.

This large range in refractive state would require an elaborate accommodatory apparatus, and more recently, Sivak and Woo (1975) questioned whether any functional accommodation exists in lampreys at all. They failed to see any changes in refractive state after tricaine methane sulphonate (MS 222) anaesthesia and found small optical changes, in marked con-

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trast to the very large changes reported by Franz (1932) when the cornealis and other head muscles of *Petromyzon marinus* were stimulated. Therefore, as an alternative hypothesis, could Franz (1932) have failed to take into account the fact that the lamprey lens is nonspherical, and misinterpreted his large range of measurements as different levels of accommodative excitation? This suggestion is supported by many published values for the lamprey eye during development, in postmetamorphic animals, or in adults where the shape of the lens is either not clear or appears nonspherical (e.g., in Dickson and Graves 1981).

Not all aquatic vertebrates possess spherical lenses. Among teleosts, nonspherical lenses occur in the sandlance, *Limnichthyes fasciatus* (Collin and Collin 1988*a*), the mesopelagic species *Trachipterus trachypterus* and *T. arcticus* (Munk 1986), several species of deep-sea angler fishes, and the gulper eel (Munk 1984). The lenses of the "four-eyed fish," *Anableps anableps* (Sivak 1976), and the intertidal mudskipper, *Periophthalmus* (Graham 1972), are also nonspherical and are adapted for aquatic as well as aerial vision. A nonspherical lens is predominantly found in the eyes of elasmobranchs (Sivak 1978), the equatorial diameter exceeding the axial diameter by various amounts even though these fish are under the same optical constraints as teleosts. However, there are also exceptions in this group, the lenses of the dogfish *Mustelis canis* and *Squalus acanthias* being almost spherical (unpublished data). Holosteans (now reclassified as members of the Ginglymodi group) also possess spherical lenses (Collin and Collin 1992).

This large variation in lens shape in aquatic gnathostomes has led us to reevaluate the shape of the lens in an agnathan, the silver lamprey, *Ichthyomyzon unicuspis*, to gain some insight into the evolution and the functional constraints of lens shape in aquatic vertebrates.

Methods

The eyes of 10 postmetamorphic *Ichthyomyzon unicuspis*, ranging between 10.5 and 16.0 cm in length, were examined. All individuals were juveniles (2–6 months postmetamorphic and possessing specialized mouthparts), i.e., not considered to be adults. Adults reach lengths exceeding 34 cm, with associated increases in eye size. This study concentrates on a particular developmental stage, since little is known of the developmental changes in the optical elements of the lamprey eye. Prior to sacrifice, all animals were maintained at constant temperature (8°C) refrigerated aquaria in the laboratory. The silver lampreys were collected from the Mississippi River near Guttenberg, Iowa.

To calculate the dimensions of the orbit, lens, and cornea, and assess the true shape of the lens, *in vivo* and without shrinkage, three lampreys (just after metamorphosis) were anaesthetized in MS 222 (1:2000) and the eyes carefully excised, leaving the extraocular muscles and surrounding tissue intact. These blocks of tissue containing the eyes were then immediately immersed in a mixture of dry ice and absolute alcohol and embedded in an aqueous 30% sucrose solution on a freezing sledge microtome (American Optical). An Olympus dissecting microscope fitted with a 35-mm single reflex camera was mounted above the specimen stage, which was illuminated by an optic-fibre lamp. A photograph was taken of the block after the removal of each section (20 μm in thickness). One eye was cut in the axial (transverse) plane and the other in the equatorial (horizontal) plane. The photograph showing the greatest lens thickness was assumed to represent a section through the geometric axis of the eye (Sivak 1978). Intraocular dimensions and the radii of curvature of the surfaces of the lens were calculated from photographic enlargements (taken on Panatomic 32 ASA film) of frozen material by means of a pair of calipers and a graduated compass.

TABLE 1. Ocular dimensions of the silver lamprey, *Ichthyomyzon unicuspis*, measured from frozen material

Parameter measured	Eye (mm)	Lens (mm)
Equatorial diameter (*A*)	1.55	0.80
Vertical diameter (*B*)	1.31	0.69
Axial diameter (*C*)	1.66	0.73
Ratio *A*:*B*	1.18	1.10
Ratio *A*:*C*	0.93	1.10
Ratio *B*:*C*	0.79	0.95
Radius of curvature		
Anterior lens	0.48	
Posterior lens (nasal)	0.45	
Posterior lens (temporal)	0.44	
Cornea	1.02	
Lens radius	0.36	
Vitreous chamber depth	0.60	
Corneal thickness	0.12	
Matthiessen's ratio	2.66	
Retinal thickness	0.12	

NOTE: All values represent the mean from three eyes of postmetamorphic individuals 10.5 cm in length. The radii of curvature are measured in the equatorial plane. No anterior chamber depth is given, since the corneal surface apposes that of the anterior lens. Matthiessen's ratio depicts the relationship between the posterior nodal distance and the lens radius.

The remaining animals were used to assess the shape of the lens in living (nonfrozen) and fixed tissue. These animals were also anaesthetized with MS 222 (1:2000) and the eyes excised and placed in either lamprey Ringer solution at 8°C (Rovainen 1974) or 2.5% glutaraldehyde in 0.1 M phosphate buffer (pH 7.4) at 8°C overnight. Following their removal from the orbit, different aspects of the unfixed lenses were examined in Ringer solution, photographed, and compared with those of the frozen material. The immersion-fixed eyes and lenses were also photographed and then embedded in epoxy resin and horizontal sections (2–3 μm) were cut using a glass knife (in the plane of the equatorial diameter of the lens). These sections were stained with Richardson's stain and examined on an Olympus compound microscope (BH-2). The section with the largest axial lens diameter was considered to represent the geometric centre of the lens. Fixed lenses were photographed to illustrate the suture pattern of the lens fibres.

Results

The eyes of *Ichthyomyzon unicuspis* are slightly elongated in the horizontal or equatorial plane but greatly elongated in the mediolateral aspect or axial plane (Table 1, Figs. 1 and 2). Likewise, the pupil is elongated in the horizontal plane, with the lens filling the dorsal region of the eye, leaving a space between the lens and the ventral margin of the pupil (Fig. 3A). In the living, frozen, and fixed states, the lens is irregularly shaped, with its equatorial diameter exceeding its axial diameter (thickness) (Table 1). The back of the lens is also flattened dorsoventrally to form a ridge along its equatorial diameter. Thus, the lens is somewhat egg-shaped, with the blunt end directed towards the cornea (Figs 2, 3D). There is also a slight asymmetry in the shape of the back of the lens. On the nasal aspect, the lens has a convex shape close to the pointed apex, in contrast to the temporal aspect which is slightly concave (Figs. 2, 3). The radius of curvature of the front of the lens bordering the anterior chamber is 0.48 mm, whereas the back of the lens, within the vitreous, is cone-shaped, with radii of curvature of 0.45 mm (nasal) and 0.44 mm (temporal) for the posterior lens surfaces (Table 1).

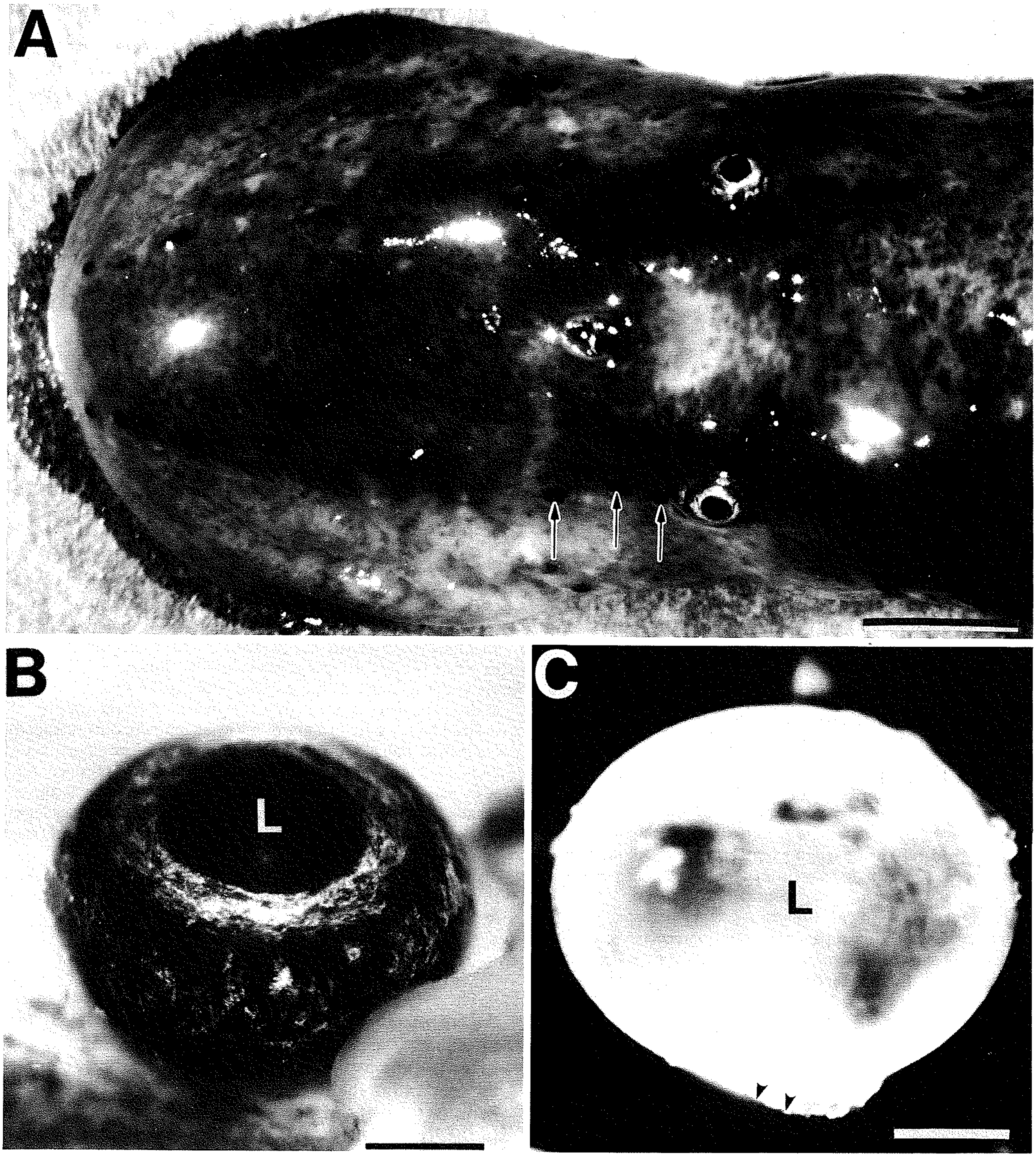

FIG. 1. (A) Dorsal view of a postmetamorphic silver lamprey, *Ichthyomyzon unicuspis*, showing the lateral position of the eyes. The positions of the gill openings on one side are indicated by arrows. (B) Magnified view of the right eye, showing the position of the lens (L) in the orbit. (C) View of the axial plane of the living lens photographed in Ringer solution and illuminated by two optic-fibre lights. Note that the lens is not spherical but cone-shaped posteriorly, with a convexity on its nasal edge (arrowheads). Scale bars: A, 4.0 mm; B, 0.5 mm; C, 0.2 mm.

The lens is held in place by the vitreous body posteriorly, the scleral cornea anteriorly, and the pupillary margins of the iris laterally. Overall, the curvatures of the lens and dermal cornea are in register on the visual axis and both show a pronounced asymmetry, the radius of curvature being much greater in the dorsoventral plane. Six extraocular eye muscles are found (Fritzsch et al. 1990), but no extraocular cornealis muscle (Duke-Elder 1958) is observed inserting into the transparent dermal cornea.

The lens is surrounded by a thick basement membrane, the lens capsule, with the anterior lens surface covered by a single layer of cuboidal epithelial cells. The coarse lens fibres are irregularly arranged in a circular mass, appearing to meet along two suture planes, horizontal on both the anterior and

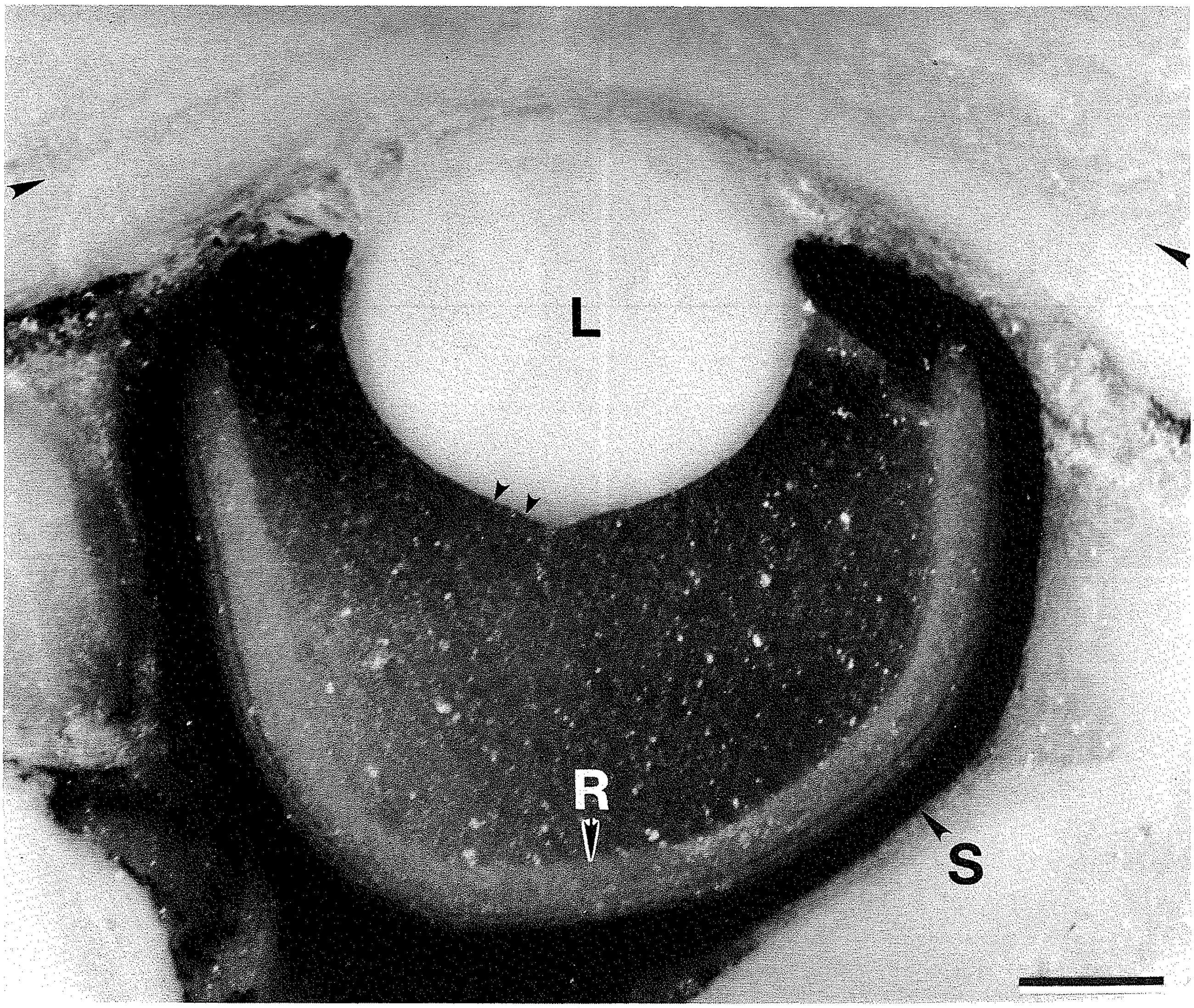

FIG. 2. Photograph of the hemisected eye of a postmetamorphic silver lamprey (10.5 cm in length) cut in the horizontal (equatorial) plane on a freezing microtome. This section illustrates the greatest axial lens diameter and is considered to represent the geometric centre of the lens. All intraocular measurements presented in Table 1 are carried out on similarly unfixed frozen tissue. The large arrowheads depict the outer boundary of the corneal epithelium, while the small arrowheads depict the slight nasal convexity in the posterior pole of the lens (L). R, retina; S, sclera. Scale bar = 0.25 mm.

posterior faces (Figs. 3 and 4). The density of the lens fibres changes markedly from the surface to the centre, with a high concentration of fibres lying in a ring adjacent to the lens capsule (Fig. 4A) and a second, central area of more darkly stained material, presumably the lens nucleus. These central nuclear fibres also contain small granular inclusions of various sizes, possibly the light-yellow pigment granules described by Walls and Judd (1933).

Discussion

Our data disagree with the scheme of a spherical lens in lampreys (Franz 1932; Walls 1942; Duke-Elder 1958; Kleerekoper 1972; Dickson and Graves 1981), at least for the silver lamprey, *Ichthyomyzon unicuspis*. In contrast, the data indicate that, in this species, the lens is lateromedially flattened, as alluded to by Capraro (1934) and Nicol (1989) and as described for elasmobranchs (see summary by Sivak 1990) and some teleosts (Graham 1972; Munk 1984; 1986; Collin and Collin 1988*a*). The pointed ridge along the posterior edge of the lens (Figs. 2, 3D, and 4B) has not been previously noted and the refraction of light at this surface is not well understood. If light is focussed on the anterior part of the lens, the coarse lens fibres situated just below the lens capsule appear to focus the light on the apex of this ridge (Fig. 3D). This indicates that the optical properties of the lens may be nonuniform, as exemplified by the variation in staining of the lens and as previously suggested by Hess (1912). Lenses of postmetamorphic lampreys of other species such as *Petromyzon marinus* need to be examined to reveal whether these findings for the lens of *I. unicuspis* constitute general properties of all lamprey lenses.

If nonspherical lenses are common in lampreys, at least at this stage in development, this could indicate that nonspherical lenses are a primitive vertebrate trait found in two groups of primary aquatic myopterygians, the petromyzontiformes and the elasmobranchs (including the chimaeras; unpublished data). However, nonspherical lenses in bony fish are appar-

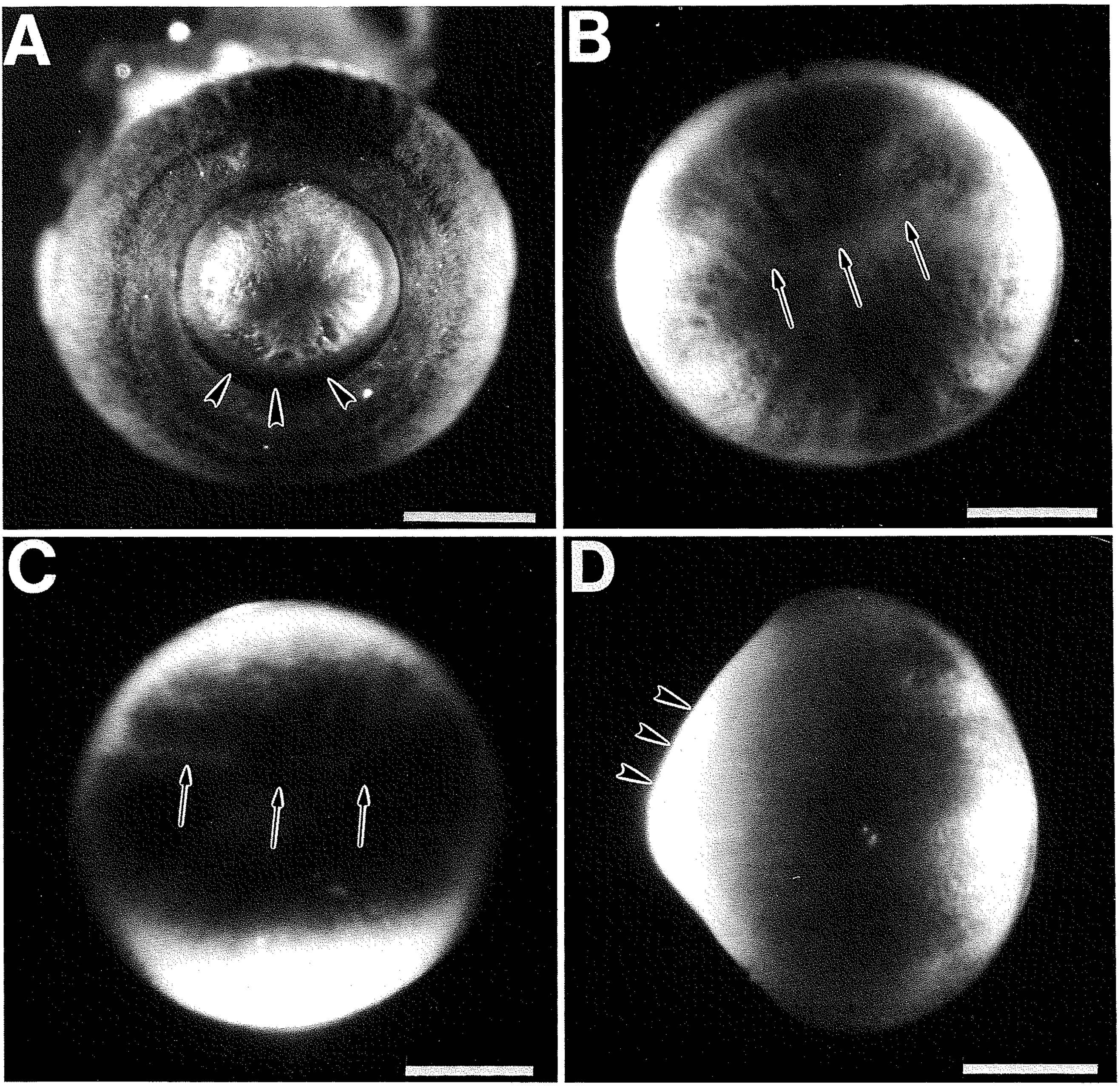

FIG. 3. (A) Lateral view of the eye of the silver lamprey after fixation, showing the horizontal suture along the equatorial plane of the lens and the ventral space between the lens and the pupil (arrowheads). (B and C) The horizontal suture planes, indicated by arrows in the lateral (B) and medial (C) views of the lens. (D) Note the nonspherical shape of the lens when viewed in the axial plane and the asymmetric curvature of the nasal slope (arrowheads) of the posterior apex in relation to the temporal slope. Scale bars: A, 0.5 mm; B, C, and D, 0.25 mm.

ently an adaptive trait and may be elongated in the mediolateral plane, like the oval lens of the "four eyed fish" (Sivak 1976), the long axis corresponding to the ventral (aquatic) pupil axis and the short axis corresponding to the upper (aerial) pupil axis and the unique optical system of the sandlance, *Limnichthyes fasciatus* (Collin and Collin 1988*a*, 1988*b*). Other flattened teleost lenses are also found in the mormyrid *Marcusenius longianalis* (Franz 1920), a number of ceratioid angler fishes, the gulper eel, *Saccopharynx ampullaceus* (Munk 1984), and the mesopelagic species *Trachipterus trachypterus* and *T. arcticus* (Munk 1986). Direct measurements of the optical properties of the dissected lens of *I. unicuspis* are needed to show whether the shape of this lens can be interpreted as an adaptation to specific optical needs or, rather, reflect historical constraints on the form of the lens.

One explanation of the unique shape of the lens of this lamprey may be found by comparing it with the similarly egg-shaped lenses of the mesopelagic teleosts *T. trachypterus* and *T. arcticus*, which are thought to possess different focal lengths for parallel rays entering the eye from different directions (Munk 1986). Using theoretical considerations, it is thought that these egg-shaped lenses will focus light entering the eye on the visual axis at a shorter distance than light entering the eye from other directions. It has been suggested that, in this way, the lens is multifocal or varifocal (Munk 1986). Without ray-tracing analyses it is not known whether the lam-

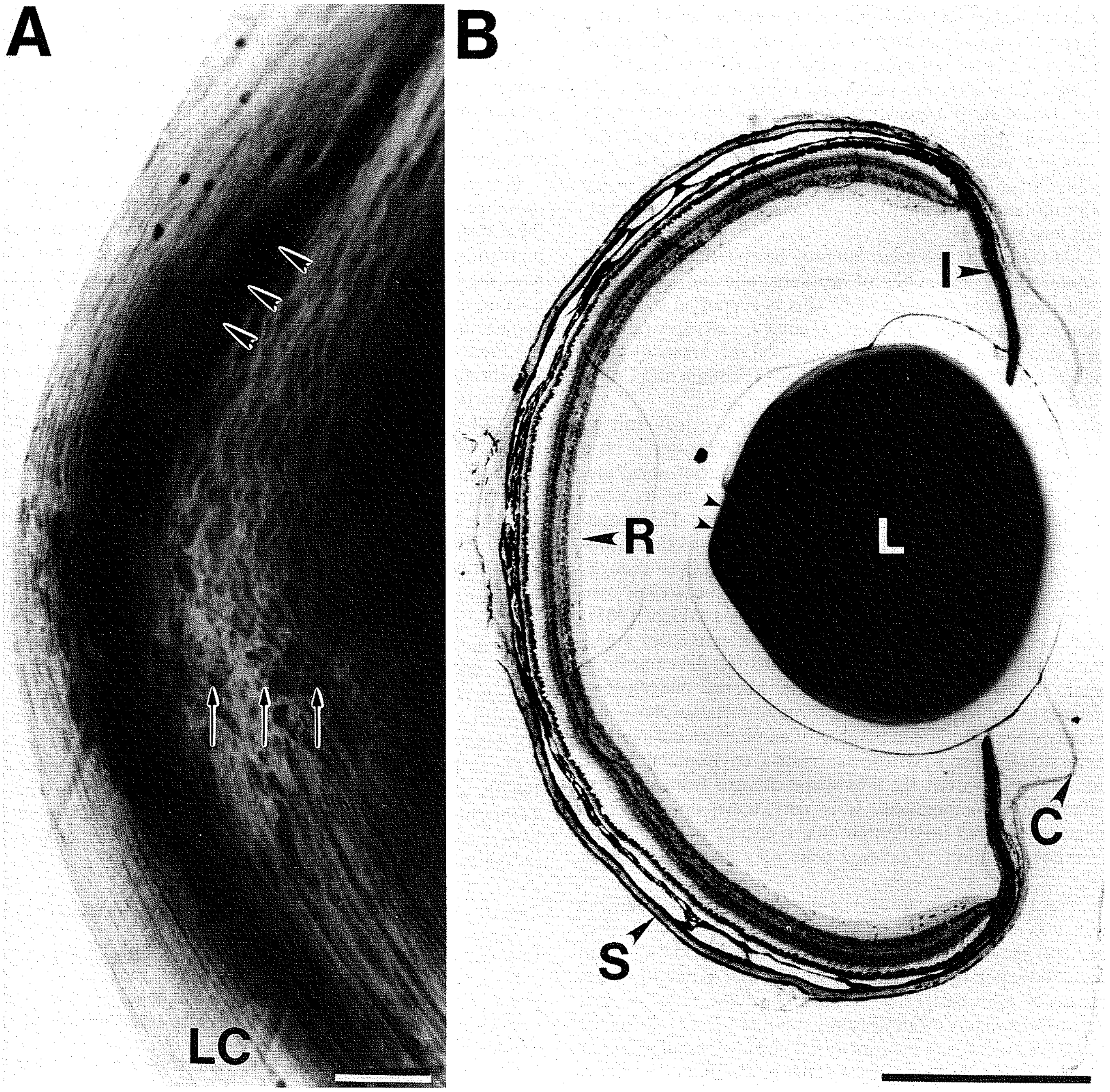

FIG. 4. Horizontal section (2 μm) of the posterior apex of the fixed lens of *Ichthyomyzon unicuspis*. The arrows indicate the area where the lens fibres interdigitate in a suture, while the arrowheads show an area surrounding the lens and beneath the lens capsule (LC) in which the lens fibres are more concentrated and therefore more darkly staining. (B) Horizontal section (2 μm) of the fixed eye, showing the relative size and shape of the lens (L) in the orbit of a lamprey 16 cm in length. Note that the convex shape of the nasal aspect of the posterior apex (arrowheads) observed in living and frozen material is unchanged. The cornea (C) is usually closely apposing the surface of the lens but has lifted in histological processing. I, iris; R, retina; S, sclera. Scale bars: A, 25 μm; B, 0.4 mm.

prey lens is multifocal, but this may be conceivable given its similarity in shape.

Assuming that the lamprey lens is multifocal, what could be the optical advantage of such a lens? Owing to the small eye size of these postmetamorphic lampreys (less than 2 mm in diameter), the retinal image formed would be similarly small. However, since the size of the image is directly proportional to the focal length, an image formed in the central retina of an object situated along the visual axis would be smaller than an image falling on more peripheral parts of the retina. Therefore, the size of the image will vary depending on the position of the object relative to the lens axis (Munk 1986), with a larger image sampled by the peripheral retina.

Could the putative multifocal capabilities of this lens, in association with the asymmetry in the curvature of the posterior part of the lens and its dorsal displacement, enable the lamprey to see a well-focussed image on the photoreceptor layer in the peripheral retina? A clue may lie in the fact that in *I. unicuspis*, an analysis of the topography of the total population of retinal ganglion cells in an individual of similar size reveals a higher concentration of glanglion cells in the peripheral retina, especially in the dorsal region, with little specialization of the retina on the visual axis (Fritzsch and Collin 1990). Therefore, this peripheral increase in ganglion cell density would allow a greater sampling of an image and therefore provide higher spatial resolving power in this region. One may expect some refraction of light on the visual axis peripherally, given a different radius of curvature for the anterior (0.48 mm) and posterior (0.45 mm nasal and 0.44 mm temporal) lens surfaces.

Could the lens in the *adult* lamprey be spherical, however, as stipulated by a number of workers, and the lens shape change throughout development? This is supported by observations of a change in lens shape in adult *I. unicuspis* (unpublished data) and a peripheral migration of areas of high ganglion cell density in older individuals (Fritzsch and Collin 1990).

However, the postmetamorphic lamprey eye may still be optically adjusted, given that it obeys Matthiessen's ratio (Matthiessen 1880). A value of 2.66 (the posterior nodal distance divided by the lens radius) is well within the recorded limits of 2.40 and 2.82 found for most teleosts. This would mean that the smaller egg-shaped lens, just after metamorphosis, may at least be adjusted for focussing light even though, theoretically, the limit of lens resolution may be greater than the retinal resolution at this stage (Fernald and Wright 1985). The shape and focussing ability must be examined in a premetamorphic specimen in order to assess the developmental changes in this agnathan visual system, but this phenomenon of changing the shape of the lens through metamorphosis has previously been found in a number of amphibians during their progression from an aquatic to a terrestrial environment (Sivak et al. 1985). However, the lens shape changes from spherical to flattened in amphibians. It is not known how the lens changes shape, but it is thought that a change in volume and in the configuration of existing cells may take place (Sivak 1988).

In the European lamprey, *Lampetra fluviatilis*, the lens radius was calculated to be 1.21 mm (1.165 using axis measurement) and the focal length determined to be 2.54 mm with a static refraction of −8 dioptres, which corresponds to a sight distance of 12.5 cm (Franz 1932). Thus, the ratio of focal length to lens radius (Matthiessen's ratio) is 1:2.1 (1:2.2 using axis measurement) and appears to fall outside the range 2.40:1 to 2.82:1 found by Matthiessen (1880). The failure to attain this ratio and the fact that Franz (1932) also gave two measurements (one as the lens diameter and the other as the diameter of the lens on the visual axis) may be an indication that the lens was not spherical. However, is it possible that during his ophthalmoscopic examinations of the accommodatory power of the eye of *L. fluviatilis*, his values of 73 dioptres (positive) and 28 dioptres (negative) were measured off the visual axis? Since he made measurements on unrestrained animals, his large variation in focal length (attributed to a unique accommodatory apparatus, i.e., the cornealis muscle, which flattened the cornea and therefore pushed the juxtaposed lens towards the retina) may be unrelated to the active focussing ability of the eye and reflect measurements taken of the eye and lens at different angles, and possibly of individuals of different age. Alternatively, given the small size of the eyes of these animals, and that the equivalent in millimetres of a change in ophthalmoscopic focus given in dioptres is inversely related to the size of the globe (Murphy and Howland 1987), Franz (1932) may also have focussed the retinal plane over a wide range of ophthalmoscopic settings and mistakenly regarded this range of values as a measure of accommodatory power. These large accommodative changes have also been refuted by Sivak and Woo (1975), who could not elicit a change in refractive state during anaesthesia with MS 222 or after electrical stimulation.

The lamprey lens differs from that of gnathostomes by the presence of pigment granules, which lie diffusely in one of three distinct fibre layers. In *I. unicuspis*, what appear to be pigment granules are concentrated in the oldest region of the lens, the centre, and are irregular in size and shape. These we assume to be the light-yellow pigments found in the central nuclear fibres by Walls and Judd (1933). The cell nuclei are not limited to a distinct zone, which is the condition in other vertebrates, but are diffused throughout the lens periphery. The horizontal suture pattern on the anterior and posterior surfaces of the lens, which is formed by the alignment of lens fibres, was thought by Capraro (1934, 1937) not to exist at all in *Petromyzon*. This pattern seems to differ from that of sharks and many teleosts, which possess a vertical suture on the anterior face and a horizontal suture on the posterior face (Nicol 1989). Other teleosts also have sutures in a stellate pattern (Prince 1956).

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