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Pupil shapes and lens optics in the eyes of terrestrial vertebrates

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Summary

Animal eyes that are primarily used under low-light conditions usually have optical systems of short depth of focus, such that chromatic defocus may lead to considerable blurring of the images. In some vertebrates, the problem is solved by multifocal lenses having concentric zones of different focal lengths, each of which focuses a different relevant spectral range onto the retina. A partially constricted circular pupil would shade the peripheral zones of the lens, leading to the loss of well-focused images at relevant wavelengths. The slit pupil, however, allows for use of the full diameter of the lens even in bright light. We studied species of terrestrial vertebrates from a variety of phylogenetic groups to establish how widespread multifocal lenses are and how pupil shapes are adapted to the optical systems. We found that multifocal lenses are common from amphibians to mammals, including primates. Slit pupils were only present in animals having multifocal optical systems. Among the felids, small species have multifocal lenses and slit pupils, while large species have monofocal lenses and round pupils. The Eurasian lynx, a cat of intermediate size, has an intermediate eye design. The functional significance of the absence of multifocal optical systems in large felids remains mysterious, because such systems are present in other large-eyed terrestrial vertebrates. Multifocal optical systems in nocturnal prosimians suggest that those animals have colour vision despite being described as cone monochromats.

Key words: physiological optics, chromatic aberration, multifocal lens, slit pupil, evolution.

Introduction

Many animals use colour vision to detect objects against the background and recognise them by colour (e.g. Maximov, 2000). To be able to distinguish between colours, an animal has to have at least two types of photoreceptor expressing different visual pigments as well as mechanisms to compare the outputs from spectrally different photoreceptors (Sharpe et al., 1999). Depending on the species, vertebrate photopic vision ranges from monochromatic (e.g. in a number of strictly nocturnal species and most aquatic mammals; Peichl et al., 2001) to pentachromatic (in some birds; Pichaud et al., 1999). Most mammals are dichromats (Jacobs, 1993).

The quality of the optical system may limit the amount of information that can be made available to the brain since the retina can only encode information that is present in the image. Blur due to defocus reduces the information content of the retinal image, and exact adjustment of focus is particularly important if an animal has eyes adapted for use under low-light conditions. For maximum light-gathering ability, the eyes of nocturnal and crepuscular vertebrates have pupils that are large relative to the focal lengths of the optical systems, i.e. the *f*-numbers are small (*f*-number=focal length/pupil diameter). If the *f*-number is small, depth of focus is short and even small amounts of defocus lead to considerable blurring of the image (Smith and Atchison, 1996).

Ocular media are colour-dispersive, i.e. their refractive indices increase with decreasing wavelength of light (Sivak and Mandelman, 1982; Kröger, 1992). Consequently, the focal length of the optical system is a function of wavelength [longitudinal chromatic aberration (LCA)]. Focal length is shortest for short wavelengths (blue) and longest for long wavelengths (red). If an animal is capable of colour vision and has eyes of small *f*-number, LCA is a major source of blur (chromatic defocus) that cannot be eliminated by accommodation.

In the African cichlid fish *Astatotilapia* (formerly *Haplochromis*) *burtoni* (Günther 1893), well-focused colour images are formed by the crystalline lens alone since the cornea has negligible refractive power in water (Matthiessen, 1882, 1886). The lens has longitudinal spherical aberration (LSA) of complex shape that leads to several focal lengths (multifocal lens). Each focal length is used to create a well-focused image for one of the spectral types of cone photoreceptor in the retina (Fig. 1). Multifocal lenses have carefully controlled gradients of refractive index, possibly including discontinuities at the borders between zones of different focal lengths (Kröger et al., 1999).

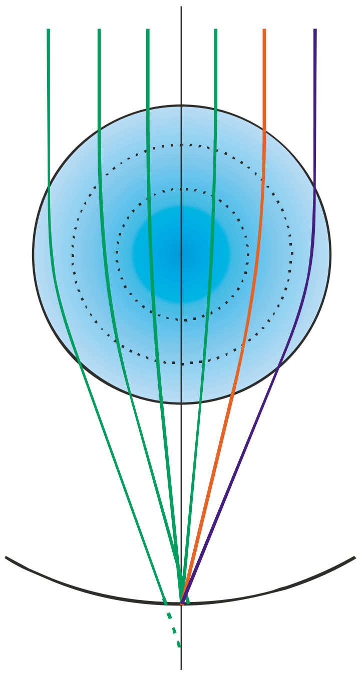

Fig. 1. Schematic illustration of the function of a colour-corrected multifocal fish lens. The spherical lens has a number of discrete zones, three in this example, of different focal lengths for monochromatic light of intermediate wavelength (green). Because of colour dispersion, the lens refracts light of short wavelength (blue) more strongly than green light, such that the zone of the lens having too long a focal length for green light focuses blue light on the retina. Accordingly, the zone of the lens having too short a focal length for green light focuses light of long wavelength (red) on the retina. By this mechanism, a sharp colour image is created by a single lens. That image, however, is contaminated by defocused light having passed through 'wrong' zones of the lens (e.g. the peripheral and intermediate zones for green light).

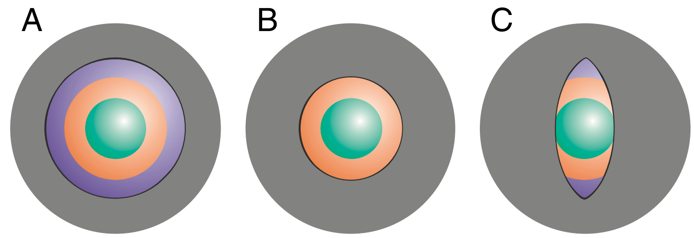

Fig. 2. The functional significance of the slit pupil in combination with a multifocal lens. In the fully dilated state of the pupil (A), all zones of the lens (shown in the colours they are focusing) can be used. A concentrically constricting iris (B) would cover the outer zone of the lens such that a spectral range (blue in this example) could not be focused on the retina. By contrast, all lens zones can be used if the pupil constricts to a slit (C).

Eye design is more complicated in terrestrial vertebrates, because in air the cornea is added as a refractive element. One therefore cannot understand the optical function of the eye by only studying the crystalline lens. Fortunately, multifocal optical systems can be detected in living animals by using eccentric slope-based infra-red videorefractometry (Schaeffel et al., 1987, 1993). A few terrestrial species have been studied and it was found that animals having colour vision and eyes of small *f*-numbers also have multifocal optical systems (Kröger et al., 1999). In the present work, we have studied terrestrial vertebrates from a variety of phylogenetic groups in order to determine how common multifocal optical systems are and whether mono- and multifocal systems are present in closely related species with different lifestyles.

If an eye has a multifocal optical system, pupil shape is of relevance. In many fishes, the pupil is unresponsive to light. Light flux is regulated in the retina instead (Douglas and Wagner, 1982). By contrast, variable pupil sizes are the rule in terrestrial vertebrates (Walls, 1942). If the lens has concentric zones of different focal lengths, a constricted circular pupil would prevent the peripheral zone(s) of the lens from focusing light on the retina (Fig. 2). The problem can be solved by a slit pupil or other specifically adapted pupil shape that allows the animal to use several refractive zones of its lenses even in bright light (Fig. 2). We therefore also determined pupil shapes to correlate pupillary adaptations with the properties of the optical systems. Furthermore, we searched for transitional forms in order to gain information on how evolution has optimized eye designs to the needs of the animals.

Materials and methods

Animals

Wild animals in captivity were used out of preference in order to avoid genetic problems that may be present in domesticated animals. We cooperated with a number of zoological gardens and animal parks in Sweden. Domestic animals were used if no wild animals were available for study in an interesting phylogenetic group. All animals were investigated unrestrained in their usual surroundings.

A total of 20 species from the following phylogenetic groups was investigated: amphibians (subgroup: anurans), reptiles (subgroups: geckos, snakes and crocodiles) and mammals (subgroups: rodents, artiodactyls, carnivores and primates). Except for the crocodiles, which both had slit pupils, at least one species in each subgroup had a circular pupil and at least one other had a different pupil shape. In some additional species, only pupil shapes were determined.

Refractometry

Eccentric slope-based infrared videorefractometry is a method to determine the refractive state of the eye in non-cooperative subjects such as human infants and animals (Schaeffel et al., 1987, 1993). If applied on human eyes, accuracy of measurement is ~0.5 dioptres. Multifocal optical systems can be detected because different zones of the eye are focused at different distances if monochromatic light is used. Multiple focal lengths manifest themselves as ring-shaped structures in photorefractive images of the pupil (Kröger et al., 1999). We used a digital infrared-sensitive video camera (DCR-TRV 730E; Sony, Tokyo, Japan) in combination with an infrared photoretinoscope consisting of four rows of infrared light-emitting diodes at eccentricities ranging from 5 to 23 mm (Kröger et al., 1999). The distance between the retinoscope and the studied subject was 2 m maximum. The experiments were performed in dim light, and infrared light was used to prevent pupil constriction. Acquired video sequences were loaded onto a computer and single frames grabbed as still images using Premiere 6.0 software (Adobe, San Jose, CA, USA).

Pupil shapes

Pictures of animal eyes were taken using a digital camera (DSC-F707; Sony) under lighting conditions eliciting pupil constriction. Where possible, a flashlight was used to induce eye shine. This was especially useful in animals with dark irises. In one case (*Mus musculus*), infrared illumination had to be used because of an almost perfectly black iris and small eye size (the camera's flashlight did not illuminate the eye at close distance).

Results

Both multi- and monofocal optical systems were found in all studied groups and subgroups of vertebrates, ranging from amphibians to primates (Fig. 3). All species having distinct slit pupils also had clearly visible rings in videorefractive images of the dilated pupil (Table 1).

In prosimians, two nocturnal species described as cone monochromats (*Galago senegalensis*, lesser bushbaby, and *Nycticebus coucang*, slow loris) were found to have multifocal optical systems and slit pupils (Fig. 3). Two of the studied species, *Orthriophis taeniurus* (beauty snake) and *Mus musculus* (house mouse), have multifocal lenses in combination with circular pupils (Fig. 4).

In felids, we detected differences between small- and large-eyed species. The domestic cat (*Felis sylvestris domestica*) has multifocal optics and slit pupils (Fig. 5A,B). Its large relative, the Siberian tiger (*Panthera tigris altaica*), has monofocal optics and circular pupils (Fig. 5E,F). The eye of the Eurasian lynx (*Lynx lynx*) is intermediate between those of the domestic cat and the Siberian tiger. In lynx eyes, rings were barely detectable in videorefractive images and pupil shape is oval or rhomboid (Fig. 5C,D). The lynx is also intermediate in body and eye size between cat and tiger.

A similar difference between small and large species may be present in canines. The small European red fox (*Vulpes vulpes*) has slit pupils and multifocal lenses (Fig. 6A,B). Its large relatives, the grey wolf (*Canis lupus lupus*) and domestic dogs (*Canis lupus familiaris*), have round pupils (Fig. 6D). The photorefractive images obtained from *C. lupus* are, however, inconsistent. Some domestic dogs had smooth reflexes indicative of monofocal optics, while others had clear rings in the reflexes (Fig. 6C,E). Pictures obtained from a group of tame wolves show central zones of irregularity (Fig. 6F).

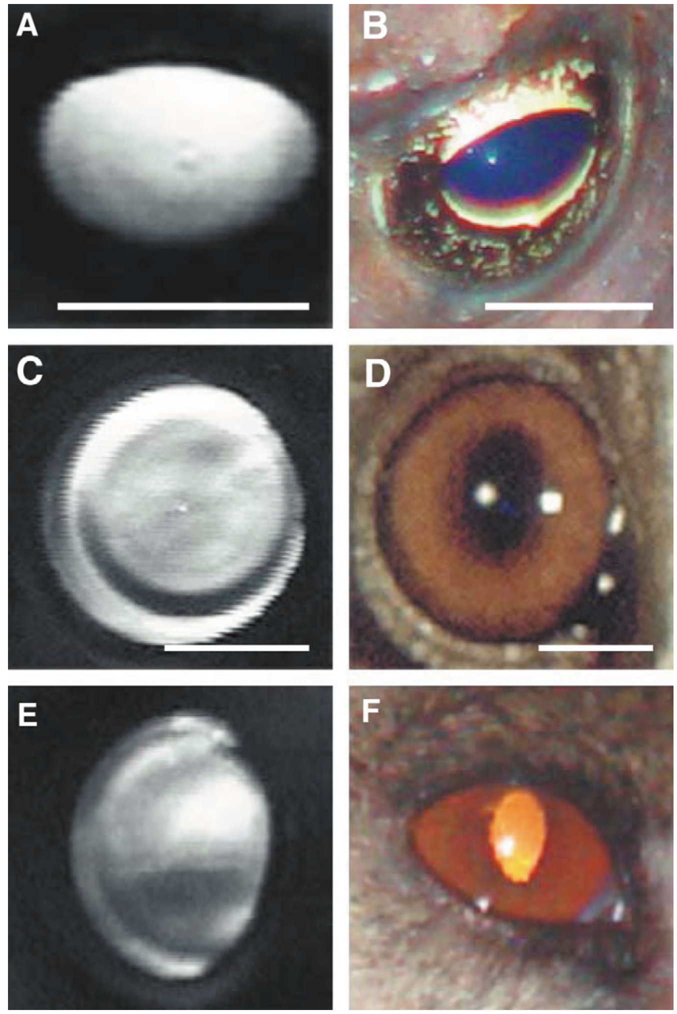

Fig. 3. Multifocal optical systems were found in all studied groups of terrestrial vertebrates, ranging from amphibians (A,B) to primates (C–F). Ring-like structures are visible in the photorefractive images (A,C,E). Because of larger eye size, the rings are more prominent in the primates (C,E) than in the toad (A). All three species have slit pupils; horizontal in the toad (B) and vertical in the primates (D,F). Scale bars are 5 mm. Species: *Bufo marinus* (A,B), *Nycticebus coucang* (C,D), *Galago senegalensis* (E,F).

There is no general correlation between eye size and the presence or absence of multifocal optical systems and slit pupils. Some large-eyed artiodactyls (e.g. *Ovis aries domesticus*) have multifocal optical systems and horizontal slit pupils (Fig. 7A,B). Horizontal slit pupils are also present in other large artiodactyls such as elk (*Alces alces*), red deer (*Cervus elaphus*) and reindeer (*Rangifer tarandus*) (Fig. 7C; Table 1), as well as in the domestic horse (*Equus caballus domesticus*) (Kröger et al., 1999). Vertical slit pupils in combination with multifocal optics were found in large and small crocodiles (*Crocodylus niloticus* and *Osteolaemus tetraspis*) (Fig. 7D).

Table 1. *Summary of results*

Phylogenetic group	Species	Common name	Lifestyle	Cone types	Eye diameter	Pupil shape	Multifocal optics	Reference – lifestyle	Reference – cone types
Amphibia									
Anura	*Bufo marinus* Linnaeus 1758	Cane toad	N	*3–4*	6	–	+	Meyer (1927)	Kelber et al. (2003)
	Phyllobates bicolour Duméril and Bibron 1841	Black-legged poison frog	D	*3–4*	4	O	–	Hanström (1962)	
Reptilia									
Serpentes	*Python molurus* Linnaeus 1758	Indian python	N	*2*	8	|	+	Mattison (2003)	Sillman et al. (1999)
	Orthriophis taeniurus friesi Werner 1926	Taiwan beauty snake	P	?	6	O	+	Schulz (1996)	–
Gekkonidae	*Tarentola chazaliae* Mocquard 1895	Helmeted gecko	N	*3*	5	|[1]	+	Welch (1994)	Loew et al. (1996)
	Phelsuma abbotti chekei Meier 1995	Chekes day gecko	D	*3*	5	O	–		Ellingson et al. (1995)
Crocodylidae	*Crocodylus niloticus* Laurenti 1768	Nile crocodile	N	*4*[2]	35	|	+	Wettstein (1937)	Sillman et al. (1991)
	Osteolaemus tetraspis Cope 1861	African dwarf crocodile	N	*4*[2]	5	|	+		
Mammalia									
Rodentia	*Mus musculus* Linnaeus 1758	House mouse	N	2	5	O	+	Nowak (1999a)	Szél et al. (1992)
	Hydrochaeris hydrochaeris Linnaeus 1766	Capybara	D	*2*	15	O	–		Ahnelt and Kolb (2000)
Artiodactyla	*Ovis aries domesticus* Linnaeus 1758	Domestic sheep	D	2	25	–	+	Nowak (1999a)	Jacobs et al. (1998)
	Sus scrofa domesticus Linnaeus 1758	Domestic pig	C,N	2	25	O	–		Neitz and Jacobs (1989)
	Alces alces Linnaeus 1758	European elk	C,D	*2*	25	–	?		Jacobs (1993)
	Cervus elaphus Linnaeus 1758	Red deer	C	*2*	25	–	?		
	Rangifer tarandus Linnaeus 1758	Reindeer	D	*2*	25	–	?		
Felidae	*Felis sylvestris domestica* Schreber 1775	Domestic cat	C,N	2	15	|	+	Nowak (1999a)	Linberg et al. (1998)
	Lynx lynx Linnaeus 1758	Eurasian lynx	C,N	2	20	(|)	(+)		Ahnelt et al. (2000)
	Panthera tigris altaica Linnaeus 1758	Siberian tiger	C,N	*2*	30	O	–		
Canidae	*Vulpes vulpes* Linnaeus 1758	Red fox	C,N	2	12	|	+	Nowak (1999a)	Jacobs et al. (1993)
	Canis lupus Linnaeus 1758	Grey wolf	N,D[3]	2	20	O	uncertain[4]		Peichl et al. (2001)
Primata	*Nycticebus coucang* Boddaert 1785	Slow loris	N	(*1*)	15	|	+	Nowak (1999b)	Ahnelt and Kolb (2000)
	Galago senegalensis Geoffroy 1796	Lesser bushbaby	N	*1*	12	|	+		Wikler and Rakic (1990)
	Lemur catta Linnaeus 1758	Ring-tailed lemur	D	(3)	13	O	–		Blakeslee and Jacobs (1985)

Lifestyles: D, diurnal; C, crepuscular; N, nocturnal; P, polyphasic. Cone types: number of spectrally different cone types. Eye diameters are estimated values in mm. Pupil shapes: O, circular; –, horizontal slit; |, vertical slit. Multifocal optics: +, present; –, absent. Italics indicate that data were available from closely related species; parentheses indicate that a characteristic is uncertain or weakly developed; question marks indicate that data were unavailable.

[1]The pupil of *T. chazaliae* constricts to a slit in moderately bright light. At full daylight, it constricts to four small, vertically aligned apertures.

[2]Four cone pigments are present in *Alligator mississippiensis*

[3]Wolves are mainly diurnal in cold climates.

[4]The photorefractive images obtained from tame wolves and domestic dogs were inconsistent (see text for details).

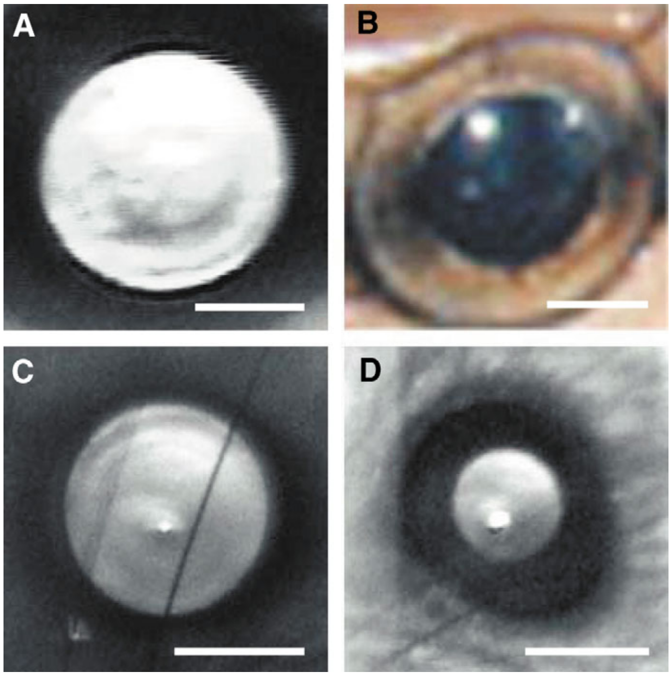

Fig. 4. Multifocal optical systems in combination with circular pupils are present in the beauty snake (*Orthriophis taeniurus friesi*; A,B) and house mouse (*Mus musculus*; C,D). The partially constricted pupil of the house mouse was visualized using infrared light because in the visual range the iris was as black as the pupil and the flashlight of the camera did not illuminate the eye at close range. Scale bars are 2 mm.

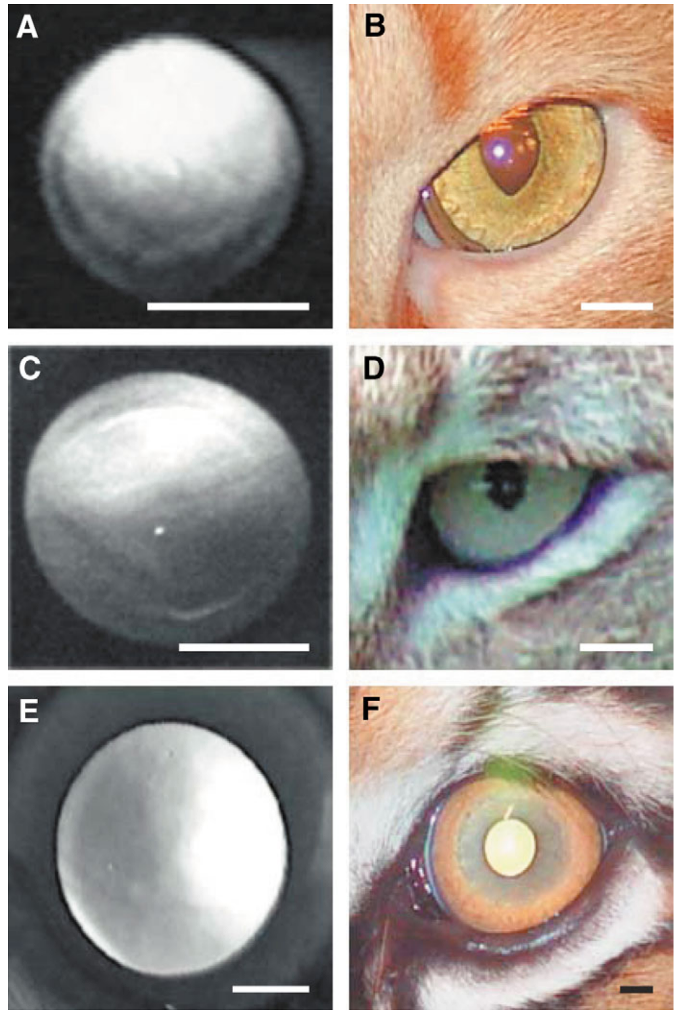

Fig. 5. The eyes of felids. The domestic cat (*Felix sylvestris domestica*; A,B) has a multifocal optical system (indicated by the ring-like structure in the photorefractive image) and a slit pupil. The Siberian tiger (*Panthera tigris altaica*; E,F) has a monofocal optical system (the photorefractive reflex has a smooth intensity gradient) and a circular pupil. The pupil appears slightly oval in both images because the tiger did not look at the camera. The photorefractive reflex is appearing sideways because the animal was lying on its side. The Eurasian lynx (*Lynx lynx*; C,D) has an eye of intermediate size and design. A faint ring-like structure is visible in the photorefractive image and the pupil is oval to rhomboid in shape. Scale bars are 5 mm.

Discussion

The origin of ring-like structures in videorefractive images

In our work, we have assumed that the observed structures in videorefractive images were caused by spherical aberration, a symmetrical monochromatic aberration. It has been shown that asymmetrical aberrations, such as coma, can also lead to structured videorefractive images (Campbell et al., 1995; Roorda et al., 1995). Nevertheless, we think that multifocal optical systems can be detected by eccentric videorefraction with excellent confidence, at least in the types of eye we have studied. Ring-like structures have only been observed in the eyes of animals active under low-light conditions. In such eyes, the lens is thick, in some cases almost spherical. Furthermore, its centre is close to the centre of curvature of the cornea (Vakkur and Bishop, 1963; Hughes, 1979; Campbell et al., 1982; Martin, 1983; Remtulla and Hallett, 1985). Asymmetrical aberrations should therefore play a minor role. Although asymmetrical aberrations are more likely to play a significant role in the eyes of diurnal species having high *f*-numbers and flat lenses, ring-like structures were not observed in such eyes. We therefore conclude that ring-like structures in videorefractive images are generally indicative of multifocal systems, although it cannot be excluded that there may be a few exceptions to this rule. Such rare cases, however, would not change the conclusions to be drawn from our results.

Lens optics and pupil shape

Our results indicate that multifocal optical systems are widespread among terrestrial vertebrates. In an earlier study, it was found that a number of fishes have multifocal lenses (Kröger et al., 1999). Taken together, these findings strongly suggest that correction of chromatic aberration by multifocal optical systems is common in vertebrates.

In our sample of terrestrial vertebrates, there were no species having slit pupils in combination with monofocal optical systems. The slit pupil therefore usually seems to be an adaptation to multifocal optical systems. However, there are exceptions to this general rule. Many cephalopods have horizontal slit (octopuses) or W-shaped pupils (some squids and cuttlefishes), despite the fact that most species are monochromats (Williamson, 1995). Even the firefly squid (*Watasenia scintillans* Berry 1911), one of a few cephalopod species known to have several visual pigments (Seidou et al., 1990), has a monofocal lens (Kröger and Gislén, 2004) and, interestingly, a circular pupil (Kinya Narita, personal communication). LCA is compensated for by a banked retina (Kröger and Gislén, 2004). In cetaceans, being monochromats (Peichl et al., 2001), the pupil often has a flat U-shape. In very bright light, two distinct pupillary openings remain (Dawson et al., 1979). Complex pupil shapes are present in a number of fishes (Walls, 1942). This indicates that multifocal optical systems are not the only possible reason for the evolution of non-circular pupils. Use as a focus indicator (Murphy and Howland, 1990), camouflage of the eye (Walls, 1942; Douglas et al., 2002) and optimization of the light path through the eye (Kröger and Kirschfeld, 1993) are some of the known reasons for the occurrence of unusual pupil shapes. Clearly, one cannot deduce from pupil shape alone whether or not an eye has a multifocal optical system.

It is also true that the circular pupil is usually correlated with a monofocal optical system. However, two of the species in our sample had multifocal optical systems and circular pupils (Table 1; Fig. 4). Such an eye design can be useful for animals with small eyes of limited spatial resolution or large eyes of intermediate *f*-numbers. If the pupil is fully dilated, depth of focus may be so short that several focal lengths are necessary. When the pupil constricts in response to increasing light intensity, depth of focus increases, such that a monofocal optical system may be sufficient. To test this hypothesis, one would have to create optical models of the eyes in question and investigate the sampling density of the retina. One would also have to know whether the animals use colour vision when their pupils are fully dilated. Such an investigation was beyond the scope of this study.

In addition to the animal groups examined in this study, there are birds with slit pupils, namely the *Rhynchops* genus of

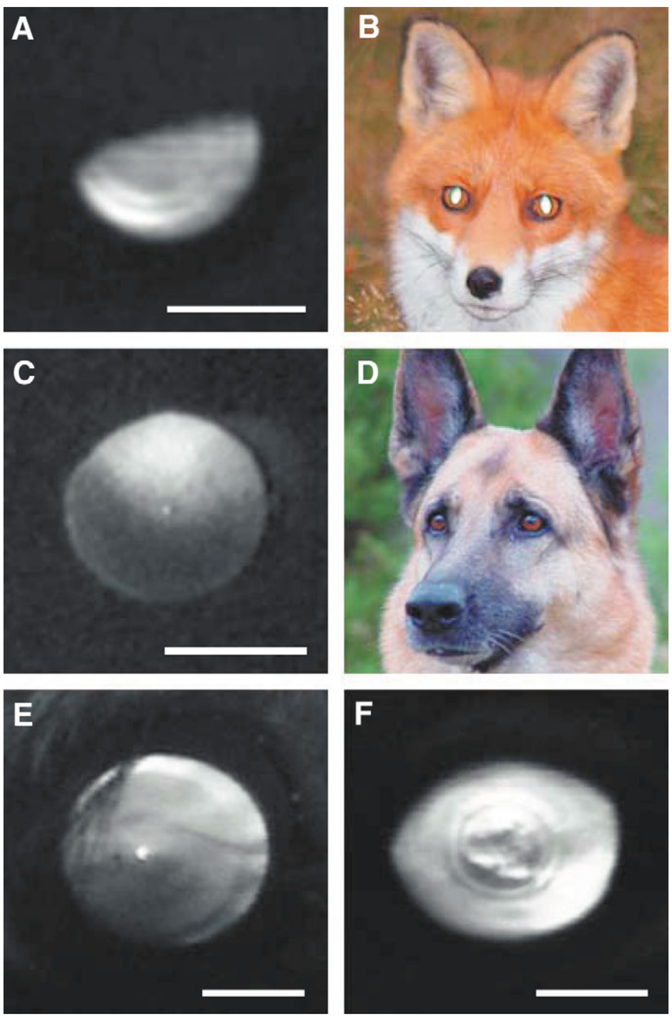

Fig. 6. The eyes of canines. The red fox (*Vulpes vulpes*) has vertical slit pupils and multifocal optical systems (A,B). Grey wolves and dogs (*Canis lupus lupus* and *Canis lupus familiaris*, respectively) have circular pupils (D). The status of their optical systems is unclear, because some dogs have smooth photorefractive reflexes (dachshund; C), while others have clear ring-like structures (giant schnauzer; E). All members of a group of four closely related tame wolves had a central region of irregularity in photorefractive images (F). Scale bars are 5 mm.

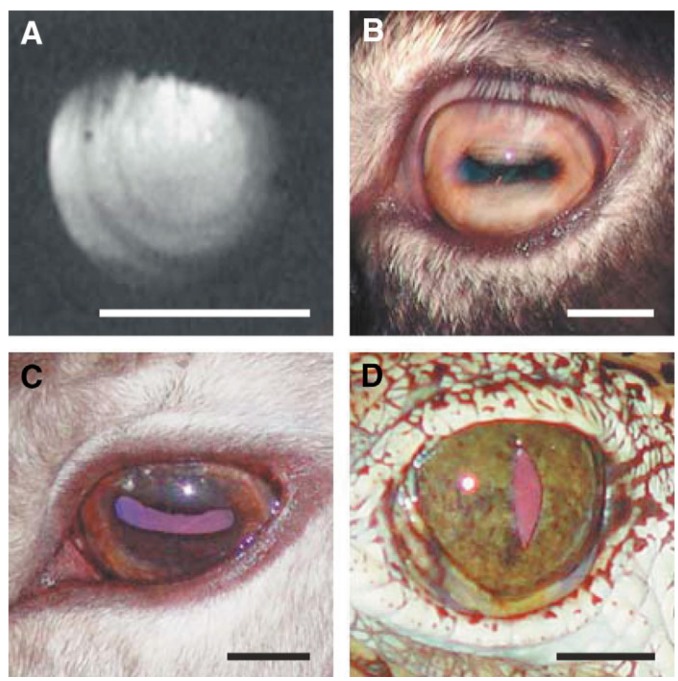

Fig. 7. Multifocal optical systems and slit pupils in large-eyed terrestrial vertebrates. Clearly visible ring-like structures were observed in photorefractive images of the eyes of domestic sheeps (*Ovis aries domesticus*; A) which have horizontal slit pupils (B). Similar pupil shapes were found in other artiodactyls, such as the reindeer (*Rangifer tarandus*; C). The Nile crocodile (*Crocodylus niloticus*; D) has a vertical slit pupil in combination with a multifocal optical system. Scale bars are 10 mm.

partially nocturnal, fishing birds (skimmers). Since birds are of the same descent as reptiles and most species have colour vision (Pichaud et al., 1999), the skimmers may also have multifocal lenses. We would very much welcome a study of these animals to which we could not get access. Skimmers have most likely descended from birds that had circular pupils and monofocal optical systems. It would therefore be highly interesting to know whether or not they have multifocal optical systems.

The results obtained from nocturnal prosimians indicate that the animals have multifocal optical systems, which in turn suggests that they are capable of colour vision. However, both studied species, the slow loris (*Nycticebus coucang*) and lesser bushbaby (*Galago senegalensis*), seem to have only one spectral type of cone (Wikler and Rakic, 1990; Tan and Li, 1999; Ahnelt and Kolb, 2000). Dichromatism by rod–cone interactions is unlikely, because the photorefractive images suggest the presence of three distinct refractive zones. The animals therefore may have hitherto undiscovered cone types. A more revolutionary idea is that several spectrally different types of rod may have evolved in nocturnal primates.

Evolutionary transitions

The occurrence of mono- and multifocal optical systems as well as circular and slit-shaped pupils in closely related species in a variety of phylogenetic groups indicates that transitions between these eye designs have occurred frequently and in short evolutionary times. This gives rise to the interesting question of whether multifocal optical systems have developed polyphyletically, i.e. independently several times during evolution. If so, one may ask whether the mechanisms controlling the refractive index profiles of the lenses are homologous and similar in all vertebrates or are also of polyphyletic origin and therefore different in various groups of vertebrates. It may be, however, that mono- and multifocal optical systems are manifestations of the same mechanism, i.e. optimization of the optical properties of the eye by feedback of information on image quality from the retina or brain to the lens and perhaps the cornea. This question could be answered by studying genetically manipulated animals that lack a visual pigment present in the wild type of the species.

Small eyes with multifocal optical systems and circular pupils (e.g. in the house mouse and beauty snake; Fig. 4) suggest that evolutionary transitions from multifocal systems combined with slit pupils to monofocal systems combined with round pupils, and *vice versa*, may have been achieved *via* small eyes of limited spatial resolution. However, our findings in cats suggest that transitions by gradual decrease of the differences in focal lengths as well as pupil asymmetry are also possible. It remains a puzzle how intermediate eye designs, such as in the Eurasian lynx, are optimally adapted to the needs of the animals.

Conclusions

Multifocal optical systems are common in the eyes of terrestrial vertebrates. In many, but not all cases, the slit pupil seems to be an adaptation to a multifocal optical system. Despite being complex organs, vertebrate eyes have undergone rapid evolutionary changes involving a variety of components. Several paths appear to be possible for evolutionary transitions between mono- and multifocal optical systems.

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