CHAPTER NINETEEN

The Tarsier Fovea: Functionless Vestige or Nocturnal Adaptation?

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THE FOVEA AND HAPLORHINE/ANTHROPOID ORIGINS

The retinal fovea is a specialization of the visual system that is widespread among vertebrates, but among mammals is restricted to haplorhine primates. All anthropoids have foveae, although that of *Aotus* the nocturnal owl monkey is morphologically distinct and appears to be degenerate (Webb and Kaas, 1976). The foveae of tarsiers are reported to be variably (Castenholtz, 1965 Woollard, 1925), or universally present (Hendrickson, personal communication). Foveae are occasionally present in galagos (one *Otolemur crassicaudatus* and one *Galago senegalensis* out of 18 animals [De Bruyn et al., 1980]) (Stone and Johnston, 1981), although they are less well developed. Reports of foveae in Lemuridae (*Lemur catta* and *Hapalemur griseus*, Pariente, 1975, 1979) are based on ophthalmoscopic investigations and remain to be confirmed using histological techniques.

The retinal fovea of tarsiers and anthropoids is of interest for the study of anthropoid origins because it may be a synapomorphy of a tarsier–anthropoid clade (Haplorhini) exclusive of other primates (Cartmill, 1980; Kay et al., 1997; Martin, 1990; Ross, 1996, 2001; Ross et al., 1998). As such, the fovea

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may tell us about the ecological context, particularly the diel periodicity (i.e., nocturnal or diurnal), in which haplorhines arose and diversified. Although most extant and all basal anthropoids are diurnal (Heesy and Ross, 2002; Kay and Cartmill, 1977; Kay and Kirk, 2000), both extant tarsiers and the likely sister taxon of the tarsier–anthropoid clade (omomyiforms) are exclusively nocturnal.[1] Consequently, the last common ancestor of tarsiers and anthropoids is most parsimoniously reconstructed as nocturnal (Heesy and Ross, 2001). In contrast, some workers hypothesize that the haplorhine fovea evolved in a diurnal lineage (Le Gros Clark, 1959). Cartmill proposed that the fovea evolved as an adaptation for improved visual acuity and that it persisted in the lineage leading to extant *Tarsius* when that lineage reverted to nocturnality (Cartmill 1980; Kay et al., 1997; Martin 1990; Ross, 1996, 2000). In support of this argument, a fovea is most often found in diurnal animals (Cartmill, 1980), tarsiers lack a tapetum, a structure typically present in nocturnal mammals, suggesting that the tarsier lineage lost its tapetum in a diurnal ancestor (Cartmill, 1980; Martin, 1973, 1979), and a fovea may be absent in some tarsier individuals (Castenholtz, 1965; Woollard, 1925).

This lack of consilience (Lee and Doughty, 1997) between the activity pattern optimized for the tarsier–anthropoid node (nocturnality) and that expected to be associated with the fovea also present at that node (diurnality), can be resolved in a number of ways. The functional and comparative arguments mustered by Martin and Cartmill might be incorrect. The haplorhine fovea may have arisen in a nocturnal environment (Figure 1B and D), be retained in extant populations of *Tarsius* because it confers an adaptive advantage under scotopic, or low light, conditions, and have been co-opted (or exapted) for the adaptive benefits it confers under the diurnal conditions under which most anthropoids live. Alternately, Martin and Cartmill's argument might be correct, the fovea may have arisen in a diurnal ancestor (Figure 1A and C), the fovea of extant tarsiers might have been co-opted (or exapted) for adaptive benefits it confers under nocturnal conditions, and the fovea of anthropoids might have been retained in extant anthropoids because of its adaptive value under diurnal conditions.

How to choose between these possible scenarios? If one could discriminate traits that are maintained in lineages by natural selection from those retained

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[1] Here I follow Ross et al. (1998) in excluding the diurnal form *Rooneyia* from Omomyiformes, instead placing it as Primates *incerta sedis*.
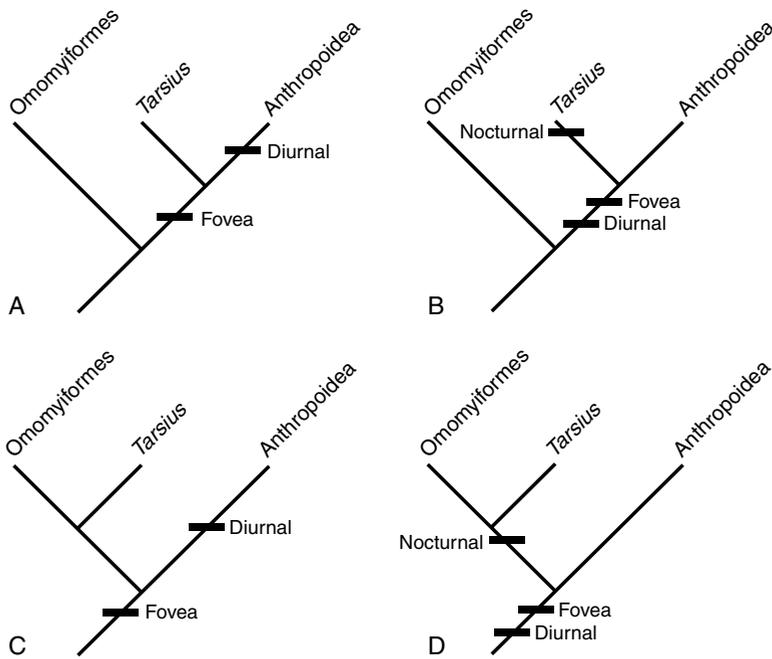
Figure 1. Cladograms of alternate hypotheses of haplorhine (anthropoid–tarsier–omomyid) relationships and the evolution of activity pattern and retinal fovea assuming that the primitive condition for Primates is nocturnal and afoveate. (A) Phylogeny advocated by Cartmill (1980), Martin (1990), Kay et al. (1997), Ross et al. (1998) with most parsimonious optimization of characters. (B) Same phylogeny as in A, but with character state evolution hypothesized by Cartmill (1980) and Ross (1996, 2000). (C) Alternate phylogeny similar to that advanced by some workers (e.g., Szalay and Delson, 1979) with *Tarsius* deriving from some omomyiform lineage. Most parsimonious pattern of character state evolution is illustrated. (D) Same phylogeny as in C but with diurnality, loss of tapetum and origin of fovea in stem lineage leading to the last common ancestor of tarsiers and anthropoids. This model assumes that Cartmill's evolutionary scenario is correct but his phylogeny is incorrect.

by "phylogenetic inertia," this question might be resolved. For example, if the anthropoid fovea evinces traits characteristic of "phylogenetic inertia" and the tarsier fovea appears to be adaptive, the "nocturnal origin" of both foveae and crown Haplorhini would be supported. Conversely, if the anthropoid fovea is adaptive and the tarsier fovea is "inertial," then "diurnal origins" of both foveae and crown Haplorhini are indicated. Traits indicative of phylogenetic inertia might include variable presence in the extant populations, lack of
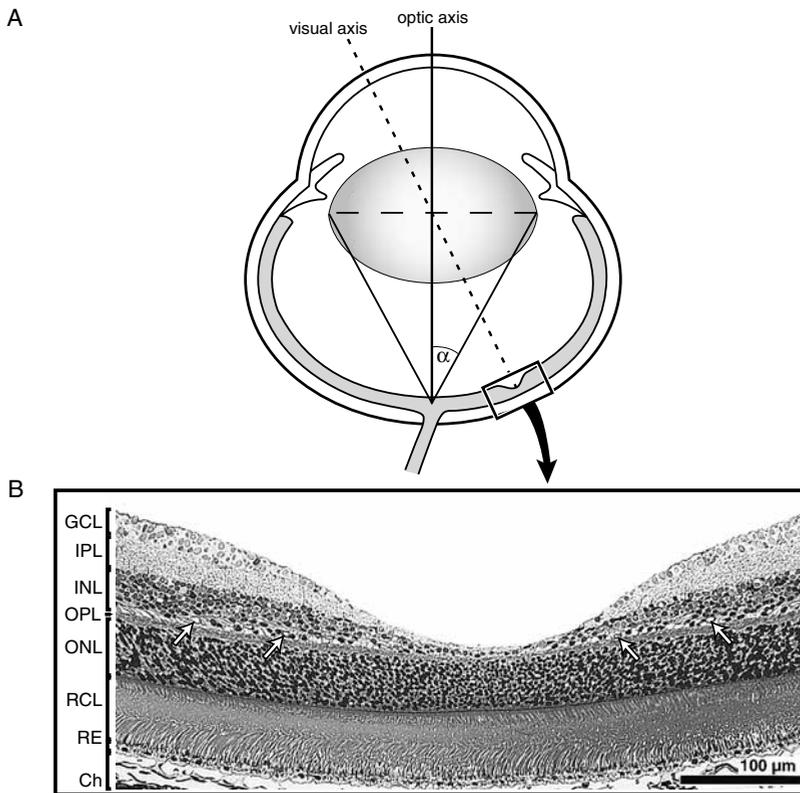
Figure 2. Diagram of anatomy of tarsier eye and retina. (A) Eye of *Tarsius*, redrawn from Castenholtz (1984). Angle α was calculated using the diameter of the lens and the distance from the center of the lens to the retina (Castenholtz, 1984). (B) Photograph of histological section of retina around and at the fovea of *Tarsius spectrum*. Abbreviations: Ch, choroid; RE, retinal epithelium; RCL, "rods and cones" layer; ONL, outer nuclear layer; OPL, outer plexiform layer; INL, inner nuclear layer; IPL, inner plexiform layer; GCL, ganglion cell layer; ILM, internal limiting layer. The adjectives used to describe their relative positions, inner and outer, refer to the direction of the vitreous and the choroid respectively. The outermost layer, adjacent to the choroid, is the nonneural *retinal epithelium*.[4] Moving towards the vitreous of the eye, the "*rods and cones*" layer contains the photosensitive outer segments of the photoreceptor cells, the rods and cones. The cell bodies of the photoreceptors lie in the *outer nuclear layer* (ONL) separated from the rods-and-cones layer by the *external limiting membrane*, the outer boundary of the neuroglial cells. The centrally (vitread) directed processes of the photoreceptors synapse on the axons and dendrites of the bipolar and horizontal cells in the *outer plexiform layer*

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[4] In humans this layer is called the retinal pigment epithelium (Williams and Warwick, 1980) but it is not pigmented in all vertebrates, so the more general term is preferred here.

plausible function, and functional "degeneracy," all of which have been argued to characterize the fovea of *Tarsius*. This chapter uses biomechanical data to determine whether the tarsier fovea has a plausible function.

Another way to choose between these scenarios is to use comparative data to determine whether foveae can arise in nocturnal lineages, or whether they always arise in diurnal lineages, as has been assumed (Cartmill, 1980; Ross, 1996, 2001). This chapter presents comparative data on the distribution of foveae among vertebrates and evaluates, using data on phylogenetic related-ness, whether foveae can arise in scotopically adapted lineages.

ANATOMY OF THE FOVEA

The vertebrate eye forms an image by refracting incoming light rays to bring to a focus on the retina all rays from a common source (Figure 2). The light rays reflected by the object of fixation are focused onto the retina at the visual axis, and it is at this point on the retina where a fovea is found in many verte-brates. The fovea of *Tarsius spectrum* is illustrated in Figure 2 (Hendrickson, personal communication). The fovea is usually characterized by a relatively high density of photoreceptors and ganglion cells, a pit in the inner layers of the retina, and the absence of intraretinal blood vessels.

The retina contains photoreceptor cells ("rods and cones") that transduce light energy into neural signals, first order neurons (bipolar cells), and interneurons (horizontal and amacrine cells) that combine and process the sig-nals from the photoreceptors, and second order neurons (ganglion cells) that relay these signals to the brain. Compared with other parts of the retina, the fovea exhibits increases in the density of photoreceptors and ganglion cells,

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Figure 2.   *Continued*

(OPL). The cell bodies for the bipolar cells and horizontal cells lie in the *inner nuclear layer* (INL) along with the somata of the amacrine cells. The bipolar and amacrine cells synapse on the ganglion cells in the *inner plexiform layer* (IPL), and the ganglion cell somata lie in the *ganglion cell layer* (GCL). The axons of the ganglion cells form the next layer, the *ganglion cell axon* or *nerve fiber layer*. The innermost layer, next to the vitreous, is the *internal limiting layer* or *membrane*, composed of terminal processes of retinal glial cells, a basement membrane, and collagen fibrils derived from the vitreous.
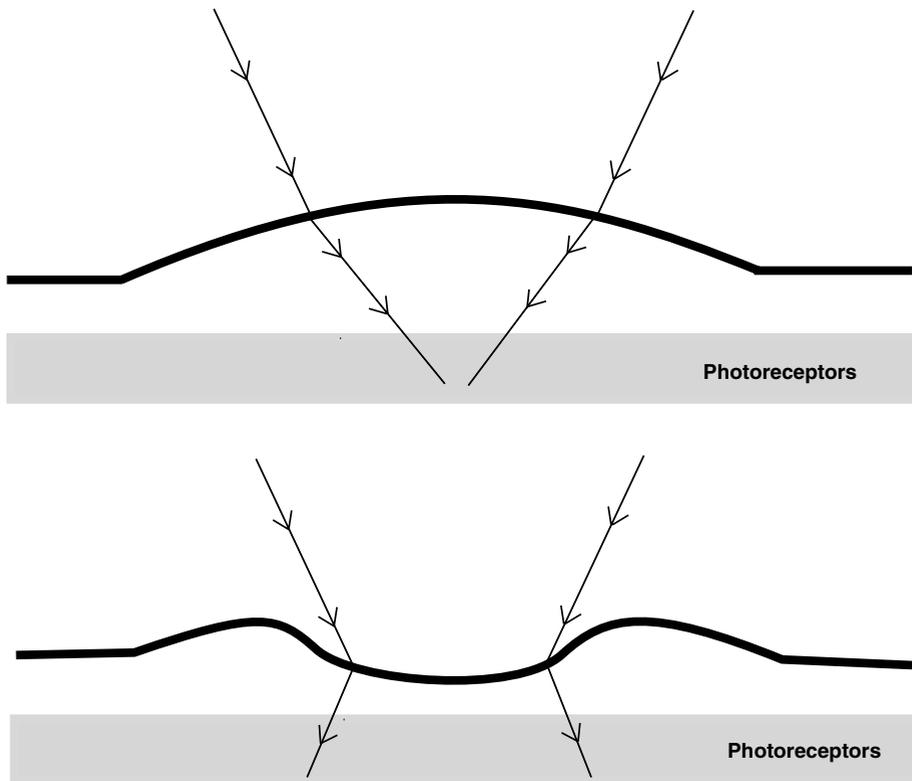
Figure 3. Diagrams illustrating function of the fovea according to Walls (1937). Top: Concentration of cells in the inner layers of the retina at the area centralis causes a doming of the retina. This would result in a refraction of incoming light rays such as to reduce image size. Bottom: The fovea reverses the direction of the light refraction, enlarging the image.

and in the ratio of ganglion cells to photoreceptors. This is true whether the foveal photoreceptors are predominantly cones, as in diurnal anthropoids such as humans and macaques (Curcio et al., 1990; Packer et al., 1989; Perry and Cowey, 1985; Wikler et al., 1990), or rods as in nocturnal *Aotus* (Ogden, 1974, 1975) or *Tarsius* (Hendrickson et al., 2000). In addition to being more numerous, the photoreceptors have a smaller diameter and are elongated, as has long been known for primates (Curcio et al., 1987; Hendrickson, 1992; Hendrickson and Yuodelis, 1984; Polyak, 1941; Rohen and Castenholtz, 1967). Also, in tarsiers and many anthropoids there are fewer short-wavelength sensitive cones (S-cones) in the fovea than in the parafoveal retina (Calkins, 2001; Hendrickson et al., 2000; Martin and Grünert, 1999).

Increases in photoreceptor density, ganglion cell density, and in the ganglion cell:photoreceptor ratio at the fovea suggest that the fovea functions to enhance visual acuity above and beyond that of the surrounding retina. This is true whether the photoreceptors involved are cones or rods, although rods do not afford as great an increase in acuity if they show high summation (i.e., many rods connected to few ganglion cells). The decrease in S-cones in the foveae of some primates also increases acuity by ameliorating the chromatic abberation that is particularly problematic at short wavelengths (Calkins, 2001) and in large eyes (Martin and Grünert, 1999).

The cells of the vertebrate retina are arranged in layers (Figure 2) (Rodieck, 1988), and the word *fovea* (Latin for "pit") refers to the depression in the retina caused by centrifugal displacement of the inner layers of the retina: The nerve fiber, ganglion cell, inner plexiform, and inner nuclear layers. In *Tarsius*, the inner nuclear layer is still present in the fovea, but is greatly thinned (Figure 2). Walls (1937) observed that increase in cell numbers in the inner retinal layers of the area centralis make the retina thickest there, doming the retinal surface into the vitreous, an effect that has been documented in *Lemur, Indri*, and *Propithecus* (Rohen and Castenholtz, 1967). Because the retina has a higher index of refraction than the vitreous (Steenstrup and Munk, 1980; Valentin, 1897; Walls, 1940), this doming of the retinal surface causes incoming light rays to be refracted ("bent") and to converge onto a smaller area, spreading the image over a smaller number of photoreceptors, decreasing visual acuity (Figure 3). Walls (1937) argued that the fovea counters this decrease in image size by spreading the image over a larger area (Figure 3).

Walls identified two shapes to the foveal pits of vertebrates: The concave-sided (concaviclivate) form seen in humans and other primates, including *Tarsius*, and the convex-sided (convexiclivate) form found in most birds and lepidosaurs (Figure 4). When Walls calculated the increase in image size associated with the two different fovea shapes he found that the amount of refraction associated with the concaviclivate form was insufficient to produce a significant increase in visual acuity, while the image produced by the convexiclivate form was significantly enlarged. Walls argued from this that the concaviclivate fovea was actually a degenerate form of the convexiclivate fovea and that all forms with concaviclivate foveae were descended from animals with convexiclivate foveae (Walls, 1940, 1942). Pumphrey (1948) took issue with Walls' interpretation of the function of the convexiclivate fovea. He demonstrated that the highly curved pit at the bottom of a convexiclivate fovea
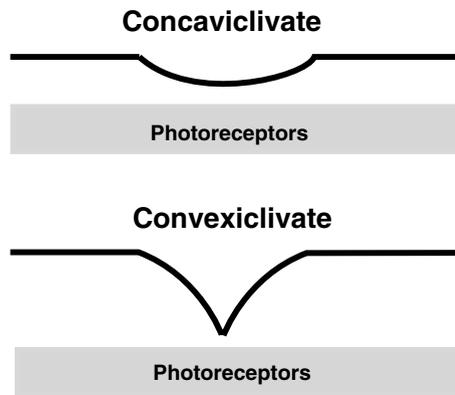
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Concaviclivate

Photoreceptors

Convexiclivate

Photoreceptors

Figure 4. Diagrams of convexiclivate (convex sided) and concaviclivate (concave sided) foveae.

severely distorts an image lying across it, arguing against Walls' assumption that the convexiclivate fovea is a superior version of the concaviclivate fovea. Pumphrey argued that the convexiclivate fovea transforms a "radially symmetrical image into an asymmetrical one except when there is exact coincidence between the axes of symmetry of the fovea and the object," facilitating "maintenance of accurate fixation." This effect results from the rapid changes in slope moving away from the center of the convexiclivate fovea. Because the degree of refraction of a light ray is in part a function of the slope of the interface between the vitreous and retina, rapid changes in fovea slope result in rapid changes in the "gain," or degree of displacement of a light ray where it strikes the rods and cones layer. Consequently, an image lying across a convexiclivate fovea will have different parts displaced to different degrees, depending on the slope of the fovea. Thus, only an image lying symmetrically across the fovea will be evenly distorted. As soon as an image moves away from this symmetrical position it will be distorted unevenly, thereby facilitating its fixation.

For these reasons, the convexiclivate fovea might also function as a movement or focus detector. Rapid changes in gain as a light ray moves across the convexiclivate fovea amplify movement of the cone of rays coming from the lens. This not only provides "sensitive appreciation of angular movements of a fixated object" (Pumphrey, 1948; p. 307) but also increases the apparent movement of the plane of focus, making the eye more sensitive to changes in focus. The convexiclivate fovea is an ideal focus detector because it only subtends a small part of the visual field, so it can perform its function without distorting the image over a broad extent of the visual field (Harkness and Bennet-Clark, 1978).

Notably, these mechanisms can work well in both scotopic (low light level) and photopic (diurnal) conditions (Harkness and Bennet-Clark, 1978; Locket, 1992), providing plausible explanations for the presence of convexiclivate foveae among animals living in dim light. Steenstrup and Munk (1980) have also suggested that the convexiclivate foveae of the deep-sea teleost family Notosudidae function to break camouflage of mesopelagic fishes using point sources of light to hide against the background illumination.

The third attribute common to most foveae is the absence of intraretinal circulation. Most foveate vertebrates (lepidosaurs, avians, many euteleost fishes) lack retinal circulation, their retinae being nourished from the choroid or directly from the vitreous humor. However, some fishes have blood vessels lying between the photoreceptor layer and the incoming light rays, either within the retina or between the retina and the vitreous, and mammals with thick retinae have two layers of blood vessels within the inner layers of the retina (Chase, 1982). Anthropoids divert this retinal circulation away from the fovea (Provis, 2001; Provis et al., 1998; Wolin and Massopust, 1970), tarsiers have been variably argued to have avascular (Hendrickson et al., 2000) or vascular (Rohen, 1966; Wolin and Massopust, 1970) foveae. Erythrocytes are thought to diffract light because of the iron attached to hemoglobin molecules, so it has been suggested that the lack of blood vessels in the fovea improves visual acuity (Weale, 1966). In support of this argument, the retinal blood vessels are not only deflected around the fovea in anthropoids, but also around the area centralis of other (afoveate) mammals (Rohen, 1966; Walls, 1942; Weale, 1966; Wolin and Massopust, 1970).

FUNCTIONAL ANALYSIS

Plausible hypotheses for the functions of convexiclivate foveae have been proposed and tested computationally (e.g., Locket, 1992), but the function(s) of concaviclivate foveae are less well understood. The anatomical bases of the hypothesized functions for convexiclivate foveae are the steepness of the walls of the fovea, the sharp reversal in the direction of curvature at the bottom of the fovea, and the refractive index of the vitreal/retinal surface. The refractive index of the vitreal/retinal surface is fairly constant across vertebrates (Steenstrup and Munk, 1980) but the slope of the foveal clivus and the shape of the bottom of the fovea vary widely. As Pumphrey (1948) noted, more gently sloping (concaviclivate) foveae without a sharp reversal at the bottom cannot be assumed to function like convexiclivate foveae. The functions

attributable to convexiclivate foveae may not be applicable to the foveae of haplorhines and other vertebrates. What then is the function of the tarsier fovea and of concaviclivate foveae in general? Specifically, does the fovea of *Tarsius* refract the incoming light rays enough for it to function as an image enlarger, focus indicator, or movement detector?

Functional Analysis Methods

If the tarsier fovea functions either to increase visual acuity by increasing the size of the retinal image, or enhances movement by amplifying it, then the retina must refract incoming light rays enough to produce gain equal to or greater than the highest spatial frequency unambiguously available to the visual system; that is, the Nyquist limit. The Nyquist limit (λ) can be related to the spacing between ganglion or photoreceptor cells by the formula

$$\lambda = \sqrt{3}a$$

where $a =$ intercell spacing in a hexagonal array. The Nyquist limit calculated from the receptive field center diameter of a ganglion cell in cats and macaques closely matches the limits of spatial resolution measured behaviorally (Wässle and Boycott, 1991), so it is reasonable to estimate the smallest spatial frequency discernable by the tarsier fovea using the formula for λ.

The intercell spacing of tarsier ganglion cells is unknown, but Tetreault et al. (this volume) report a peak ganglion cell density for *Tarsius syrichta* of 13,300/mm^2 near the fovea, suggesting a ganglion cell spacing of 0.75 μm. Corrections of foveal ganglion cell densities due to ganglion cell displacement in humans reveal higher effective ganglion cell densities in the foveola than on the foveal rim (Sjörstrand et al., 1999), suggesting that there might be even higher effective ganglion cell densities in the center of the tarsier fovea. Given that cone photoreceptors are separated by 2–3 μm, a ganglion cell spacing of 0.75 μm and higher in *Tarsius* suggests that more than one ganglion cell is connected to each foveal photoreceptor. If this is the case, then *Tarsius* resembles anthropoids in having cones in its fovea connected to more than one ganglion cell. Hendrickson et al. (2000, personal communication) report cone densities as high as 50–85,000 mm^2 at 50–100 μm from the fovea, suggesting that the "tarsier may have a steep cone gradient centered on the fovea, similar to diurnal primates" (Hendrickson et al., 2000, p. 727). At present, therefore, the most conservative estimate of the Nyquist limit of *Tarsius* is derived using the

photoreceptor spacing of primate cone cells. Curcio et al. (1990, p. 519) report a range of values for cone center–center spacing in humans ranging from 1.9–4.8 μm. These values yield Nyquist limits of 3.3–8.3 μm.

To calculate the increase in image size afforded by the fovea of *Tarsius*, the following parameters are required: (a) The degree to which incoming light rays are refracted as they pass over the retinal surface; (b) the distance from the vitreal retinal surface to the outer segments of the photoreceptors; and (c) the angle of incidence of the incoming light rays. Given these three parameters, we can calculate a parameter, called here *gain*, defined as the distance on the photoreceptor outer segments (at the inner limiting membrane) that a single light ray is deflected by the inner retinal surface.

(a) Refraction. Light is refracted as it passes across the interface between media of different optical densities. Passing from a less to a more dense medium, as in the case of the vitreous–retina interface, it is bent towards the perpendicular to the interface. Snell's law describes the relationship between the angle of incidence (Θ_1), the angle of refraction (Θ_2), and the indices of refraction of the two media (n_1 and n_2) as follows:

$$\sin\Theta_2 = \sin\Theta_1 * n_1/n_2 \tag{1}$$

The refractive index of the retina has not been measured in *Tarsius*, but Valentin (1879, in Walls, 1940, pp. 831–832) reported a range of values for mammals from 1.3407 in the green monkey, to 1.3460 in the dog, with a mammalian average of 1.34385 and the average of the green monkey and a baboon of 1.34265. The index of refraction of the vitreous in tarsiers is also unknown, but in humans it is around 1.336 (Duke-Elder, 1970). Assuming that the retina of *Tarsius* has an index of refraction of 1.343 and the vitreous an index of 1.336, the ratio of the refractive indices of vitreous:retina is 0.995 (Pumphrey, 1948; Valentin, 1879). Therefore Θ_2 can be estimated as

$$\Theta_2 = \arcsin(.995 \sin\Theta_1) \tag{2}$$

(b) Retinal depth. The contours of the vitreal surface of the retinal fovea were digitized from one published photograph of the fovea of *Tarsius bancanus* (Rohen and Castenholtz, 1967, Figure 8b) and from an image of the fovea of *Tarsius spectrum* kindly supplied by Dr Anita Hendrickson, University of Washington, Seattle, WA (Figure 2B). The digitized data consisted of "*x* values" and "*y* values" for points on the vitread surface of the fovea. In *Tarsius bancanus* the distance from the retinal surface to the "rods and cones" layer at

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the bottom of the fovea (100 μm) was calculated by subtracting the length of the photoreceptor outer segments (48 μm) from the thickness of the retina at that point (148 μm) (Rohen and Castenholtz, 1967). This "y value" was then applied to the lowest point in the digitized image and the remainder of the "y values" scaled accordingly. These values represent Y in Figure 5. For the other foveae included in this study, the scales of the images were calculated directly from the scale bars in the published figures.

   (c) Angle of incidence. An incident light ray that is perpendicular to the photoreceptor layer makes an angle of incidence (Θ_1) (relative to the perpendicular to the vitreal surface) of

$$\Theta_1 = \arctan f(x) \tag{3}$$

where $f(x)$ = the slope of the line connecting the digitized points (Figure 5). However, light arrives at the fovea in a cone. The maximum angles of the edges of a cone of light arriving at the retina can be estimated from measures of lens diameter and the distance of the center of the lens from the retina. Using data in Castenholtz (1984), $\alpha = 24.5°$ is the highest angle at which rays
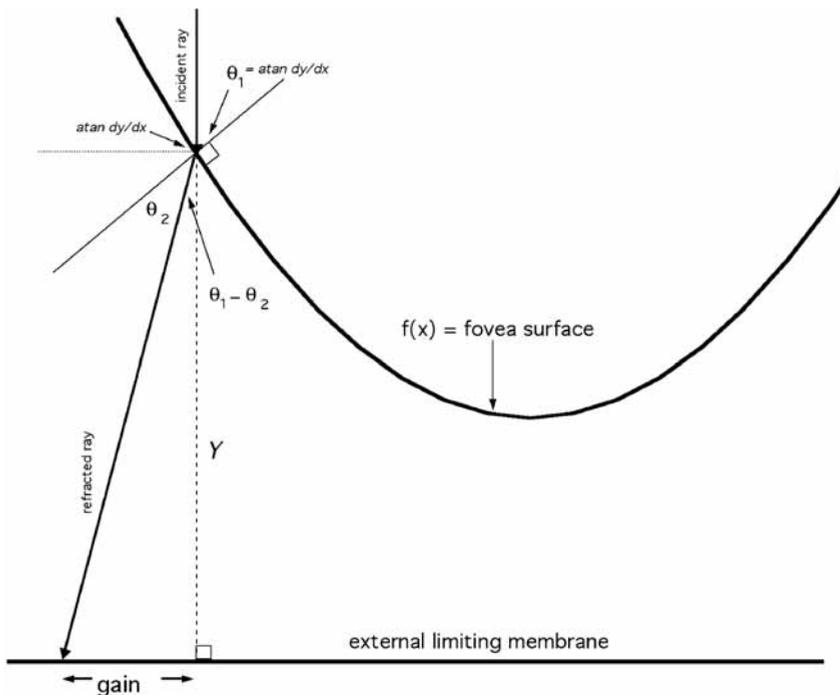

Figure 5.   Diagram illustrating method for calculating gain. See text for details.

of light can strike the fovea. If the gain for the perpendicular light rays is

$$\text{gain} = \tan(\Theta_1 - \Theta_2)\, f(x) \tag{4}$$

or, substituting Eq. (2) and (3) into Eq. (4), as

$$\text{gain} = f(x)\, \tan\{[\arctan f(x)] - [\arcsin(.995\,\sin(\arctan f(x))]\} \tag{5}$$

(See Figure 5), then the gain for the light rays at the periphery of the light cone can be calculated using the same formula, but adding 25° to the angle of incidence (Θ_1).

These calculations were performed on the digitized images of the foveae of *Tarsius bancanus* (Rohen and Castenholtz, 1967, Figure 8b) and *Tarsius spectrum* (Hendrickson, personal communication). For comparison, calculations were also performed for the foveae of some other vertebrates, including some primates with concaviclivate foveae and some birds and fish with convexiclivate foveae (Table 1). For vertebrates other than *Tarsius*, these calculations were made for light rays perpendicular to the retina only, for lack of precise estimates of the angle of incidence of rays coming through the periphery of the lens.

Results of Functional Analysis

The gains calculated for the fovea of *Tarsius spectrum* are plotted in Figure 6 and maximum values of gain for all foveae are given in Table 1. The maximum

Table 1.   Gain produced by fovea according to equation 5

Taxon	Gain (μm)[a]	
Tarsius spectrum	0.6	(1.33 at edge of light cone)[b]
Tarsius bancanus	1.52	(2.32 at edge of light cone)[b]
Cercopithecus nictitans	0.53	
Homo sapiens	0.30	
Strix aluco	1.12	
Asio otus	0.64	
Asio flammeus	1.35	
Tyto alba	0.22	
Alepocephalus bairdi	3.99	
Falco berigora (nasal fovea)	2.63	
Falco berigora (temporal fovea)	1.55	
Halcyon sancta (nasal fovea)	12.9	
Halcyon sancta (temporal fovea)	3.12	

[a]Highest absolute value of gain (rightward or leftward deflection of a light ray) for a
   ray of light perpendicular to the photoreceptor layer.
[b]Highest absolute value of gain (rightward or leftward deflection of a light ray) given
   by a ray of light arriving at the retinal surface at an angle of 25° to the perpendicular.
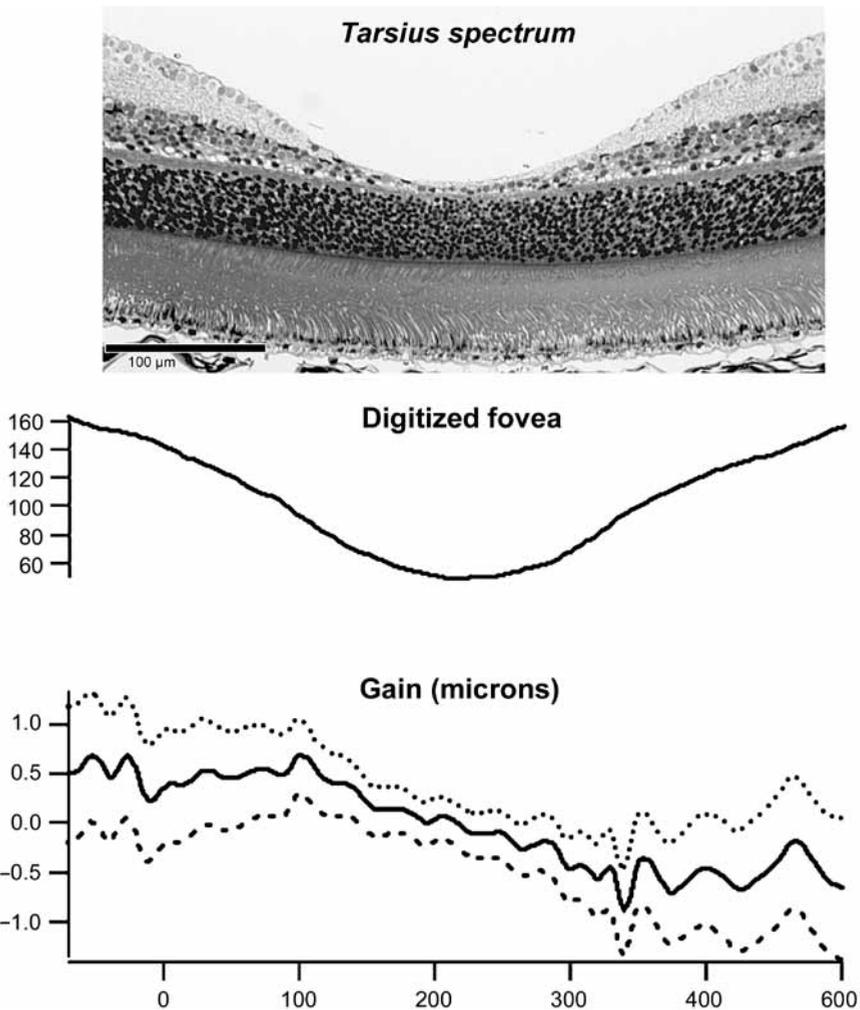
Figure 6. Results of gain calculations for *Tarsius spectrum*. Top: Image of fovea supplied by Dr A. Hendrickson. Middle: digitized outline of fovea. Light arrives at the retina in a cone with a maximum included angle of 50° (see text). Bottom: Plot of gain calculations for the three light rays defining the center and edges of the light cone. The solid line represents gain for incoming light rays at the center of the cone, the dotted and dashed lines the gains for the right and left edges of the cone. Gain is plotted at all positions along the fovea. Note that maximum gain is 1.33 μm.

gain produced in the tarsier fovea is 1.5 μm for the perpendicular rays, roughly 1.5 times the width of one photoreceptor. The maximum values obtained for the edges of the cone of light rays are 2.3 μm in *Tarsius bancanus* when the edge of the cone passes across the sloping side of the fovea. If the minimum detectable gain required for a detectable optical effect is 3.3–8.3 μm, then

tarsiers are not sensitive to the gain derived from foveal refraction. Notably, nor does this number exceed the limits of acuity demonstrated for diurnal macaques, suggesting that the gain produced by the tarsier fovea would be insignificant to tarsiers, even if they had the visual acuity of diurnal anthropoids.

Low gains are also seen in *Cercopithecus, Homo*, and the owls *Tyto, Asio,* and *Strix*, forms with shallow foveae with gently sloping walls. Without knowing maximal pupillary diameter and the distance from the lens center to the retina, precise values for maximal gain cannot be calculated. However, note that much higher gains are seen in the convexiclivate foveae of the kingfisher *Halcyon sancta*, the falcon, *Falco berigora*, and the deep-sea teleost, *Alepocephalus bairdi*.

COMPARATIVE ANALYSIS

Comparative Methods

The evolutionary hypothesis being tested is that foveae are most likely to arise in diurnal lineages and are retained in nocturnal lineages either by stabilizing selection or by some kind of unspecified constraint (Cartmill, 1980; Ross, 1996, 2000; Walls, 1942). To evaluate this hypothesis, data on the occurrence of foveae in vertebrates were gathered from the literature and are summarized in Tables 2–4. The activity patterns and/or habitats of foveate vertebrates and their close relatives are also supplied. Hypotheses about the sequence of evolutionary events can only be tested by mapping the distributions of character states onto phylogenies. The most recent phylogenies for the relevant groups were obtained from the literature. In one case (lepidosaurs) it was possible to apply Maddison's (1990) concentrated changes test to determine whether foveae are more likely to evolve in those parts of the trees that represent diurnal lineages. Because the number of changes involved in each tree is relatively small, Schluter et al.'s (1997) maximum likelihood approach was not required. The concentrated changes test requires full resolution of tree branching patterns, so polytomies were arbitrarily resolved.

Results of Comparative Analysis

Fishes: Eleven genera of bathypelagic fish (fish living below a depth of 1000 m) exhibit a fovea in an all-rod retina (Table 2). Numerous fishes living near the surface in photopic environments also exhibit foveae. Fishes therefore provide an excellent group in which to determine the probability of a fovea evolving in a "nocturnal" or scotopic environment.

Table 2. Occurrences of foveae and tapeta in Teleostei

Classification	Species	Retinal specializations	Recorded depth and diet	References
Elopocephala				
Elopomorpha				
Anguilliformes				
Serrivomeridae	*Serrivomer beani*	No fovea or area.	Epipelagic/ abyssopelagic (150–3000 m)	Collin and Partridge, 1996; Nicol, 1989
Synaphobranchidae	*Synaphobranchus kaupi*	No fovea or area.	Benthypelagic (400–4800 m); mobile piscivore	Collin and Partridge, 1996; Whitehead et al., 1986
Clupeocephala				
Euteleostei				
Protacanthopterygii				
Argentiniformes				
Argentinoidei				
Microstomatidae	*Nansenia groenlandica*	Temporal area, multiple banks of rods	Mesopelagic	Munk, 1966b
Microstomatinae				
Bathylagini	*Bathylagus benedicti, B. pacificus*	Concaviclivate temporal fovea, 6 banks of receptors in fovea, 3 elsewhere; pure rod retina	Epipelagic and mesopelagic; gelatinous predators (zooplanktonivores)	Vilter, 1954a, 1954c and Munk, 1966b, in Locket, 1977; Nicol, 1989; Gartner et al., 1997
	B. stilbius	No fovea, pure rod retina	Epipelagic	Munk, 1966b
Opisthoproctidae	*Bathylychnops exilis*	No fovea, pure rod retina	Epipelagic	Munk, 1966b; Weitzman, 1997
	Rhynchohyalus natalensis	No fovea, pure rod retina	Epipelagic and mesopelagic (down to 550 m)	Munk, 1966b; Weitzman, 1997
	Opisthoproctus grimaldii	No fovea, pure rod retina	Mesopelagic (200–600 m)	Munk, 1966b; Weitzman, 1997
	Winteria telescopa	No fovea, pure rod retina	Mesopelagic and Bathypelagic (500–1250 m)	Munk, 1966b; Weitzman, 1997

Alepocephaloidei				
Platytroctidae	*Searsia koefoedi*	Convexiclivate temporal fovea; pure rod retina	Mesopelagic (450–1500 m)	Marshall, 1966, in Locket, 1977, p. 173; Collin and Partridge, 1996
	Platytroctes apus	Convexiclivate temporal fovea; pure rod retina	Bathypelagic (seldom <900 m)	Collin and Partridge, 1996
	Platytroctegen mirus	Deep convexiclivate fovea; pure rod retina	Bathypelagic	Munk, 1966b, in Locket, 1977: 173
Bathylaconidae	*Bathylaco nigricans*	Deep convexiclivate fovea; pure rod retina.	Meso- and bathypelagic	Munk, 1968; Collin and Partridge, 1996
Alepocephalidae	*Bathytroctes microlepis*	Convexiclivate temporal fovea; pure rod retina	Engybenthic/ bathypelagic (1100–2700 m)	Collin and Partridge, 1996
	Bajacalifornia drakei	Convexiclivate temporal fovea; pure rod retina	—	Locket, 1985
	Rouleina attrita	No fovea; pure rod retina	Engybenthic (1400–2100 m); mucous predator	Collin and Partridge, 1996; Gartner et al., 1997
	Leptoderma macrops	Convexiclivate fovea; pure rod retina	—	Locket, 1977, p. 173, Figure 61
	Alepocephalus rostratus	Convexiclivate temporal fovea; pure rod retina	Engybenthic (300–3600 m); Macroplanktonivore, hover-and-wait	Collin and Partridge, 1996; Gartner et al., 1997
	Alepocephalus bairdi	Convexiclivate fovea; pure rod retina	Macroplanktonivore, hover-and-wait	Locket, 1992; Gartner et al., 1997
	Conocara murrayi	Convexiclivate temporal fovea; pure rod retina	Engybenthic (1200–2600 m), Diet unknown.	Collin and Partridge, 1996; Gartner et al., 1997
	Xenodermichthys copei	Convexiclivate temporal fovea, pure rod retina	Mesopelagic (100–1000 m)	Marshall, 1966, in Locket, 1977, p. 173; Collin and Partridge, 1996

Table 2. *Continued*

Classification	Species	Retinal specializations	Recorded depth and diet	References
Neoteleostei				
Stenopterygii				
Stomiiformes				
Sternoptychidae (hatchetfishes)	*Argyropelecus aculeatus, A. sladeni, A. olfersi*	No fovea	Mesopelagic zooplanktonivores	Munk, 1966b; Collin and Partridge, 1996; Gartner et al., 1997
	Sternoptyx	No fovea	Mesopelagic; zooplanktonivores	Gartner et al., 1997
Stomiidae	*Malacosteus niger* (incl. indicus?)	No fovea, tapetum	Mesopelagic; zooplanktonivore	Munk, 1977; Gartner et al., 1997
Aulopiformes				
Chlorophthalmoidei				
Chlorophthalmidae	*Chlorophthalmus albatrossis*	No fovea. Guanine tapetum	Down to 1440 m	Tamura, 1957 and Somiya and Tamura 1971 in Munk, 1977
Ipnopidae	*Bathypterois dubius* (tripodfishes)	No fovea. Yellow eyeshine	Benthic (750–950 m); - sit and-wait ambush micronekton feeder (copepods)	Collin and Partridge, 1996
	Ipnops murrayi	No fovea		Munk, 1959
Notosudidae	*Ahliesaurus berryi, Scopelosaurus hoedti*	All(?) cone retina; temporal convexiclivate fovea in cone area	Meso- and bathypelagic, hovering and darting predation	Nicol, 1989; Marshall, 1966, in Locket, 1977, p. 173; Munk, 1975
	Scopelosaurus lepidus	temporal convexiclivate fovea in cone area; rest of retina rods; retinal tapetum around groups of rods	Meso- or benthopelagic (745–650 m); zooplanktonivore	Munk, 1977

Alepisauroidei				
Alepisauridae	*Omosudis lowei*	Cone dominated retina. No fovea, Tapetum lucidum around each cone; no reflectors with rods	Bathypelagic (950–2500 m); active piscivorous micronectivores	Munk, 1965; Frederiksen, 1976 in Munk, 1977, p. 22; Gartner et al., 1997
Paralepididae	*Notolepis rissoi*	No fovea, tapetal cell sheaths	Mesopelagic; active piscivorous micronectivores	Locket, 1977, p. 167; Gartner et al., 1997
Evermannellidae	*Evermanella atrata*	No fovea, Tapetum lucidum	?Mesopelagic; active piscivorous micronectivores	Brauer, 1908 in Munk, 1977; Gartner et al., 1997
	Evermanella indica	No fovea	Mesopelagic; active piscivorous micronectivores	Munk, 1966b; Gartner et al., 1997
Scopelarchidae	*Scopelarchus güntheri, S. sagax, Benthalbella infans*	No fovea, *S. güntheri* tapetum lucidum	Mesopelagic (190–1855 m); active piscivorous micronectivores	Locket, 1971; Locket, 1977, p. 158; Munk, 1977; Gartner et al., 1997
	Scopelarchus michaelsarsi	No fovea	Mesopelagic (256–500 m); active piscivorous micronectivores	Collin and Partridge, 1996; Collin et al., 1998; Gartner et al., 1997
Ctenosquamata				
Myctophiformes				
Myctophidae	*Myctophum punctatum, Lampanyctus macdonaldi*	No fovea	Mesopelagic, migratory?; zooplanktonivores	Collin and Partridge, 1996; Gartner et al., 1997
Acanthomorpha				
Gobiesociformes				
Gobiesocidae	*Lepadogaster candollei*	Fovea		Vrabec, 1969 in Munk, 1975
Beryciformes				
Diretmidae	*Diretmus argenteus*	No fovea. Retinal tapetum	Mesopelagic (<1000 m)	Munk, 1966a
Gasterosteiformes				
Syngnathoidei				

Table 2. *Continued*

Classification	Species	Retinal specializations	Recorded depth and diet	References
Syngnathidae	*Entelurus aequoreus, Nerophis ophidion, Siphostoma fuscum, S. acus, S. tenuiorostris*	Fovea		Munk, 1975; Slonaker, 1897 in Munk, 1975; Krause, 1889; Verrier, 1928; Kahmann, 1936 in Munk, 1975
	Hippocampus hippocampus, H. ramulosus	Convexiclivate central fovea Fovea	Shallow water	Krause, 1886a in Locket, 1977, p. 173 Kahman, 1934, 1936; Kolmer, 1936; Rochon-Duvigneaud, 1943
	Syngnathus typhle	Temporal, asymmetrical, slit-like, convexiclivate fovea, (Two foveae according to Rauther, 1925)	Shallow water	Locket, 1977, p. 173
Scorpaeniformes Cottoidei Agonidae	*Agonus cataphractus*	Fovea		Kahmann, 1936 in Munk, 1975
Perciformes Percoidei Serranidae	*Serranus cabrilla, S. hepatus, S. scriba, Paralabrax clathratus, P. maculofasciatus, P. nebulifer*	Fovea	Predators of mobile prey	Verrier, 1928, Kahmann, 1936 Schwassmann, 1968 in Munk, 1975

Labroidei				
Labridae	*Coris julis, Julis lunaris, Pseudocheilinus hexataenia, Thalassoma pavo*	Fovea		Verrier, 1933; Kahmann, , 1934, 1936 in Munk, 1975
Scaridae	*Cryptotomus roseus*	Fovea		Ali et al., 1973, in Munk, 1975
Trachindoei				
Trachinidae	*Trachinus draco, T. vipera*	Fovea		Kahmann, 1934, 1936 in Munk, 1975
Blennioidei	—	—	Near shore, benthic	—
Blenniidae	*Blennius basiliscus, B. gattorugine, B. ocellaris, B. pavo, B. sanguinolentus, B. tentacularis*	Fovea	Benthonic, sit-and-wait ambush predator of invertebrates, small fish	Rochon-Duvigneaud, 1943
Clinidae	*Dialammus fuscus, Mnierpes macrocephalus*	Fovea	Amphibious fish specialized for amphibious vision	Munk, 1969; Graham and Rosenblatt, 1970; Graham, 1970, 1971 in Munk, 1975
	Clinus dorsalis, Malacoctenus hubbsi, Paraclinus sini	Fovea		Munk, 1971
Chaenopsidae	*Acanthemblemaria crockery, Chaenopsis alepidota*	Fovea		Munk, 1971
Pholidodidae	*Pholis gunnellus*	Fovea		Verrier, 1933; Kahmann, 1934, 1936 in Munk, 1975

Table 2. *Continued*

Classification	Species	Retinal specializations	Recorded depth and diet	References
Tetraodontiformes				
Balistoidei				

Balistidae	*Balistapus aculeatus,*
	  Balistes carolinensis
		Fovea		Kahmann, 1934, 1936 in
				  Munk, 1975

Ostraciontidae	*Ostracion cornutus,*
	  O. cubicus
		Fovea		Kahmann, 1936 in
				  Munk, 1975

Tetraodontoidei				
Tetraodontidae	*Tetrodon fluviatilis*	Fovea		Kahmann, 1934, 1936 in Munk, 1975

Notes: Definitions of habitat and dietary guilds primarily from Gartner et al. (1997). Information on Blennius from Munk (1971).
Benthic, fishes in physical contact with the bottom and not very mobile; Demersal, fishes spending most of time near bottom (<5 m) and moving actively over
it; Benthopelagic, pelagic forms that spend only part of life cycle near the bottom; Pelagic, midwater fishes; Epipelagic, species residing above 200 m;
Mesopelagic, species residing 200 m to 1000 m; Bathypelagic, species residing primarily below 1000 m.

The environments and diets of foveate fishes and their relatives are given in Table 2. Water attenuates light transmission in various ways and to various degrees depending on the optical properties of the water. However, under the best conditions the scotopic threshold lies at a depth of about 1000 m, below which down-welling light is not visible (Nicol, 1989), and in most circumstances, the mesopelagic environment may be considered scotopic as well. The phylogenetic relationships of fishes used here derive from Johnson and Patterson (1993, 1996; Baldwin and Johnson, 1996) and Stiassny et al. (1996).

Protacanthopterygii. Foveae are not reported in elasmobranchs (sharks, skates, and rays), non-tetrapod sarcopterygians, "chondrosteans" (Polypteriformes and Acipenseriformes), Ginglymodi (*Lepisosteus*), Haleocomorphi (*Amia*), or in basal teleosts Osteoglossomorpha, Elopomorpha, and Clupeomorpha. Among euteleosts, foveae first appear among the Protacanthopterygii, a monophyletic sister taxon to all other euteleosts (i.e., Eurypterygii, Esociformes, and other stomiiforms) (Johnson and Patterson, 1996). Protacanthopterygii consist of three groups, the Salmoniformes, Argentinoidei, and Alepocephaloidei, with the latter two united in the order Argentiniformes (Figure 7).

The phylogenetic relationships of basal euteleosts are presented in Figure 7 along with data on the presence/absence of foveae and the depths at which the fish are found (see also Table 2). Visual system data are available for three taxa that were not included in the most recent phylogenetic analysis (Johnson and Patterson, 1996). *Conocara* and *Xenodermichthys* are here placed at the base of the Alepocephalidae and *Platytroctegen* is placed in with the other platytroctids, *Platytroctes* and *Searsia*, in an unresolved trichotomy.

Among basal euteleosts, foveae appear to have evolved twice among argetiniforms: Once among alepocephaloids and once among argentinoids. All alepocephaloids that have been examined possess an all-rod retina and all possess a temporally positioned convexiclivate fovea except *Rouleina*, which exhibits a temporal area with a relatively high concentration of ganglion cells (Collins et al., 1996). Regardless of the phylogenetic positions of *Xenodermichthys, Conocara*, and *Platytroctegen* (and the retinal anatomy of the six unsampled genera) a temporally positioned convexiclivate fovea is a synapomorphy of the Alepocephaloidei. All but one genus of Alepocephaloidei is found in either the mesopelagic or the bathypelagic zones. Three genera are both bathy- and mesopelagic (*Searsia, Bathylaco, Leptochilichthys*), one genus (*Bajacalifornia*) ranges from the epipelagic through bathypelagic zones, and *Xenodermichthys*
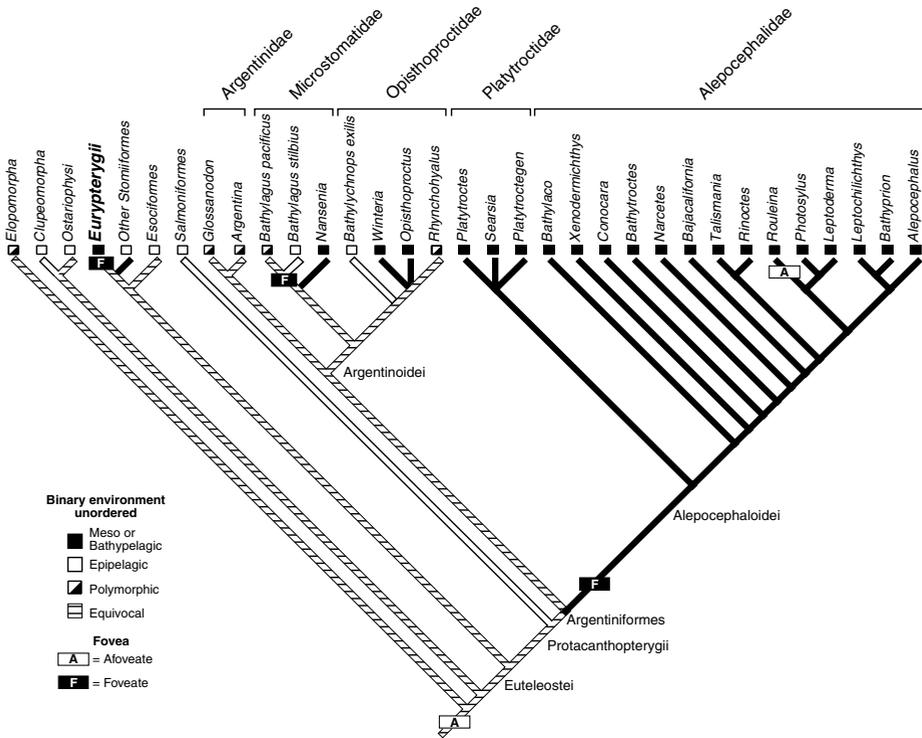
Figure 7. Phylogeny of euteleost fishes with environment mapped on the branches and most parsimonious hypotheses for gains and losses of foveae indicated with boxes. Note that foveae evolve twice more among Eurypterygii. See Table 4 for data.

is only recovered from between 100–1000 m. Thus, the stem lineages of Alepocephaloidei and Alepocephalidae were in possession of a convexiclivate fovea and either mesopelagic (200–1000 m depth) or bathypelagic (>1000 m).

Within the Argentinoidei, two species of *Bathylagus, B. pacificus*, and *B. benedicti* (*B. euryops*?) have been confirmed as possessing a temporally positioned concaviclivate fovea in an all-rod retina (Locket, 1977; Munk, 1966b; Vilter, 1954a,b). The retinae of the other seven bathylagine genera are unstudied. The only microstomatine microstomatid genus sampled, *Nansenia groenlandica*, is afoveate (Munk, 1966b). Five out of a total of six opisthoproctid genera have been sampled (*Opsithoproctus, Dolichopteryx, Rhynchohyalus, Winteria, Bathylychnops*), and they all lack foveae (Ali and Hanyu, 1963; Collin et al., 1997; Munk, 1966b). Among Argentinidae, *Argentina silus* lacks a fovea (Ali and Hanyu, 1963), and *Glossanodon* is unsampled. Thus, among the

Argentinoidei, a fovea has only been confirmed in the bathylagines. Argentinoids tend to reside slightly higher in the water column than ale-pocephaloids, being predominantly epipelagic and/or mesopelagic, although *Bathylagus* and opisthoproctids are sometimes recovered below 1000 m (Weitzman, 1997).

Thus, it appears that the fovea of the Alepocephaloidei evolved at least in a mesopelagic environment, and possibly a bathypelagic one. The bathylagine fovea evolved in either epipelagic, mesopelagic, or bathypelagic conditions. *Bathylagus* is sometimes recovered from bathypelagic depths. Where known, the argentiniforms are macroplanktonivores or zooplanktonivores (Table 2, data from Gartner et al., 1997), with many of their prey being bioluminescent (Herring, 1987). *Alepocephalus* feeds on gelatinous prey and incidental pelagic prey using a hover-and-wait strategy. The alepocephalids (slickheads) also exhibit marked expansion of their optic tectum (Wagner, 2001), suggesting that they may be classified as visual predators. The single exception is *Rouleina*, which may obtain organic detritus and tiny organisms from the water column by suspending mucous from the ventral and dorsal midlines, then ingesting the mucous with captured food particles (Gartner et al., 1997). It is notable that *Rouleina* is the only alepocephaloid genus that is not a visual predator and the only one lacking a retinal fovea.

The sister taxon of Argentiniformes, Salmoniformes, lives in a photopic environment but lacks any evidence of a fovea, although only 2 genera and 9 species have been sampled (Ali, 1959; Ahlbert, 1976; Beaudet et al., 1997; Schmitt and Kunz, 1989).

Euryptergians. Foveae appear again within the basal eurypterygians, the Aulopiformes. The optic specializations of 10 genera from the two largest families of Aulopiformes, the Chlorophthalmoidei and Alepisauroidei, have been studied, as have four genera of the closely related mesopelagic order, Stomiiformes. Among these taxa, only two genera, *Ahliesaurus* and *Scopelosaurus*, from the chlorophthalmoid family Notosudidae, have been shown to possess foveae. The third genus in this family has not yet been studied. The Chlorophthalmoidei consist of predominantly meso-bathypelagic predators with significant numbers of cones in the retina. The notosudids possess a temporally positioned convexiclivate fovea characterized by paired cones, in comparison with the grouped photoreceptors seen elsewhere in the retina. Foveae have not been reported among other Aulopiformes, or among Myctophiformes, suggesting that the foveae of acanthomorphs represent at

least a fourth case of independent evolution. However, only one myctophiform has been sampled and more data on the retina and the visual system in general are sorely needed for basal Neoteleostei (Wulliman, 1997).

Acanthomorpha. Among acanthomorph fishes, foveae have been documented in numerous taxa from various habitats, summarized in Table 2, but an exhaustive survey of retinal anatomy is lacking. For example, although one species of the Gobiesociformes has been reported to have a fovea (Table 2), it is not clear whether other Paracanthopterygii have been examined. No foveae have been reported for Beryciformes, but foveae are widespread among percomorph fishes. These foveae vary in shape, although some are documented to be convexiclivate, even among epipelagic fishes. At present it is impossible to determine whether a fovea is primitive for Acanthomorpha or not. Notably, nocturnal predatory acanthomorphs, such as Apogonidae (cardinal fishes) and Haemulidae (grunts) are not among those documented as possesing foveae, however, nor is it clear how well they have been sampled.

Summary of Fish Data. A fovea has evolved at least four times among fishes: A convexiclivate fovea evolved in the mesopelagic or bathypelagic stem lineage of Alepocephaloidei; a concaviclivate fovea was acquired in the mesopelagic or epipelagic stem lineage of *Bathylagus*; a convexiclivate fovea was gained once in the cone dominated retina of the epi-, meso-, and bathy-pelagic notosudid Chlorophthalmoidei; and foveae of either shape appear in several lineages of the Acanthomorpha. The convexiclivate foveae of ale-pocephaloids almost certainly evolved and were maintained in a lineage of scotopic visual predators. The concaviclivate foveae of bathylagine argentinioids may have evolved in a scotopic lineage, as all bathylagines have eyes specialized for scotopic environments, or in the epipelagic and photopic environment characteristic of bathylagines.

Lepidosauria: The distribution of foveae (Peterson, 1992), well-corroborated phylogenies (Estes and Pregill, 1988) and ecological studies (Vitt and Pianka, 1994) are available for lepidosaurs (Figure 8, Table 3). Lepidosaurs provide an interesting parallel with haplorhine primates. The distribution of activity period among extant squamates suggests that the squamate clade (lizards and snakes) was primitively diurnal, although their sister taxon is the relict nocturnal predator, *Sphenodon* (Figure 8). Isolated on tiny islands off the coast of New Zealand, *Sphenodon* is the only surviving remnant of a broader distribution of sphenodontians in the Mesozoic.

Table 3.   Occurrences of foveae and tapeta in Lepidosauria

Classification	Species	Retinal specializations	Habitat	References

Rhynchocephalia
  Squamata
    Iguania
      Iguanidae
	Sphenodon punctatus	Concaviclivate fovea	Nocturnal, ambush	Walls, 1942; Vilter, 1951

Iguanines	*Iguana iguana*	Fovea	Diurnal	Meneghini and Hamasaki, 1967, in Peterson, 1992
	Dipsosaurus dorsalis	Fovea	Diurnal, herbivorous	Peterson, 1981, in Peterson, 1992
Sceloporines	*Phrynosoma cornutum,*	Central convexiclivate fovea	Diurnal	Slonaker, 1897, in Munk, 1970; Detwiler and Laurens in Peterson, 1992
	Phrynosoma orbiculaire	Fovea	Strictly diurnal	Rochon-Duvigneaud, 1943
Anoloids	*Anolis spp.*	Temporal and nasal foveae, nasal more convexiclivate	Diurnal, sit-and-wait predators	Various authors, Peterson, 1992; Fite and Lister, 1981; Makaretz and Levine, 1980
Basliliscines	*Basiliscus plumifrons*	Fovea	Diurnal	Kahmann, 1923 in Rochon-Duvigneaud, 1943
Acrodonta Chamaeleonidae	*Chamaeleo*	Central convexiclivate fovea	Diurnal, sit-and-wait predators	Cajal, 1893, Johnson, 1927, in Peterson, 1992
Agamidae	*Agama tournevillii*	Convexiclivate fovea	Diurnal, sit-and-wait predators	Verrier, 1933
	Amphibolurus barbatus	Fovea	Diurnal, sit-and-wait predators	O'Day, 1939 in Peterson, 1992
	Physignathus leusieur	Fovea	Diurnal, sit-and-wait predators	Kahmann, 1923 in Rochon-Duvigneaud, 1943
	Uromastyx acanthinurus	Horizontal band-shaped area with fovea	Diurnal	Kahmann, 1936 in Munk, 1970.

Table 3. *Continued*

Classification	Species	Retinal specializations	Habitat	References
Scleroglossa				
Pygopodidae	*Delma, Lialis, Aprasia*	No fovea	Nocturnal, some diurnal activity	Underwood, 1970; Walls, 1942
Gekkonidae	—	—	—	—
Gekkonines	*Phelsuma spp.*	Fovea	Diurnal	Tansley, 1961, 1964 in Peterson, 1992; Pough et al., 1998
	Aristelliger cochranae	Fovea	Nocturnal/crepuscular	Underwood, 1970
	Other gekkonines	No fovea	Nocturnal/crepuscular	Underwood, 1970
Sphaerodactylines	*Sphaerodactylus*	Fovea	Diurnal	Underwood, 1970, in Peterson, 1992; Pough et al., 1998
	Gonatodes	Fovea	Diurnal	Underwood, 1970, in Peterson, 1992; Pough et al., 1998
Serpentes				
Colubridae	*Ahaetulla* (previously *Dryophis*)	Temporal concaviclivate fovea	Diurnal, arboreal predator	Rochon-Duvigneaud, 1943; Walls, 1942
	Dryophiops	Temporal concaviclivate fovea	Diurnal, arboreal predator	Walls, 1942
	Thelotornis	Temporal concaviclivate fovea	Diurnal, arboreal predator	Walls, 1942
	Oxybelis	Temporal	Diurnal, arboreal predator	Fite, personal communication

Scincomorpha				
Scincoidea				
Scincidae	*Trachydosaurus rugosus*	Horizontal band-shaped area with fovea	Diurnal, herbage, fruit, blossoms, snails, insects	Kahmann, 1936 in Munk, 1970; Kahmann, 1923 in Rochon-Duvigneaud, 1943
	Lygosoma (Leiolopisma) entrecasteauxii	Fovea	Diurnal, active predator	O'Day, 1939 in Peterson, 1992
Cordylidae	*Cordylus (Zonurus) giganteus*	Fovea	Diurnal, sit-and wait predator	Kahmann, 1923 in Rochon-Duvigneaud, 1943
Lacertoidea				
Xantusidae		Fovea lacking in most	Mostly nocturnal	Walls, 1942
Lacertiformes				
Lacertidae	*Eremias argus, Podarcis muralis*	Fovea	Most lacertids diurnal	Detwiler, 1923 in Peterson, 1992; Vilter, 1949
Teiidae	*Tupinambis sp.*	Horizontal band-shaped area with fovea.	Diurnal	Franz, 1934 in Munk, 1970.
Anguimorpha				
Varanidae	*Varanus griseus, V. niloticus*	Horizontal band-shaped area with fovea.	Diurnal, *V. niloticus* semiaquatic	Kahmann, 1933, 1936 in Munk, 1970. Kahmann, 1923 in Rochon-Duvigneaud, 1943
Helodermatidae	*Heloderma*	No fovea	Nocturnal and diurnal	

Notes: Squamates: Habitat and behavioral data come from Pough et al., 1998; Worell, 1966; Habitat and behavioral data on vine snakes are summarized by Henderson and Binder, 1980.

Among lepidosaurs, activity pattern is closely correlated with the presence
or absence of a fovea (Table 3). The presence of a fovea in *Sphenodon* and the
Iguania places a fovea in the squamate stem lineage and the last common
ancestor of lepidosaurs (Figure 8). However, the activity pattern of the lepi-
dosaurian stem lineage cannot be resolved without data on the fossil out-
groups as osteological correlates of activity pattern among lepidsauromorphs
have yet to be identified (Underwood, 1970). Among squamates the change
to nocturnality in gekkonines, Xantusidae, *Lanthanotus*, and helodermatids
was accompanied by loss of the fovea. Most nocturnal gekkos lack foveae, but
those gekkos that secondarily evolved diurnality also regained a fovea (Röll,
2001). Snakes also lacked a fovea primitively, probably because of a phase as
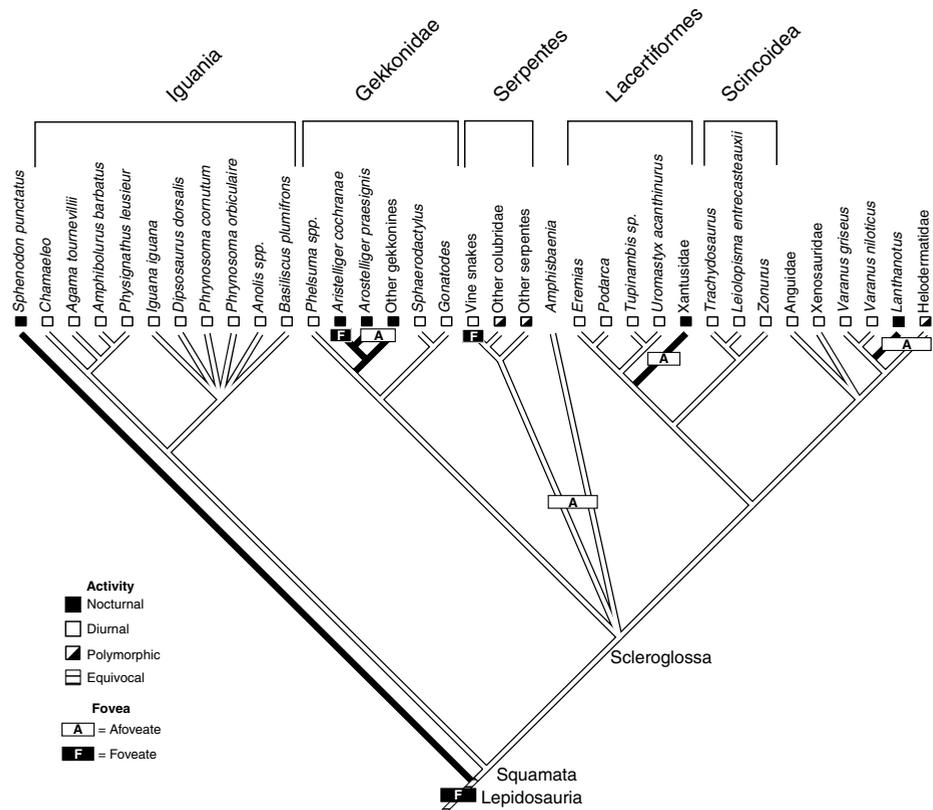burrowing animals (Figure 8). However, within Serpentes, several taxa

Figure 8. Phylogeny of Lepidosauria with environment mapped on the branches and
most parsimonious hypotheses for gains and losses of foveae indicated with boxes. See
Table 3 for data.

referred to as "vine snakes" have evolved a temporal fovea as an adaptation to arboreal predation (Walls, 1942; Fite, personal communication). Other adaptations to this lifestyle include a key-hole shaped pupil, an aphakic gap in some taxa (a similarity to bathylagine fishes), and a "siting" groove down the side of the snout which lines up with the fovea and aphakic gap (Henderson and Binder, 1980). By all accounts "vine snakes" is a polyphyletic assemblage (Henderson and Binder, 1980), suggesting that they evolved their foveae and other visual specializations independently.

One of the few comparative studies of ecological correlates of fovea shape is on anoline lizards (Fite and Lister, 1981). Anolines are the only non-avian vertebrates with two foveae in each eye, a convexiclivate central fovea and a more concaviclivate temporal fovea, as found in many predatory birds, particularly raptors. Fite and Lister report an inverse relationship between the steepness of the fovea centralis and prey size. The close correlation between activity pattern and fovea presence/absence and between ecology and foveal shape argue for the strong influence of selection on the fovea in lepidosaurs.

The correlated changes test was applied to determine the probability that the four gains and one loss of a fovea in diurnal lineages and three losses and one gain in nocturnal lineages could have occurred at random. This probability was found to be 0.00015. These results suggest a strong link between fovea presence and a diurnal activity pattern in lepidosaurs. However, in the absence of information on activity patterns of stem lepidosaurs, it is not possible to determine whether nocturnality or diurnality characterized their foveate last common ancestor.

Archosauria: When dealing with Archosauria the quality of the data varies and the limitations of a literature review must be acknowledged. Wood's (1917) data derive from ophthalmoscopic investigations only, which cannot definitively discern the presence or absence of foveae. Good histological cross sections for a variety of birds are provided by Rochon-Duvigneaud (1943), Oehme (1961), and Kajikawa (1923). Histological sections of bird eyes are also provided by workers on more restricted samples, such as Moroney and Pettigrew (1987), Fite and Rosenfield-Wessels (1975), and Reymond (1985, 1987). Sometimes the data provided are contradictory and/or the classification of the animals is in doubt. For example, Wood found no fovea for *Anas boscas*, whereas Rochon-Duvignead found a deep convexiclivate fovea for "*A. boschas*." In such cases the histological data were preferred.

Within Archosauria foveae have not been definitively reported outside of Aves. Munk (1970) reports Chievitz (1889, 1891) as attributing a fovea to

Crocodylus and *Alligator*, however, this interpretation is not accepted by Peterson (1992). Further histological examination of crocodyliforms is required before the primitive condition for archosaurs can be established.

Most birds possess foveae, and although the evidence for Palaeognathae requires confirmation with histology, Wood (1917) reports one in most of the taxa he examined. Thus, a fovea is likely to have been present in the last common ancestor of Aves. In fact, foveae were only reported to be absent in the Cape Penguin, *Spheniscus demersus*, several ducks and herons, some galliforms, some coots, two doves, a cockatoo, and the caprimulgiforms. Moreover, except in the case of caprimulgiforms and some galliforms where the reports are based on histological examinations (Pettigrew and Konishi, 1984; Pettigrew, personal communication), the absence of a fovea is based only on Wood's ophthalmoscopic investigations. Taking Wood's data at face value, these absences can be explained with reference to only six losses of foveae among birds: Once each in the ancestors of Sphenisciformes, Caprimulgiformes, and Galliformes, and once each within Columbiformes, Psitacciformes, and Gruiformes.

Many predatory birds actually possess two foveae in each eye: A concaviclivate fovea located temporally and subserving the binocular visual field, and a convexiclivate fovea centrally located and oriented into the monocular visual field. The functional hypotheses advanced by Pumphrey and that of Harkness and Bennet-Clark predict this distribution, given that binocular focus clues are not available in the monocular visual field. One might imagine that the convexiclivate fovea can be used to scan the world monocularly for movement indicating prey, whereas the concaviclivate fovea is used to improve acuity and depth perception in the binocular field, something vital for a bird attacking terrestrial prey.

Foveae occur in some nocturnal birds, but not others. Strigiformes (owls) and their probable sister-group, the Caprimulgiformes (goatsuckers, nightjars, frogmouths, potoos, and oilbirds), are active in the evening and at night. (Some owls are active during the day, such as the Snowy Owl, but data on its retinal morphology are incomplete [Wood, 1917].) A fovea has been confirmed in all owls that have been examined histologically (Table 4). Those nocturnal caprimulgiforms that have been examined lack a fovea (Pettigrew, personal communication). Strigiforms were classified with Falconiformes (diurnal raptors) for many years, a classification revived by Cracraft (1981), however, DNA hybridization studies place owls closest to the nocturnal

Table 4.   Occurrences of fovea and other retinal specializations in Archosauria

Classification	Species	Retinal specializations	Diel period	References
Crocodylia				
	Crocodylus intermedius	Horizontal band-shaped area with trough-like fovea (?)		Chievitz, 1889, 1891 in Munk, 1970; Underwood, 1970
	Alligator mississipiensis	Horizontal band-shaped area with trough-like fovea (?)		Chievitz, 1889, 1891 in Munk, 1970; Underwood, 1970
Aves				
Casuariiformes				
Casuariidae	*Casuarius occipitalis*	Fovea, Possibly a small slit-like fovea	"Somewhat nocturnal"	Wood, 1917; Kajikawa 1923; Feduccia, 1996
Struthioniformes				
Struthionidae	*Struthio camelus*	Fovea	Diurnal	Wood, 1917
Rheiformes				
Rheidae	*Rhea americana*	Fovea	Diurnal	Wood, 1917
Tinamiformes				
Tinamidae	*Rhyncotus rufescens, Calodroma elegans*	Fovea?		Wood, 1917
Apterygiformes				
Apterygidae	*Apteryx mantelli*	Fovea?	Nocturnal	Wood, 1917
Podicipediformes				
Podicipedidae	*Podicipes cristatus*	Macula and fovea	Diurnal	Wood, 1917
Sphenisciformes				
Spheniscidae	*Spheniscus demersus*	No fovea	Diurnal	Wood, 1917; Rochon-Duvigneaud, 1943

Table 4. *Continued*

Classification	Species	Retinal specializations	Diel period	References
Procellariiformes				
Procellaridae	*Puffinus griseus*	Linear fovea	Diurnal	Wood, 1917
Pelecaniformes				
Phalacrocoracidae	*Phalacrocorax carbo*	Deep wide fovea centralis	Diurnal, diver	Rochon-Duvigneaud, 1943
	Phalacrocorax penicillatus	Fovea centralis		Wood, 1917
Pelecanidae	*Pelicanus comspicillatus*	Fovea?		Wood, 1917
Sulidae	*Sula bassana*	Fovea?		Wood, 1917
Anseriformes				
Anatidae	*Anser cinereus*	Small, not very deep, elongate fovea	Diurnal	Kajikawa, 1923
	Anser domesticus	Shallow, round, small fovea centralis	Diurnal	Kajikawa, 1923
	Branta canadensis	No fovea?	Diurnal	Wood, 1917
	Anser caerulescens	Fovea	Diurnal	Wood, 1917
	Anas boschas	Deep fovea centralis	Diurnal	Rochon-Duvigneaud, 1943; Wood, 1917
	Anas boscas Dendrocygna autumnalis, Aix galericulata	No fovea	Diurnal	Wood, 1917
Phoenicopteriformes				
Phoenicopteridae	*Phoenicopterus roseus*	Slit-like fovea	Diurnal	Wood, 1917
Ciconiiformes				
Ciconiidae	*Mycteria americana*	Fovea	Diurnal	Wood, 1917

Ardeidae	*Ardea purpurea*	Deep fovea centralis	Diurnal	Kajikawa, 1923
	Ardea cineraea	Fovea centralis	Diurnal	Kajikawa, 1923
	Ardea occidentalis	No fovea	Diurnal	Wood, 1917
	Ixobrychus minutus	Fovea centralis	Diurnal	
	Nycticorax nycticorax	No fovea	Nocturnal	Wood, 1917
	Botaurus lentiginosus	Two foveae	Diurnal	Wood, 1917
	Cochlearius cochlearius	No fovea	Nocturnal	Wood, 1917
Threskiornithidae	*Plegadis falcinellus*	Fovea		Wood, 1917
	Platalea leucorodia	Fovea		Wood, 1917
Falconiformes				
Accipitridae	*Accipiter nisus*	Fovea	Diurnal	Kajikawa, 1923
	Accipiter nisus	Convexiclivate deep central fovea and shallower temporal fovea	Diurnal	Rochon-Duvigneaud, 1943
	Accipiter gentilis	Steep convexiclivate fovea centralis, more gentle convexiclivate fovea temporalis	Diurnal	Fite and Rosenfield-Wessels, 1975
	Aquila audax	Convexiclivate deep central fovea and shallower temporal fovea	Diurnal	Reymond, 1987
	Buteo buteo	Convexiclivate deep central fovea and shallower temporal fovea	Diurnal	Rochon-Duvigneaud, 1943
	Buteo latissimus	Two foveae	Diurnal	Wood, 1917
	Buteo jamaicensis	Steep convexiclivate fovea centralis, more gentle convexiclivate fovea temporalis	Diurnal	Fite and Rosenfield-Wessels, 1975
	Circus aeruginosus	Fovea centralis, no temporal fovea in several well-preserved eyes	Diurnal	Kajikawa, 1923
	Circus pratensis	Deep fovea centralis, free of rods	Diurnal	Kajikawa, 1923

Table 4. *Continued*

Classification	Species	Retinal specializations	Diel period	References
	Gypaetus barbatus	Bifoveate	Diurnal	Wood, 1917
	Haliaeetus leucocephalus	Fovea centralis (and nasalis?)	Diurnal	Wood, 1917
	Haliaeetus leucogaster	Two foveae	Diurnal	Wood, 1917
	Elanus scriptus	Bifoveate	Nocturnal	Pettigrew, personal communication
	Elanus notatus	Bifoveate	Diurnal	Pettigrew, 1983
	Milvus migrans	Convexiclivate deep central fovea and shallower temporal fovea	Diurnal	Rochon-Duvigneaud, 1943
Falconidae	*Falco sparverius*	Convexiclivate fovea centralis and temporalis	Diurnal	Fite and Rosenfield-Wessels, 1975
	Falco tinnunculus	Convexiclivate temporal fovea	Diurnal	Oehme, 1961
	Falco sparverius	Deep central fovea and shallower temporal fovea	Diurnal	Wood, 1917
	Tinnunculus alaudarius *Falco tinnunulus?*	Convexiclivate deep central fovea and shallower temporal fovea	Diurnal	Wood, 1917; Rochon-Duvigneaud, 1943
	Falco berigora	Convexiclivate deep central fovea and shallower temporal fovea	Hunts in bright daylight, dawn dusk and at night	Reymond, 1987
	Falco subbuteo	Convexiclivate deep central fovea and shallower temporal fovea	Diurnal	Rochon-Duvigneaud, 1943
	Astur plumbarius *Maybe Asturina*?	Distinct fovea centralis	Diurnal	Kajikawa, 1923
	Astur palumbarius	Convexiclivate deep central fovea and shallower temporal fovea	Diurnal	Rochon-Duvigneaud, 1943

Sagittariidae	*Sagittarius serpentarius*	Fovea centralis and temporal area	Diurnal	Wood, 1917
Galliformes				
Phasianidae		One convexiclivate fovea	Diurnal	Rochon-Duvigneaud, 1943
	Meleagris galloparvo	No macula or fovea	Domesticated	Wood, 1917
	Francolinus lathami	No fovea		Wood, 1917
	Coturnix histrionica	No macula or fovea		Wood, 1917
	Gallus domesticus	No macula or fovea	Domesticated	Wood, 1917
Numididae	*Guttera pucherani*	No macula or fovea	Domesticated	Wood, 1917
Cracidae	*Crax globosa*	No macula or fovea?		Wood, 1917
Gruiformes				
Rallidae	*Rallus aquaticus*	Fovea centralis	Diurnal	Kajikawa, 1923
	Fulica americana	No fovea?	Diurnal	Wood, 1917
	Fulica cristata	No fovea	Diurnal	Wood, 1917
	Aramides ipecaha	Fovea and macula	Diurnal	Wood, 1917
Rhynochetidae	*Rhynochetus jubatus*	Nasal fovea	Diurnal	Wood, 1917
Cariamidae	*Cariama cristata*	Two foveae?	Diurnal	Wood, 1917
Otididae	*Otis tarda, Tetrax tetrax*	Fovea centralis	Diurnal	Wood, 1917
Charadriiformes				
Charadriidae	*Vanellus*	Indistinct fovea centralis	Diurnal	Kajikawa, 1923
	Plover	Concaviclivate fovea	Diurnal	Rochon-Duvigneaud, 1943
	Squatarola squatarola	Fovea	Diurnal	Wood, 1917
	Oedicnemus scolopax	Fovea centralis	Nocturnal	Wood, 1917
Alcidae	*Cepphus columba*	Fovea	Diurnal	Wood, 1917
	Fratercula arctica			
Laridae	*Larus argentatus*	Deep, convexiclivate fovea centralis, concave temporal fovea	Diurnal	Wood, 1917; Kajikawa, 1923
	Larus canus	Distinct, streak-like central fovea (no second fovea in 6 eyes)	Diurnal	Kajikawa, 1923

Table 4. *Continued*

Classification	Species	Retinal specializations	Diel period	References
	Larus maritimus	Deep, elongated fovea	Diurnal	Kajikawa, 1923
	Larus ridibundus	Rather deep fovea centralis	Diurnal	Kajikawa, 1923
	Seagull	Fovea centralis as in "Sternes"	Diurnal	Rochon-Duvigneaud, 1943
Scolopacidae	*Gallinago*	Fovea centralis	Diurnal	Kajikawa, 1923
	Tringa totanus	Convexiclivate fovea centralis		Kajikawa, 1923
	Tringa melanoleuca	Large central fovea		Wood, 1917
	Numenius hudsonicus	Fovea		Wood, 1917
Sternidae	*Sterna albifrons*	Steep convexiclivate fovea centralis, more gentle convexiclivate fovea temporalis	Diurnal	Fite and Rosenfield-Wessels, 1975
	Sterna macrura	Fovea in frontal part of retina	Diurnal	Kajikawa, 1923
	Sterna minuta	Convexiclivate deep central fovea and shallower temporal fovea	Diurnal	Rochon-Duvigneaud, 1943
	Sterna hirundo	Two foveae		
Columbiformes				
Columbidae	*Columba domestica*	Fovea centralis, shallow, imperfect	Diurnal	Kajikawa, 1923
	Leucosarcia picata	No fovea or macula	Diurnal	Wood, 1917
	Columba palumbus	Faint, doubtful fovea	Diurnal	Wood, 1917
	Goura victoria	No fovea or macula	Diurnal	Wood, 1917
Psittaciformes				
Psittacidae	*Cacatua roseicapilla*	Fovea centralis	Diurnal	Kajikawa, 1923
	Cactua galerita	No fovea	Diurnal	Wood, 1917
	Chrysotis amazona	Fovea	Diurnal	Wood, 1917
	Strigops habroptilus	Temporal area, no fovea	Nocturnal	Wood, 1917

Apodiformes					
Apodidae	*Apus apus*	Well-developed fovea temporalis, weak fovea centralis	Diurnal	Walls, 1942	
	Swift	One shallow fovea	Diurnal	Rochon-Duvigneaud, 1943	
Caprimulgiformes					
	Podargus	No fovea reported	Crepuscular	Walls, 1942	
Caprimulgidae	*Goat suckers*	No fovea, tapetum in pigment epithelium	Crepuscular	Walls, 1942; Pettigrew, personal communication; Martin, 1985	
	Caprimulgus europaeus	No fovea?	Crepuscular	Wood, 1917	
Steatornithidae	*Steatornis*	No fovea	Nocturnal, cave living, echolocation	Pettigrew and Konishi, 1984; Walls, 1942; Feduccia, 1996	
Strigiformes					
Strigidae	*Bubo virginianus*	Gentle convexiclivate fovea temporalis	Nocturnal	Fite and Rosenfield-Wessels, 1975	
	Bubo bubo	Fovea temporalis	Nocturnal	Rochon-Duvigneaud, 1943	
	Athene cunicularia	Fovea temporalis	Nocturnal	Wood, 1917	
	Athene noctua	Fovea temporalis	Nocturnal	Rochon-Duvigneaud, 1943	
	Glaucidium radiatum	Gentle convexiclivate fovea temporalis	Nocturnal	Fite and Rosenfield-Wessels, 1975	
	Asio otus	Concaviclivate temporal fovea	Nocturnal	Oehme, 1961	
	Asio flammeus	Convexiclivate temporal fovea	Nocturnal	Rochon-Duvigneaud, 1943; Oehme, 1961	
	Strix aluco	Concaviclivate temporal fovea	Nocturnal	Wood, 1917; Oehme, 1961	
Tytonidae	*Tyto alba*	Shallow temporal fovea		Oehme, 1961	
Trochiliformes					
Trochilidae	*Calypta anna*	Two foveae	Diurnal	Wood, 1917	
Cuculiformes					
Cuculidae	*Coccyzus americanus*	One fovea		Wood, 1917	
	Cuculus canorus	One macula, fovea?		Wood, 1917	

Table 4. *Continued*

Classification	Species	Retinal specializations	Diel period	References
Coraciiformes				
Alcedinidae		Convexiclivate deep central fovea and shallower temporal fovea	Diurnal and partly aquatic	Rochon-Duvigneaud, 1943
European kingfisher	*Alcedo ispida*	Two foveae		Wood, 1917
Sacred kingfisher	*Halcyon sancta*	Convexiclivate deep central fovea and shallower temporal fovea	Diurnal and partly aquatic	Moroney and Pettigrew, 1987
Forest kingfisher	*Halcyon macleayii*	Convexiclivate deep central fovea and shallower temporal fovea	Diurnal and partly aquatic	Moroney and Pettigrew, 1987
Azure kingfisher	*Ceyx azureus*	Convexiclivate deep central fovea and shallower temporal fovea	Diurnal and partly aquatic	Moroney and Pettigrew, 1987
Laughing kookaburra	*Dacelo gigas*	Convexiclivate deep central fovea and shallower temporal fovea	Diurnal and partly aquatic	Wood, 1917; Moroney and Pettigrew, 1987
Blue-winged kookaburra	*Dacelo leachii*	Convexiclivate deep central fovea and shallower temporal fovea	Diurnal and partly aquatic	Moroney and Pettigrew, 1987
Upupidae				
Common Hoopoe	*Upupa epops*	Shallow fovea centralis	Diurnal	Wood, 1917
Meropidae—Bee-eaters				
Rainbow bee-eater	*Merops ornatus*	Convexiclivate deep central fovea and shallower temporal fovea	Diurnal, aerial feeder	Moroney and Pettigrew, 1987
Piciformes				
Picidae—Woodpeckers	*Picus minor*	Clearly visible fovea	Diurnal	Kajikawa, 1923
Green woodpecker	*Picus viridis*	Convexiclivate deep central fovea and shallower temporal fovea	Diurnal	Rochon-Duvigneaud, 1943

Northern wryneck	*Jynx torquilla*	Fovea centralis	Diurnal	Kajikawa, 1923
Red-shafted flicker	*Colaptes mexicanus*	Fovea centralis	Diurnal	Wood, 1917
Red-headed woodpecker	*Melanerpes erythrocephalus*	Fovea centralis	Diurnal	Wood, 1917
Great spotted woodpecker	*Dendrocopus major*	Convexiclivate deep central fovea and shallower temporal fovea	Diurnal	Wood, 1917; Rochon-Duvigneaud, 1943
Ramphastidae				
Sulphur-breasted toucan	*Ramphastos sulfuratus*	Temporal fovea	Diurnal	Wood, 1917
Passeriformes				
Corvidae—Crows				
Jay	*Garrulus glandarius*	Fovea centralis	Diurnal	Kajikawa, 1923
Jay	*Garrulus glandarius*	Convexiclivate deep central fovea and shallower temporal fovea	Diurnal	Rochon-Duvigneaud, 1943
Rook	*Corvus frugilugis*	Fovea centralis	Diurnal	Kajikawa, 1923
Rook	*Corvus frugilegus*	Convexiclivate deep central fovea and shallower temporal fovea	Diurnal	Rochon-Duvigneaud, 1943
	Corvus cornix	Convexiclivate deep central fovea and shallower temporal fovea	Diurnal	Rochon-Duvigneaud, 1943
Jackdaw	*Coleus monedula = Corvus monedula*	Fovea centralis within area	Diurnal	Kajikawa, 1923
Jackdaw	*Coloeus monedula = Corvus monedula*	Convexiclivate deep central fovea and shallower temporal fovea	Diurnal	Rochon-Duvigneaud, 1943
Raven	*Corvus corax*	Central fovea	Diurnal	Wood, 1917
American crow	*Corvus americanus*	Central fovea	Diurnal	Wood, 1917
Blue jay	*Cyanocitta cristata (and C. stelleri)*	Gentle convexiclivate fovea centralis	Diurnal	Wood, 1917; Fite and Rosenfield-Wessels, 1975
Black-billed magpie	*Pica pica*	Convexiclivate deep central fovea and shallower temporal fovea	Diurnal	Rochon-Duvigneaud, 1943

Table 4. *Continued*

Classification	Species	Retinal specializations	Diel period	References
Fringillidae—Finches				
Common (Red) Crossbill	*Loxia curvirostra*	Round, deep fovea centralis	Diurnal	Kajikawa, 1923
	Carduelis	Round, deep fovea centralis	Diurnal	Kajikawa, 1923
Brambling	*Fringilla montifringilla*	Fovea centralis	Diurnal	Kajikawa, 1923
Chaffinch	*Fringilla coelebs*	Fovea centralis	Diurnal	Kajikawa, 1923
Tyrannidae			Diurnal	Wood, 1917
Derby tyrant	*Pitangus derbianus*	Fovea		
Hirundinidae—Swallows			Diurnal	
Barn swallow	*Hirundo rustica*	Two foveae: centralis containing only rods, convexiclivate "fovea externa"		Wood, 1917; Kajikawa, 1923
Muscicapidae—Flycatchers			Diurnal	
	Muscicapa	Fovea centralis		Kajikawa, 1923
Bluebird	*Sialia sialis*	Bifoveate	Diurnal	Wood, 1917
Wheatear	*Oenanthe oenanthe*	Fovea centralis	Diurnal	Wood, 1917
Nectariniidae—Sunbirds	*Nectarina chalypea*	Convexiclivate fovea centralis	Diurnal	Fite and Rosenfield-Wessels, 1975
Paridae—True Tits			Diurnal	
Crested tit	*Parus cristatus*	Convexiclivate deep central fovea and shallower temporal fovea		Rochon-Duvigneaud, 1943
Laniidae				
California Shrike	*Lanius ludovicianus*	Bifoveate	Diurnal	Wood, 1917
Paradisaeidae				
Law bird of paradise	*Parotia lawii*	Nasal fovea	Diurnal	Wood, 1917
Passeridae—Sparrows			Diurnal	
Domestic sparrow	*Passer domesticus*	Deep fovea centralis		Kajikawa, 1923

Sittidae—Nuthatches			Diurnal	
Eurasian nuthatch	*Sitta europaea*	Convexiclivate deep central fovea and shallower temporal fovea		Rochon-Duvigneaud, 1943
Mimidae				
Western mockingbird	*Mimus polyglottos* and *M. orpheus*	Bifoveate	Diurnal	Wood, 1917
Sturnidae—Starlings				
European starling	*Sturnus vulgaris*	Convexiclivate fovea	Diurnal	Oehme, 1961
Turdidae—Thrushes				
	Turdus musicus	Fovea	Diurnal	Kajikawa, 1923
Blackbird	*Turdus merula*	Convexiclivate deep central fovea and shallower temporal fovea	Diurnal	Wood, 1917; Rochon-Duvigneaud, 1943

Kajikawa (1923) reviews the literature up to 1923. Primary references may be found there. Data from Kajikawa are obtained from a translation by Dr. B. Demes. Kajikawa describes the position of the area and the shape of the fovea; adjectives of mittel (average, medium); seicht (shallow); schwach (weak); tief (deep). Data in his table are not compatible with data in his text.

Caprimulgiformes. Irrespective of whether caprimulgiforms and owls are sister taxa or not, they are certainly descended from a diurnal ancestor which, like most birds, was probably diurnal and foveate.

The only other nocturnal birds exhibiting foveae are the Letter-winged kite (*Elanus scriptus*), the Stone plover ("*Oedicnemus scolopax*"), and possibly the kiwi (*Apteryx*) although histology is needed to confirm the latter two. The most notable example is that of *Elanus scriptus*, which is bifoveate and nocturnal (Pettigrew personal communication), with a diurnal bifoveate sister taxon, *Elanus notatus*. Several nocturnal birds have lost foveae: The American black-crowned night-heron (*Nycticorax nycticorax*), the Boat-billed night heron, *Cochlearius cochlearius*, and the New Zealand kakapo, *Strigops habroptilus*.

The concentrated changes test cannot be applied to the avian data because the phylogeny is too poorly known. Although further histological work on palaeognath retinae is needed, it would seem that a fovea was present in the last common avian ancestor. Whether this ancestor was diurnal or nocturnal cannot be established at present. Palaeognaths display an array of adaptions including nocturnality and crepuscularity and the activity patterns of stem avians have yet to be documented. The fovea has been lost in five lineages (Galliformes, Sphenisciformes, Columbiformes, and Caprimulgiformes, as well as within Psittaciformes), two of which are nocturnal and three of which are not. Possibly three lineages have retained foveae as they evolved from diurnal to nocturnal environments, their ancestors probably being diurnal, although for owls and kiwis this need not have been the case. In sum, it is not known whether the avian fovea originally evolved in a diurnal or a nocturnal lineage, but it is clear that a nocturnal environment is neither sufficient nor necessary to eliminate a fovea once established.

DISCUSSION

Functional Analysis

As noted above, hypotheses of foveal function invoke advantages of three features of foveae: High densities of photoreceptors and ganglion cells combined with a low ratio of ganglion cells to photoreceptors; a depression in the retina caused by centrifugal displacement of the inner nuclear, inner plexiform, ganglion cell, and nerve fiber layers (Figure 2B); and a lack of retinal circulation at the fovea.

Function of Increased Photoreceptor and Ganglion Cell Densities: All foveate vertebrates that have been examined show increases in the number of photoreceptors and ganglion cells at the fovea (Collin, 1999; Collin and Partridge, 1996; Fite and Lister, 1981; Fite and Rosenfield-Wessels, 1975; Munk, 1966). These concentrations, as well as the low ratio of photoreceptors to ganglion cells, make the fovea an area of enhanced visual acuity. Both photopic and scotopically adapted animals exhibit concentrations of photoreceptors and ganglion cells that serve as adaptations for enhanced acuity. For example, some deep-sea teleosts pack more rods into a smaller area of the retina by arranging them in multiple banks (Table 2). *Bathylagus benedicti* has six banks of rods at the fovea in comparison with three banks elsewhere in the retina, and the alepocephalid *Bajacalifornia drakei* has anywhere from 21 to 28 banks of rods at the fovea (Locket, 1985). Clearly these animals are attempting to maintain acuity while increasing retinal sensitivity. *Tarsius* evinces the highest peak ganglion cell density of any nocturnal primate (ca. 13,300 mm^2) (Tetreault et al., this volume), and very high cone densities around the fovea as well (50,000 mm^2 and 85,000 mm^2 in two individuals) (Hendrickson et al., 2000; Hendrickson, personal communication). This suggests that the tarsier fovea is also an area of enhanced visual acuity.

In the context of these adaptations for high acuity (high cone and ganglion cell densities relative to other nocturnal primates), the absence of a tapetum in *Tarsius* is expected. Tapeta increase sensitivity by reflecting photons back through the retina, but they also scatter light rays, degrading the retinal image and decreasing visual acuity. Consequently, if foveae are adaptations for high visual acuity, they are expected not to be associated with tapeta. For this reason caprimulgiforms are not only the only avians with a tapetum, but also one of very few lacking foveae. Indeed, across all vertebrates, a tapetum is only associated with a retinal fovea in *Scopelosaurus lepidus* (Tables 2, 3, 4). The lack of a tapetum in a highly visually dependent nocturnal animal like *Tarsius* is therefore expected. The hypothesis that the tapetum's absence is purely a primitive hold-over from a diurnal ancestor (Cartmill, 1980; Martin, 1979; Ross, 1996) need not be true.

Function of the Retinal Pit: The calculations made here suggest that the pit-shaped profile of the tarsier fovea does not produce visually detectable image enlargement or movement enhancement. The validity of this conclusion depends on the validity of several assumptions regarding the parameters used in calculating the pit's optical effect. There are three reasons to believe this

conclusion is robust. First, estimates of the parameters always erred in favor of the hypothesis that tarsiers have greater acuity than they probably do. Second, the tarsier fovea is morphologically similar to that of macaques, which have 3–4 ganglion cells per cone at the fovea, and a maximum behavioral visual acuity of 3.3 μm (Wässle et al., 1990). The maximum gain produced by the tarsier fovea was 2.3 μm, below values significant even to macaques, let alone a nocturnal animal with significant summation of photoreceptors to ganglion cells (Rohen and Castenholtz, 1967). The tarsier fovea—indeed, any shallow, concaviclivate fovea—cannot function to enhance movement or improve acuity in the absence of a detectable optical effect. Third, the human fovea is similar to that of *Tarsius* in the steepness of its clivus, and Walls (1940) found the gain produced by the human fovea to be functionally insignificant. Similar comments have been made about the shallow bathylagine fovea (Locket, 1985) and are probably valid for many owls as well (Table 1).

What then is the function of the concaviclivate fovea? Details on the optical properties of different layers of retinal tissues are scant and these studies have not separated the effects of cell bodies from those of capillaries. Ohzu and Enoch (1972) estimated the ability of the foveal retina to transfer an image by determining the modulation transfer function of isolated retinal tissues. The modulation transfer function (MTF) describes the changes (modulation) in quality of an image transferred by the retina at different spatial frequencies (Ohzu et al., 1972). Ohzu and Enoch (1972) calculated the MTF for a sinusoidally varying grating transferred by the foveal and parafoveal regions in freshly obtained retinal tissues of three humans. They found that the foveal region transferred the image better than the parafoveal region, evidence that Hughes (1977) cites in support of the hypothesis that the inner layers of the retina degrade image quality. Ohzu and Enoch also note that the MTF of the human fovea is better than that of the albino rat nonfoveal retina reported in Ohzu et al. (1972). However, measures of MTF are sensitive to the time elapsed since the retina was removed from the eye: The longer the retina is outside the eye, the worse its MTF. Moreover, the MTF of the fovea deteriorates slower than the surrounding tissues (Ohzu and Enoch, 1972), suggesting that the MTF of the human fovea might be better than the parafoveal region because it has deteriorated less postmortem.

The best data available on the optical properties of different regions of the human retina come from the laboratory of Jean-Marie Gorrand. Rather than passing an image through the retina, a technique limited to the ex vivo environment, Gorrand measured image quality by reflecting the image off the retina in vivo. He found the degree of light scattering in the retina to be least

at the fovea and to increase away from the fovea and the MTF to be highest at the fovea and to decrease away from the fovea (Gorrand, 1979). Subsequent work on two individuals confirmed that the MTF is higher on the fovea than off it, but that the mean irradiance (image brightness) is not consistently higher or lower off the fovea than on it (Gorrand, 1989).

Being based only on humans and only on a few individuals, these data cannot be indiscriminately applied to all vertebrates. However, they support the hypothesis that the concaviclivate fovea improves image quality by increasing the MTF and hence the quality of the image received by the photoreceptors. If these data are applicable to all vertebrates, then this is a plausible function for the gently sloping foveae of some primates (tarsiers and anthropoids), some lepidosaurs (including *Sphenodon*), and some birds, including owls.

Function of the Absence of Blood Vessels: Weale (1966) argued that the inner layers of the retina are not a significant impediment to acuity because they are highly transparent and are juxtaposed to the photoreceptors. He instead argued that the real impediment to high acuity vision came from the capillaries and the blood cells within them refracting and absorbing photons. Behavioral observations on humans and anatomical observations on *Macaca* and *Saimiri* suggest that the retinal vasculature might indeed be a significant impediment to high acuity vision in primates. Snodderly and colleagues (1978) used early eye-tracking technology to precisely map the position on the retina of images presented in different parts of the visual field. They found that subjects found it more difficult to see images presented to the parts of the visual field that projected onto the capillaries within the retina. Moreover, Adams and Horton (2002) recently noted that the blood vessels also cast a shadow on the projection of the visual field into primary visual cortex. This suggests that the blood vessels have the capability of significantly decreasing image quality or brightness. This result takes on special significance when we consider that on average 40% of the retinal surface area outside the fovea is obscured by blood vessels in *Macaca fascicularis* (Snodderly et al., 1992) and *Saimiri* (Snodderly and Weinhaus, 1990). This means that 40% of the photons reaching the photoreceptors have passed through and been refracted or absorbed by capillaries and the blood cells in them!

Comparative data support the hypothesis that blood vessels within the retina or on its vitread surface are an impediment to high acuity vision. All vertebrates except eels[2] have blood vessels in the choroid (choriocapilliaris) that

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[2] Eels have an intraretinal blood supply, like mammals, but possess neither an *area* nor a fovea.

supply the "rods and cones" layer from behind, but the largest distance over which oxygen can diffuse from the choriocapillaris is about 143μm (data from humans, Dollery et al., 1969). Thus, vertebrates with thicker retinae, or with retinal thickenings such as seen in areae centrales around foveae, need to augment retinal nutrition from the vitread side or within the retina. There are various ways of doing this.

In mammals retinal vascularization occurs between the layers of the retina, not on the surface, and is associated with retinal thicknesses over 143 μm (Chase, 1982). The retinae of some rodents, some bats, and some marsupials are avascular and must receive their nutrients from the choroid (Buttery et al., 1990). Primates have intraretinal vasculature (see Michaelson, 1954, Wolin and Massopust, 1970) except for the foveal region of haplorhines, which is avascular. *Tarsius bancanus* is reported to have capillaries in its parafoveal region (Rohen, 1966; Figure 2; Wolin and Massopust, 1970), although Hendrickson et al. (2000) report the *Tarsius spectrum* fovea to be avascular. The image of the fovea of *T. spectrum* supplied by Hendrickson reveals blood vessels lying in the outer edge of the inner nuclear layer (Figure 2B). Large caliber vessels are not seen within 350 μm of the center of the foveal pit, and small vessels can only be seen approximately 100 μm from the fovea center. Although these latter vessels are located within the retina underlying the sloping edges of the fovea, in a position similar to those reported by Wolin and Massopust (1970), the very center of the fovea (foveola) is devoid of blood vessels.

Some workers have argued that the lack of retinal vasculature in the mammalian fovea accounts for the absence of ganglion cells and interneurons in the fovea (Rodieck, 1988; Weale, 1966), implying that the pit itself does not have a function, but is merely an effect of the absence of blood vessels. Provis et al. (1998) refined this argument by suggesting that in anthropoids the foveal ganglion cell and inner nuclear layers migrate centrifugally toward the encroaching retinal vasculature because of the lengthening of the photoreceptor outer segments during ontogeny. Foveal photoreceptors are more densely packed than in the peripheral retina because they have smaller diameters and longer outer segments. As a result, the whole photoreceptor layer is thicker in the fovea than elsewhere in the retina. Photoreceptors are the principal consumers of oxygen from the choroid capillary bed (Provis et al., 1998, p. 575), so their increased numbers and increased length might be starving the inner layers of the retina of oxygen. Certainly mammals with thick retinae tend to have vascular retinae, whereas those with thin retinae are avascular (Chase,

1982), suggesting constraints on retinal thickness. Moreover, absolute fovea area is conserved across a wide range of body and eye sizes in anthropoids, even though this results in the fovea subserving a progressively smaller angle of the visual field with increasing eye size (Franco et al., 2000). This is also suggestive of a physiological constraint on fovea size (Franco et al., 2000).

In birds the retina is thicker than that of mammals (300μm), but there is no intraretinal circulation and no vessels traverse the retina at the vitread surface. The retina instead receives its nutrients from (in addition to the choroid) the vitreous, which is supplied by the pecten, a large vascular appendage projecting into the vitreous from the optic disk. To diffuse nutrients from the pecten, birds have evolved an unusual cyclotorsional component to saccadic eye movements (Pettigrew et al., 1990). The absence of blood vessels in front of the photoreceptor layer in birds seems to have encouraged the evolution of foveae. The same may also be true of lepidosaurs, among which foveae are widely distributed, and which resemble birds in lacking retinal vessels and manifesting a (nonhomologous) richly vascularized cone (conus papillaris) extending vitread from the optic disk. Among lepidosaurs, only snakes have blood vessels on the vitread surface of the retina. The relationship of these blood vessels to the fovea in "vine snakes" is unknown.

Thus, the comparative data suggest that high acuity vision, foveae, and blood vessels do not mix, but they also suggest that foveae can develop, as in birds and lizards, even in the absence of intraretinal blood vessels. This calls into question the hypothesis that the foveal pit develops merely as an effect of the absence of blood vessels (Provis et al., 1998). It also suggests that birds, lizards, and therefore possibly primates, derive some benefit from centrifugal displacement of the inner retinal layers, whether or not this is associated with exclusion of blood vessels from the fovea. Finally, it is noteworthy that among teleosts, the relationship of the vitreal circulation to the fovea has only been reported in one taxon, the sandlance, *Limnichthyes fascaitus*, in which the convexiclivate fovea is richly vascularized (Collin and Collin, 1988a, 1988b).

Comparative Analysis

The comparative analysis reported here evaluated the hypothesis that foveae typically arise among diurnal forms. Given the likely functional differences between convexiclivate and concaviclivate foveae, it is necessary to distinguish between them.

Foveae have arisen in four lineages of teleost fishes. The mesopelagic or bathypelagic stem lineage of Alepocephaloidei evolved a convexiclivate fovea; the mesopelagic or epipelagic stem lineage of *Bathylagus* evolved a concaviclivate fovea; and the epi-, meso-, and bathypelagic notosudid Chlorophthalmoidei acquired a convexiclivate fovea as an adaptation to scotopic vision (Steenstrup and Munk, 1980). Foveae are widespread among the Acanthomorpha but a lack of precise morphological data on fovea shape and poor sampling in most taxa renders definitive conclusions impossible. Wulliman (1997) has postulated that there was a rearrangement of the visual brainstem at the origin of acanthomorphs concomitant with their invasion of reef habitats in the Late Cretaceous. Possible links between these brainstem arrangements and retinal anatomy remain to be explored. In sum, among fishes convexiclivate foveae have evolved in low light levels, with a convexiclivate fovea being strongly associated with a scotopic environment. The concaviclivate foveae of bathylagines may have arisen in either a scotopic or photopic environment.

Among lepidosaurs there is a strong link between the presence of a fovea and a diurnal activity pattern. Several nocturnal lineages lose foveae; gekkos reevolve one on returning to diurnality (Röll, 2001). In the absence of information on activity patterns of stem lepidosaurs, it is not possible to determine whether nocturnality or diurnality characterized their foveate last common ancestor.

Among archosaurs, a nocturnal environment is neither sufficient nor necessary to eliminate a fovea once it is established. A fovea was probably present in the last common avian ancestor although it is currently impossible to determine whether this ancestor was diurnal or nocturnal. Palaeognaths display an array of adaptions including nocturnality and crepuscularity, and histological work on palaeognath retinae is needed.

Among primates, crown group haplorhines (tarsiers and anthropoids) have foveae, but tarsiers are dedicated nocturnal animals and anthropoids are predominantly diurnal. The probable outgroup to the tarsier–anthropoid clade, the Omomyidae, was wholly nocturnal,[3] as the stem lineage of primates probably was. The most parsimonious reconstructions of character state evolution among tarsiers, anthropoids, and omomyids have the fovea arising in a nocturnal lineage (Figure 1).

Overall, the comparative data suggest that convexiclivate foveae can arise in either diurnal or nocturnal lineages. However, it is noteworthy that there is

[3] *Rooneyia* is not an omomyid (Kay et al., 1997; Ross et al., 1998).

no instance in which a concaviclivate fovea of the kind possessed by haplorhines definitively evolved in a scotopic setting. Those scotopically adapted vertebrates that have gently sloping foveae (*Tarsius*, *Sphenodon*, Strigiformes) are all sister-groups to diverse radiations of diurnal visually adapted animals, providing some support for Cartmill's (1980) hypothesis.

The Function of the Tarsier Fovea

What then is the function of the tarsier fovea? The high concentration of cones and ganglion cells, the high ratio of ganglion cells to photoreceptors, the exclusion of blood vessels from the foveola, and the lack of a tapetum are arguably adaptations for increased visual acuity related to sit-and-wait ambush predation. *Tarsius* and owls share many features cited as adaptations to nocturnal sit-and-wait ambush predation, including large eyes protruding from the skull; a long olfactory tract displaced dorsally by the enlarged orbits; a well-developed auditory apparatus used for locating prey; loss of optic mobility with concomitant increase in cervical mobility; and enlarged semicircular canals (Niemitz, 1985). To these might be added the presence of postorbital ossifications to deflect jaw adductors around the orbital contents (Ross, 1996, 2000), and concaviclivate retinal foveae.

Although the comparative data suggest that the concaviclivate foveae of owls, tarsiers and tuataras are useful in nocturnal settings, recent observations suggest that tarsiers might be active in light levels supporting cone vision. Gursky reports that in contrast with most nocturnal mammals, spectral tarsiers increase their activity levels on moonlit nights (1999). Hendrickson et al. (2000, p. 729) report:

"Recent behavioral observations of *T. spectrum* in the large home cages of their colony at Bogor find that they become active several hours before sundown, are relatively quiet in the middle of the night, and then active again just before and after dawn (D. Sajuthi, personal communication). Light intensities in the tropics during these hours are high enough to support cone vision."

These observations suggest that although tarsiers are nocturnal in the sense of being active at night, they may be adapted to function in light levels in which their cone rich foveae can provide relatively high acuity vision. Likely adaptations for these conditions include cone densities as high as 50–85,000 mm^2, a fovea, no tapetum, and relatively high degrees of orbital convergence. Given that these features also perform the same functions in extant anthropoids, it is reasonable to hypothesize that they were also present

in the last common ancestor of tarsiers and anthropoids. Whether or not that animal was nocturnal or diurnal, it was adapted for activity in high light levels.

CONCLUSIONS

The increase in photoreceptors, ganglion cells, and the ganglion cell:photoreceptor ratio in the tarsier fovea, and the lack of a tapetum behind it, argue for a role in improving visual acuity. The fovea does not provide a demonstrable increase in image size, nor does it provide significant gain for movement detection. Blood vessels are found in the periphery of the tarsier fovea, but not in the foveola, supporting the hypothesis that the fovea is related to exclusion of blood vessels from the foveal region. It is therefore plausible that the fovea (and lack of a tapetum) function to improve image quality by displacing inner layers of the retina and blood vessels away from the path of incoming light. Although this effect is of uncertain significance for scotopically adapted animals like tarsiers with extensive summation of photoreceptors to ganglion cells, the comparative data do indicate that shallow foveae with gently sloping sides are found in scotopically adapted visual predators, particularly of a sit-and-wait ambush variety: That is, owls, tuataras, bathylagine argentinioids, and tarsiers. These animals might profit from the thinning of the foveal retina, because it removes either cells, blood vessels, or both from the inner retinal layers, thereby improving image quality. More and better data are needed on the optical properties of the retinae, and on the distribution and size of blood vessels in the foveal regions of these animals. In addition, Woollard (1925) and Castenholtz (1965) both report that not all tarsiers have a fovea. More data are needed on the prevalence of foveae among living tarsiers, sphenodons, slickheads, and owls.

The comparative evidence does not corroborate Walls' hypothesis that foveae only arise with a convexiclivate shape and are only concaviclivate as degenerate "primitive retentions." Rather, concaviclivate foveae can appear *de novo*. However, the comparative data do support the hypothesis that concaviclivate foveae are most likely to evolve in diurnal lineages: There are no definitive instances of concaviclivate foveae arising in a nocturnal lineage, as, tuataras, owls, and tarsiers have diurnal, foveate close relatives, and bathylgines migrate up into the epipelagic, photopic environment.

The haplorhine fovea initially functioned to improve the quality of the image falling on the retina. Image quality in these stem haplorhines would have been improved by convergence of the optic on the visual axis associated

with the increased orbital convergence characteristic of primates in general. Whether the improved image quality facilitated the shift to diurnality in stem haplorhines or evolved in response to it cannot be determined from the available data. Regardless, it provided the substrate on which the remarkable visual acuity of extant anthropoids would subsequently be developed.

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REFERENCES

Adams, D. L., and Horton, J. C., 2002, Shadows cast by retinal blood vessels mapped in primary visual cortex, *Science* **298**:572–576.

Ahlbert, I.-B., 1976, Organization of the cone cells in the retinae of salmon (*Salmo salar*) and trout (*Salmo trutta trutta*) in relation to their feeding habits, *Acta Zool. (Stockholm)* **57**:13–35.

Ali, M. A., 1959, The ocular structure, retinomotor and photobehavioral responses of juvenile pacific salmon, *Can. J. Zool.* **37**:965–996.

Ali, M. A., Anctil, M., and Raymond, N., 1973, La rétine de quelques poisssons marins du littoral brésilien, *Revta Biol. Lisb.* **9**:101–114.

Ali, M. A., and Hanyu, I., 1963, A comparative study of retinal structure in some fishes from moderately deep waters of the western north Atlantic, *Can. J. Zool.* **41**:225–241.

Baldwin, C. C., and Johnson, G. D., 1996, Interrelationships of Aulopiformes, in: *Interrelationships of Fishes*, M. L. J., Stiassny, L. R., Parenti, and G. D., Johnson, eds., Academic Press Inc, San Diego, pp. 355–404.

Beaudet, L., Novales Flamarique, I., and Hawrhyshyn, C. W., 1997, Cone photoreceptor topography in retina of sexually mature pacific salmonid fishes, *J. Comp. Neurol.* **383**:49–59.

Brauer, A., 1908, *Die Tiefsee-Fische, 2. Anatomischer Teil.* Fischer, Jena.

Buttery, R. G., Haight, J. R., and Bell, K., 1990, Vascular and avascular retinae in mammals. A fundascopic and fluorescin angiographic study, *Brain Behav. Evol.* **35**:156–175.

Calkins, D. J., 2001, Seeing with S cones, *Prog. Retin. Eye Res.* **20**:255–287.

Cartmill, M., 1980, Morphology, Function and Evolution of the Anthropoid Postorbital Septum, in: *Evolutionary Biology of the New World Monkeys and Continental Drift*, R. L., Ciochon, and A. B., Chiarelli, eds., Plenum Press, New York, pp. 243–274.

Castenholtz, E., 1965, Über die Struktur der Netzhautmitte bei Primaten, *Z. Zellforsch.* **65**:646–661.

Castenholtz, A., 1984, The Eye of *Tarsius*, in: *Biology of Tarsiers*, C., Niemitz, ed., Gustav-Fisher Verlag, Stuttgart, pp. 303–318.

Chase, J., 1982, The evolution of retinal vascularization in mammals. A comparison of vascular and avascular retinae, *Ophthalmology* **89**:1518–1525.

Chievitz, J. H., 1889, Untersuchungen über die Area centralis retinae, *Arch Anat. (Physiol.)* **1889**:332–366.

Chievitz, J. H., 1891, Über das Vorkommen der Area centralis retinae in den vier höheren Wirbelthierklassen, *Arch. Anat. Entw.* **1891**:11–334.

Collin, S. P., 1999, Behavioural Ecology and Retinal Cell Topography, in: *Adaptive Mechanisms in the Ecology of Vision*, S. N., Archer, M. B. A., Djamgoz, E. R., Loew, J. C., Partridge, and S., Vallerga, eds., Kluwer Academic Publishers, Dordrecht.

Collin, S. P., and Collin, H. B., 1988a, The morphology of the retina and lens of the sandlance, *Limnichthyes fasciatus* (Creeiidae), *Exp. Biol.* **47**:209–218.

Collin, S. P., and Collin, H. B., 1988b, Topographic analysis of the retinal ganglion cell layer and optic nerve in the sandlance *Limnichthyes fascaitus* (Creeiidae, Perciformes), *J. Comp. Neurol.* **278**:226–241.

Collin, S. P., Hoskins, R. V., and Partridge, J. C., 1997, Tubular eyes of deep-sea fishes: A comparative study of retinal topography, *Brain Behav. Evol.* **50**:335–357.

Collin, S. P., Hoskins, R. V., and Partridge, J. C., 1998, Seven retinal specializations in the tubular eye of the deep-sea Pearl-Eye, *Scopelarchus michaelsarsi*: A case study in visual optimization, *Brain Behav. Evol.* **51**:291–314.

Collin, S. P. and Partridge, J. C. 1996, Retinal specializations in the eyes of deep-sea teleosts, *J. Fish Biol.* **49** (Suppl. A): 157–174.

Cracraft, J., 1981, Toward a phylogenetic classification of the recent birds of the world (class Aves), *Auk* **98**:681–714.

Curcio, C. A., Sloan, K. R. J., Packer, O., Hendrickson, A. E., and Kalina, R. E., 1987, Distribution of cones in human and monkey retina: Individual variability and radial asymmetry, *Science* **236**:579–582.

Curcio, C. A., Sloan, K. R. J., Kalina, R. E., and Hendrickson, A. E., 1990, Human photoreceptor topography, *J. Comp. Neurol.* **292**:497–523.

DeBruyn, E. J., Wise, V. L., and Casagrande, V. A., 1980, The size and topographic arrangement of retinal ganglion cells in the galago, *Vision Res.* **20**:315–327.

Dollery, C. T., Bulpitt, C. J., and Kohner, E. M., 1969, Oxygen supply to the retina from the retinal and choroidal circulations at normal and increased arterial oxygen tensions, *Invest. Ophthalmol.* **8**:588–594.

Estes, R., and Pregill, C. L., 1988, *Phylogenetic Relationships of the Lizard Families*, Stanford University Press, Stanford.

Feduccia, A., 1996, *The Origin and Evolution of Birds*, Yale University Press, New Haven.

Fite, K., and Lister, B. C., 1981, Bifoveate vision in anolis lizards, *Brain Behav. Evol.* **19**:144–154.

Fite, K., and Rosenfield-Wessels, S., 1975, A comparative study of deep avian foveas, *Brain Behav. Evol.* **12**:97–115.

Franco, E. C. S., Finlay, B. L., Silveira, L. C. L., Yamada, E. S., and Crowley, J. C., 2000, Conservation of absolute foveal area in New World monkeys, *Brain Behav. Evol.* **56**:276–286.

Franz, V., 1934, Vergleichende Anatomie des Wirbeltierauges, in: *handbuch der vergleichenden Anatomie der Wirbeltiere 2*, L., Bolk, E., Göppert, E., Kallius, and W., Lubosch, eds., Berlin & Wien, Berlin, pp. 989–1292.

Frederiksen, R. D., 1976, Retinal tapetum containing discrete reflectors and photore-ceptors in the bathypelagic teleost *Omosudis lowei*, *Vidensk. Meddr dansk naturh. Foren.* **139**:109–146.

Gartner, J. V., Crabtree, R. E., and Sulak, K. J., 1997, Feeding at Depth, in: *Deep-Sea Fishes*, R. J., Randall, and A. P., Farrell, eds., Academic Press, San Diego, pp. 115–193.

Gorrand, J.-M., 1979, Diffusion of the human retina and quality of the optics of the eye on the fovea and the peripheral retina, *Vision Res.* **19**:907–912.

Gorrand, J.-M., 1989, Reflection characteristics of the human fovea assessed by reflecto-modulometry, *Ophthal. Physiol. Opt.* **9**:53–60.

Graham, J. B., and Rosenblatt, R. H., 1970, Aerial vision: unique adaptation in an intertidal fish, *Science* **168**:586–588.

Harkness, L., and Bennet-Clark, H. C., 1978, The deep fovea as a focus indicator, *Nature* **272**:814–816.

Heesy, C. P., and Ross, C. F., 2001, Evolution of activity patterns and chromatic vision in primates: Morphometrics, genetics and cladistics, *J. Hum. Evol.* **40**:111–149.

Heesy, C. P., and Ross, C. F., 2002, Mosaic Evolution of Activity Pattern, Diet, and Color Vision in Haplorhine Primates, in: *Anthropoid Origins: New Visions*, C. F., Ross, and R. F., Kay, eds. Kluwer Academic/Plenum Publishers, New York, this volume.

Henderson, R. W., and Binder, M. H., 1980, The ecology and behavior of vine snakes (*Ahaetulla, Oxybelis, Thelotornis, Uromacer*): A review, *Contrib. Biol. Geol.* **37**:1–38.

Hendrickson, A. E., 1992, A morphological comparison of foveal development in man and monkey, *Eye* **6**:136–144.

Hendrickson, A. E., Djajadi, H. R., Nakamura, L., Possin, D. E., and Sajuthi, D., 2000, Nocturnal tarsier retina has both short and long/medium-wavelength cones in an unusual topography, *J. Comp. Neurol.* **424**:718–730.

Hendrickson, A. E., and Yuodelis, C., 1984, The morphological development of the human fovea, *Ophthalmology* **91**:603–612.

Herring, P. J., 1987, Systematic distribution of bioluminescence in living organisms. *J. Biolumin. Chemolumin.* **1**:147–163.

Hughes, A., 1977, The Topography of Vision in Mammals of Contrasting Life Style: Comparative Optics and Retinal Organization, in: *The Visual System in Vertebrates*, F., Crescitell, ed., Springer-Verlag, Berlin, pp. 613–765.

Johnson, G. D., and Patterson, C., 1993, Percomorph phylogeny: A survey and a new proposal, *Bull. Mar. Sci.* **52**:554–626.

Johnson, G. D., and Patterson, C., 1996, Relationships of Lower Teleostean Fishes, in: *Interrelationships of Fishes*, M. L. J., Stiassny, L. R., Parenti, and G. D., Johnson, eds., Academic Press Inc, San Diego, pp. 251–332.

Kahmann, H., 1936, Über das foveale Sehen der Wirbeltiere, *Albrecht v. Graefes Arch. Ophthal.* **135**:265–276.

Kajikawa, J., 1923, Beiträge zur Anatomie und Physiologie des Vogelauges, Albrecht Von *Graefes Arch. Ophthalmol.* **112**:260–346.

Kay, R. F., and Cartmill, M., 1977, Cranial morphology and adaptations of *Palaechthon nacimienti* and other paromomyidae (Plesiadapoidea, ?Primates), with description of a new genus and species, *J. Hum. Evol.* **6**:19–53.

Kay, R. F., and Kirk, E. C., 2000, Osteological evidence for the evolution of activity pattern and visual acuity, *Am. J. Phys. Anthropol.* **113**:235–262.

Kay, R. F., Ross, C. F., and Williams, B. A., 1997, Anthropoid origins, *Science* **275**:797–804.

Krause, W., 1889, Die retina II.Die Retina der Fische, *Int. Mschr. Anat. Physiol.* **6**:206–223 & 250–269.

Le Gros Clark, W. E., 1959, *The Antecedents of Man*, Harper, New York.

Lee M. S. Y., Doughty P., 1997, The relationship between evolutionary theory and phylogenetic analysis, *Biol. Rev.* **72**:471–495.

Locket, N. A., 1971, Retinal structure in *Platytroctes apus*, a deep-sea fish with a pure rod fovea, *J. Mar. Biol. Ass. U.K.* **51**:79–91.

Locket, N. A., 1975, Some Problems of Deep-Sea Fish Eyes, in: *Vision in Fishes. New Approaches in Research*, M. A., Ali, ed., Plenum Press, New York, pp. 645–655.

Locket, N. A., 1977, Adaptations to the Deep-Sea Environment, vol. 7/5. in: *The Visual System in Vertebrates. Handbook of Sensory Physiology*, F., Crescitelli, ed., Springer-Verlag, Berlin, pp. 67–192.

Locket, N. A., 1985, The multiple bank fovea of *Bajacalifornia drakei*, an alepocephalid deep-sea teleost, *Proc. R. Soc. Lond*., B, **224**:7–22.

Locket, N. A., 1992, Problems of deep foveas, *Aust. NZ. J. Ophthalmol.* **20**:281–295.

Maddison, W. P., 1990, A method for testing the correlated evolution of two binary characters: Are gains and losses concentrated on certain branches of a phylogenetic tree? *Evolution* **44**:539–557.

Makaretz, M., and Levine, R. L., 1980, A light mircoscopic study of the bifoveate retina in the lizard *Anolis carolensis*: General observations and convergence ratios, *Vision Res.* **20**:679–686.

Marshall, N. B., 1966, Family Scopelosauridae, *Sears Found. Mar. Res., Mem.* **1,5**:194–204.

Martin, G. R., 1985, Eye, in: *Form and Function in Birds*, A. S., King, and J., McLelland, eds., Academic Press, New York, pp. 311–373.

Martin, P. R., and Grünert, U., 1999, Analysis of the short wavelength-sensitive ("blue") cone mosaic in the primate retina: Comparison of New World and Old World monkeys, *J. Comp. Neurol.* **406**.

Martin, R. D., 1973, Comparative anatomy and primate systematics, *Symp. Zool. Soc. Lond.* **33**:301–337.

Martin, R. D., 1979, Phylogenetic Aspects of Prosimian Behavior, in: *The Study of Prosimian Behavior*, G. A., Doyle, and R. D., Martin, eds., Academic, New York, pp. 45–78.

Martin, R. D., 1990, *Primate Origins and Evolution. A Phylogenetic Reconstruction*, Princeton University Press, Princeton.

Meneghini, K. A., and Hamasaki, D. I., 1967, The electroretinogram of the iguana and Tokay gecko, *Vision Res.* **7**:243–251.

Michaelson, I. C., 1954, *Retinal Circulation in Man and Animals*, Charles C. Thomas, Springfield.

Moroney, M. K., and Pettigrew, J. D., 1987, Some observations on the visual optics of kingfishers (Aves, Coraciformes, Alcedinidae), *J. Comp. Physiol.* **160**:137–149.

Munk, O., 1959, The eye of *Ipnops murrayi* Günther, 1878, *Galathea Rep.* **3**:79.

Munk, O., 1965, *Omosudis lowei* Günther, 1887, A bathypelagic deep-sea fish with an almost pure-cone retina, *Vidensk. Medd. Fra Dansk naturh. Foren.* **128**:341–355.

Munk, O., 1966a, On the retina of *Diretma argenteus* Johnson, 1863 (Diretmidae, Pisces), *Vidensk. Medd. Dan. Haturist. Foren. KBH.* **129**:73–80.

Munk, O., 1966b, Ocular anatomy of some deep-sea teleosts, *Dana-Report* No. **70**: 1–71.

Munk, O., 1968, On the eye and the so-called preorbital light organ of the isospondylous deep-sea fish, *Bathylaco nigricans* Goode and Bean, 1896, *Galathea Rep.* **9**:211–218.

Munk, O., 1969, The eye of the "four-eyed" fish *Dialommus fuscus* (Pisces, Blenioidea, Clinidae). *Vidensk. Meddr. dansk naturh. Foren.* **132**:7–24.

Munk, O., 1970, On the occurrence and significance of horizontal band-shaped retinal areae in teleosts, *Vidensk. Meddr. dansk naturh. Foren.* **133**:85–120.

Munk, O., 1971, On the occurrence of two lens muscles within each eye of some teleosts, *Vidensk. Meddr. dansk naturh. Foren.* **134**:7–19.

Munk, O., 1975, On the eyes of two foveate notosudid teleosts *Scopelosaurus hoedti* and *Ahliesaurus berryi, Vidensk. Meddr. dansk naturh. Foren.* **138**:87–125.

Munk, O., 1977, The visual cells and retinal tapetum of the foveate deep-sea fish *Scopelosaurus lepidus* (Teleostei), *Zoomorph.* **87**:21–49.

Nicol, J. A. C., 1989, *The Eyes of Fishes*, Clarendon Press, Oxford.

Niemitz, C., 1985, Can a primate be an owl?—Convergences in the same ecological niche, *Fort. Ddr Zool.* **30**:667–670.

O'Day, K. J., 1939, The visual cells of Australian reptiles and mammals, *Trans. Ophthalmol. Soc. Aust.* **1**:12–20.

Oehme, H., 1961, Vergleichend-histologische Untersuchungen an der Retina von Eulen, *Zool. Jb. Anat.* **79**:439–478.

Ogden, T. E., 1974, The morphology of retinal neurones of the owl monkey *Aotes, J. Comp. Neurol.* **153**:399–428.

Ogden, T. E., 1975, The receptor mosaic of *Aotes trivirgatus*: Distribution of rods and cones, *J. Comp. Neurol.* **163**:193–202.

Ohzu, H., and Enoch, J. M., 1972, Optical modulation by the isolated human fovea, *Vision Res.* **12**:245–251.

Ohzu, H., Enoch, J. M., and O'Hair, J. C., 1972, Optical modulation by the isolated retina and retinal receptors, *Vision Res.* **12**:231–244.

Packer, O., Hendrickson, A. E., and Curcio, C. A., 1989, Photoreceptor topography of the adult pig-tailed macaque, *J. Comp. Neurol.* **288**:165–183.

Pariente, G., 1979, The Role of Vision in Prosimian Behavior, in: *The Study of Prosimian Behavior*, G. A., Doyle, and R. D., Martin, eds., Academic Press Inc., New York, pp. 411–459.

Perry, V. H., and Cowey, A., 1985, The ganglion cell and cone distributions in the monkey's retina: Implications for central magnification factors, *Vision Res.* **25**:1795–1810.

Peterson, E., 1981, Regional specialization in retinal ganglion cell projection to optic tectum of *Dipsosaurus dorsalis* (Iguanidae), *J. Comp. Neurol.* **196**:225–252.

Peterson, E., 1992, Retinal Structure, in: *Biology of the Reptilia, Volume 17, Neurology C. Sensorimotor Integration*, C. Gans, and P. S. Ulinski, eds., University of Chicago Press, Chicago, pp. 1–135.

Pettigrew, J. D., 1983, A note on the eyes of the Letter-Winged Kite *Elanus scriptus, The Emu* 82 Supplement: 305–308.

Pettigrew, J. D., and Konishi, M., 1984, Some observations on the visual system of the oilbird, *Steatornis caripensis, National Geographic Society Research Reports.* **16**:439–450.

Pettigrew, J. D., Wallman, J., and Wildsoet, C. F., 1990, Saccadic oscillations facilitate ocular perfusion from the avian pectin, *Nature* **343**:362–363.

Polyak, S., 1941, *The Retina*, University of Chicago Press, Chicago.

Provis, J. M., 2001, Development of the primate retinal vasculature, *Prog. Retin. Eye Res.* **20**:799–821.

Provis, J. M., Diaz, C. M., and Dreher, B., 1998, Ontogeny of the primate fovea: A central issue in retinal development, *Prog. Neurobiol.* **54**:549–581.

Pumphrey, R. J., 1948, The theory of the fovea, *J. Exp Biol.* **25**:299–312.

Reymond, L., 1985, Spatial visual acuity of the eagle *Aquila audax*: A behavioural, optical and anatomical investigation, *Vision Res.* **27**:1859–1874.

Reymond, L., 1987, Spatial visual acuity of the falcon *Falco berigora*: A behavioural, optical and anatomical investigation, *Vision Res.* **25**:1477–1491.

Rochon-Duvigneaud, A., 1943, *Les Yeux et La Vision des Vertébrés*, Masson, Paris.

Rodieck, R. W., 1988, The Primate Retina, in: *Comparative Primate Biology, Volume 4: Neurosciences.* H. D. Stecklis, and J. Erwin, eds., Alan R. Liss Inc., New York, pp. 203–278.

Rohen, J. W., 1966, Zur Histologie des Tarsiusauges, *Albrecht v. Graefes Arch. klin. exp. Ophthal.* **169**:299–317.

Rohen, J. W., and Castenholtz, A., 1967, Über die Zentralisation der Retina bei Primaten, *Folia primat.* **5**:92–147.

Röll, B., 2001, Gecko vision—retinal organization, foveae and implications for binocular vision, *Vision Res.* **41**:2043–2056.

Ross, C. F., 1996, An adaptive explanation for the origin of the Anthropoidea (Primates), *Am. J. Primatol.* **40**:205–230.

Ross, C. F., Lockwood, C., Fleagle, J. G., and Jungers, W. L., 2001, Adaptation and Behavior in the Primate Fossil Record, in: *Reconstructing Behavior in the Primate Fossil Record*, J. M. Plavcan, R. F. Kay, W. L. Jungers, and C. P. van Schaik, eds., Kluwer Academic/Plenum Publishers, New York, pp. 1–41.

Ross, C. F., Williams, B. A., and Kay, R. F., 1998, Phylogenetic analysis of anthropoid relationships, *J. Hum. Evol.* **35**:221–306.

Schluter, D., Price, T., Mooers, A. O., and Ludwig, D., 1997, Likelihood of ancestor states in adaptive radiation, *Evolution* **51**:1699–1711.

Schmitt, E., and Kunz, Y. W., 1989, Retinal morphogenesis in the rainbow trout, *Salmo gairdneri, Brain Behav. Evol.* **34**:48–64.

Schwassman, H. O., 1968, Visual projection upon the optic tectum in foveate marine teleosts, *Vision Res.* **8**:1337–1348.

Slonaker, J. R., 1897, A comparative study of the area of acute vision in vertebrates, *J. Morph.* **13**:445–492.

Snodderly, D. M., Leung, W. P., Timberlake, G. T., and Smith, D. P. B., 1978, Mapping Retinal Features in a Freely Moving Eye with Precise Control of Retinal

Simulus Position, in: *Frontiers in Visual Science*, S. J., Cool, and E. L., Smith, eds., Springer, New York, pp. 79–92.

Snodderly, D. M., Weinhaus, R. S., and Choi, J. C., 1992, Neural-vasculature relationships in central retina of macaque monkeys (*Macaca fascicularis*), *J. Neurosci.* **12**:1169–1193.

Steenstrup, S., and Munk, O., 1980, Optical function of the convexiclivate fovea with particular regard to notosudid deep-sea teleosts, *Optica acta* **27**:949–964.

Stiassny, M. L. J., Parenti, L. R., and Johnson, G. D., 1996, *Interrelationships of Fishes*, Academic Press Inc, San Diego.

Stone, J., and Johnston, E., 1981, The topography of primate retina: A study of the human, bushbaby and New- and Old-World monkeys, *J. Comp. Neurol.* **196**:205–223.

Szalay, F. S., and Delson, E., 1979, *Evolutionary History of the Primates*, Academic Press, New York.

Tamura, T., 1957, A study of visual perception in fish, especially on resolving power and accommodation, *Bull. Jap. Soc. Scient. Fish.* **22**:536–557.

Tansley, K., 1961, The retina of a diurnal gecko, *Pflugers Arch. Ges. Physiol.* **272**:262–269.

Tansley, K., 1964, The gecko retina, *Vision Res.* **4**:33–37.

Tetreault, N., Hakeem, A., and Allman, J., this volume, The Distribution and Size of Retinal Ganglion Cells in *Cheirogaleus medius* and *Tarsius syrichta*: Implications for the Evolution of Sensory Systems in Primates, in: *Anthropoid Origins: New Visions*, C. F. Ross and R. F. Kay, eds., New York: Kluwer Academic/Plenum Publishers.

Underwood, G., 1970, The Eye, in: *Biology of the Reptilia. Volume 2, Morphology B*, C. Gans, and T. S. Parsons, eds., Academic Press, London.

Valentin, G., 1897, Ein Beitrag zur Kenntniss der Brechungsverhältnisse der Thiergewebe, *Pflügers Arch. ges. Physiol.* **19**:78–105.

Verrier, M.-L., 1928, Sur la Présence et la structure d'une fovea rétinienne chez un percidé: Serranus cabrilla L., *C. R. hebd. Séanc. Acad. Sci. (Paris)* **186**:457–459.

Verrier, M.-L., 1933, Recherches sur la vision des reptiles, *Bull. Biol. France Belg.* **67**:350–370.

Vilter, V., 1951, Recherches sur les structures foveales dans la retine du *Sphenodon punctatus, Comptes Rendu des Séances de la Société Biologie.* **145**:26–29.

Vilter, V., 1954a, Différenciation fovéale dans l'appareil visuel d'un poisson abyssal, le *Bathylagus benedicti, Comptes Rendu des Séances de la Société Biologie.* **148**:59–63.

Vilter, V., 1954b, Relations neuronales dans la fovea à bâtonnets du *Bathylagus benedicti, Comptes Rendu des Séances de la Société Biologie.* **148**:466–469.

Vitt, L. J., and Pianka, E. R., 1994, *Lizard Ecology : Historical and Experimental Perspectives*, Princeton University Press, Princeton.

Vrabec, F., 1969, Sur la présenced'une fovea dans la rétine du *Lepadogaster*, *Vie Milieu, Ser. A* **20**:245–250.

Wagner, H.-J., 2001, Brain areas in abyssal demersal fishes, *Brain Behav. Evol.* **57**:301–316.

Walls, G. L., 1937, Significance of the foveal depression, *Arch. Ophthal.* **18**:912–919.

Walls, G. L., 1940, Postscript on image expansion at the fovea, *Arch. Ophthal.* **22**: 831–832.

Walls, G. L., 1942, *The Vertebrate Eye and Its Adaptive Radiation*, Hafner, New York.

Wässle, H., and Boycott, B. B., 1991, Functional architecture of the mammalian retina, *Physiol. Rev.* **71**:447–480.

Wässle, H., Grünert, U., Röhrenbeck, J., and Boycott, B. B., 1990, Retinal ganglion cell density and cortical magnification factor in the primate, *Vision Res.* **30**:1897–1911.

Weale, R. A., 1966, Why does the human retina possess a fovea? *Nature* **212**:255–256.

Webb, S. V., and Kaas, J. H., 1976, The sizes and distribution of ganglion cells in the retina of the owl monkey, *Aotus trivirgatus, Vision Res.* **16**:1247–1254.

Weitzman, S. H., 1997, Systematics of Deep-Sea Fishes, in: *Deep-Sea Fishes*, D. J. Randall, and A. P. Farrell, eds., Academic Press, San Diego, pp. 43–77.

Whitehead, P. J. P., Bauchot, M.-L., Hureau, J.-C., Nielsen, J., and Tortonese, E., 1986, *Fishes of the North-eastern Atlantic and the Mediterranean. Vol. I-III* Unesco, United Kingdom.

Wikler, K. C., Williams, R. W., and Rakic, P., 1990, Photoreceptor mosaic: Number and distribution of rods and cones in the rhesus monkey retina, *J. Comp. Neurol.* **297**:499–508.

Williams, P. L., and Warwick, R., 1980, *Gray's Anatomy*, 36th Edition, Churchill Livingstone, New York.

Wolff, E., 1940, *The Anatomy of the Eye and Its Orbit*, Lewis & Co., London.

Wolin, L. R. and Massopust, L. C., 1970, Morphology of the Primate Retina, in: *Advances in Primatology. Volume 1. The Primate Brain*, C. R. Noback, and W. Montagna, eds., Appleton-Century-Crofts, New York, pp. 1–27.

Wood, C. A., 1917, *The Fundus Oculi of Birds Especially as Viewed by the Ophthalmoscope*, Chicago, The Lakeside Press.

Woollard, H. H., 1925, The anatomy of *Tarsius spectrum, Proc. R. Soc. Lond.* **70**:1071–1084.

Wulliman, M. F., 1997, Major patterns of visual brain organization in teletosts and their relation to prehistoric events and the paleontological record, *Paleobiology* **23**:101–114.