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## The Evolutionary and Ecological Context of Primate Vision

*Robert D. Martin and Callum F. Ross*

### 1.1 Introduction

#### 1.1.1 Overview of primates and their phylogenetic relationships

Excluding tree-shrews, now commonly relegated to the separate mammalian order Scandentia, approximately 350 species of modern primates can currently be recognized (Groves, 2001), most of them being arboreal inhabitants of tropical and subtropical forests. As has generally been recognized in some way in all major classifications, on morphological and biogeographical grounds these living primates fall fairly clearly into six 'natural groups' (Martin, 1990): (1) Madagascar lemurs (infraorder Lemuriformes); (2) lorises and bush babies (infraorder Lorisiformes); (3) tarsiers (infraorder Tarsiiformes); (4) New World monkeys (superfamily Ceboidea); (5) Old World monkeys (superfamily Cercopithecoidea); and (6) Old World apes and humans (superfamily Hominoidea). The last two groups (Old World monkeys; Old World apes and humans) are commonly combined in the infraorder Catarrhini, distinguishing them from the infraorder Platyrrhini established for New World monkeys. Because the first three natural groups (lemurs, lorisiforms, and tarsiers) have remained relatively primitive, they have often been labeled prosimians or lower primates, to distinguish them from the more advanced simians or higher primates (monkeys, apes, and humans), which are seen as having attained a higher grade of evolution. In traditional, grade-based classifications, it has accordingly been customary to allocate prosimians to the suborder Prosimii and simians to the suborder Anthropoidea. However, there is abundant evidence indicating that, although they have

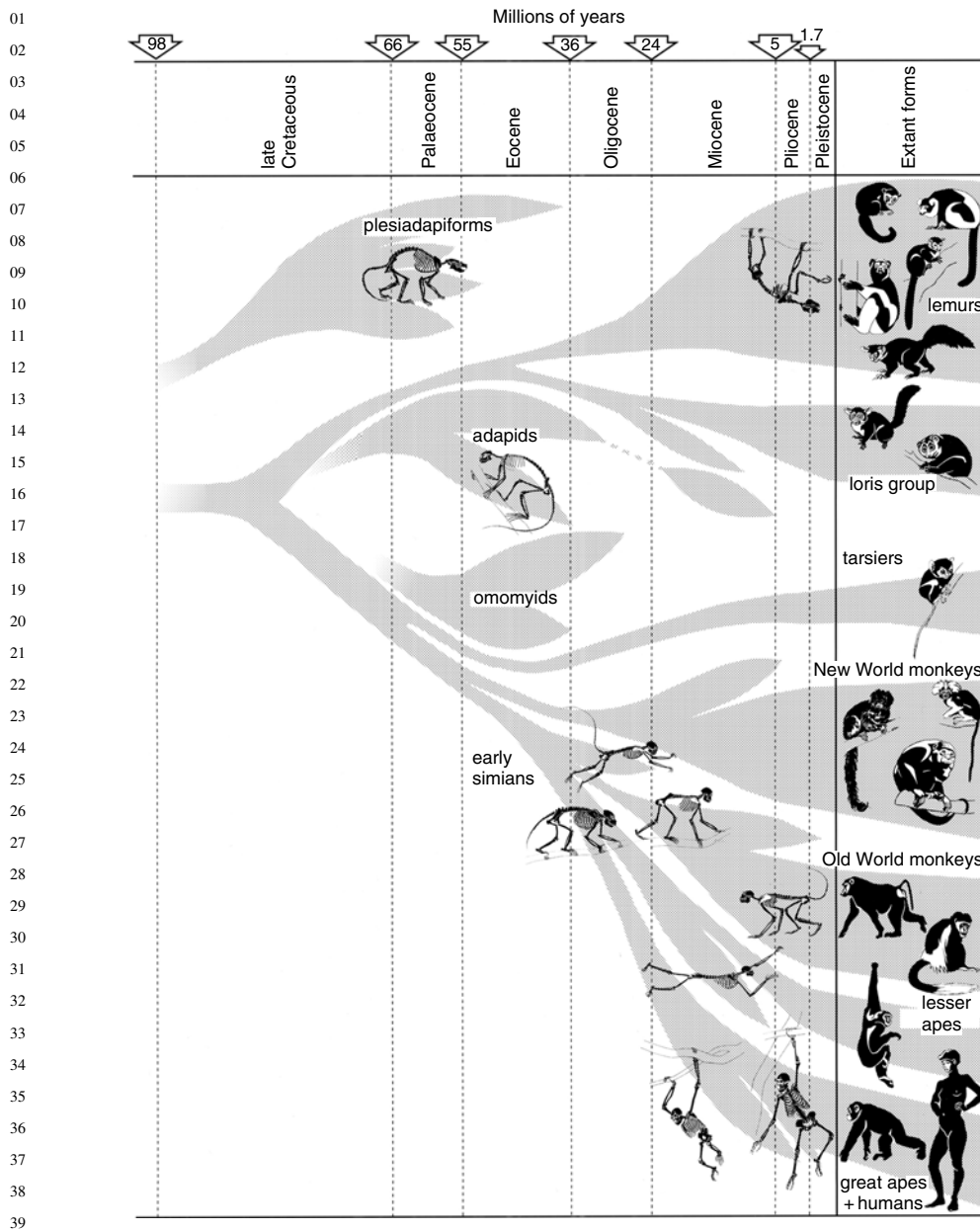
01 remained primitive in many respects, the tarsiers are in fact more closely related to the  
02 simians than to the other prosimians (Figure 1.1). In a cladistic classification (i.e. one  
03 designed to provide a direct reflection of inferred phylogenetic relationships), lemurs and  
04 lorises are hence allocated to the suborder Strepsirrhini, while tarsiers and simians are  
05 allocated to the suborder Haplorhini. Regardless of the choice of classification, which  
06 is a continuing matter of controversy, in some contexts it is convenient to distinguish  
07 between prosimians and simians in discussing primate features, whereas in others it is  
08 useful to contrast strepsirrhines with haplorhines.

09 Undoubted relatives of modern primates (euprimates or ‘primates of modern aspect’)  
10 first appear in the fossil record at the beginning of the Eocene epoch, approximately  
11 55 mya (million years ago). The Plesiadapiformes, which were predominantly present  
12 during the preceding Palaeocene epoch (55–65 mya), have traditionally been allocated to  
13 the order Primates (e.g. Simons, 1972; Szalay and Delson, 1979). However, they lack  
14 many of the defining features of primates of modern aspect (Martin, 1968, 1990; Cartmill,  
15 1972, 1974) and have been labeled ‘archaic primates’ to emphasize their distinctiveness.  
16 In fact, some authors (e.g. Martin, 1990, 1993; Kirk *et al.*, 2003) have questioned the  
17 supposed phylogenetic link between Plesiadapiformes and primates, and there have been  
18 alternative suggestions that plesiadapiforms are related to colugos (order Dermoptera)  
19 instead (Beard, 1990, 1993; Kay *et al.*, 1992). The recent discovery of a fairly complete  
20 skeleton of the plesiadapiform *Carpolestes*, which appears to show a primate-like grasping  
21 adaptation of the foot, has reopened the debate (Bloch and Boyer, 2002; but see Kirk  
22 *et al.*, 2003). Given continuing uncertainties about the status of Plesiadapiformes, the  
23 most prudent course is to treat them as a separate category in discussions of primate  
24 evolution. The present discussion will focus primarily on euprimates.

25 Fossil euprimates can be divided into two major categories. On the one hand, there  
26 are early Tertiary (predominantly Eocene) forms that can generally be allocated either  
27 to the infraorder Adapiformes or to the infraorder Omomyiformes. On the other hand,  
28 there are other, generally later, forms that can be linked more closely to the natural  
29 groups of modern primates. Direct relatives of the six modern natural groups of living  
30 primates tend to occur from the late Oligocene/early Miocene (i.e. from about 25 mya),  
31 although there are a few exceptions. For instance, the putative fossil tarsier *Tarsius*  
32 *eocaenus* is documented from the middle Eocene of China. Several authors have linked  
33 the Adapiformes to the strepsirrhine side of the primate tree and the Omomyiformes  
34 to the haplorhine side. Indeed, it has often been suggested that the Omomyiformes are  
35 specifically linked to tarsiers. However, it is possible that the Adapiformes and the  
36 Omomyiformes are not linked directly to strepsirrhines or haplorhines and that they  
37 constitute a separate adaptive radiation of early primates (Martin, 1993; Ross, 2003).  
38 It should be noted that Adapiformes and Omomyiformes have a northern continental  
39 distribution (Asia, Europe, and North America), while unquestioned strepsirrhines and  
40 haplorhines have a distribution that is predominantly confined to the southern landmasses.

### 41 42 **1.1.2 Contributions of the comparative approach**

43  
44 With respect to vision, as in many other areas of biology, a comparative interspecific  
45 approach has much to offer with respect to evolutionary and functional interpretation.  
46 Among other things, it yields a different complementary perspective that can enhance

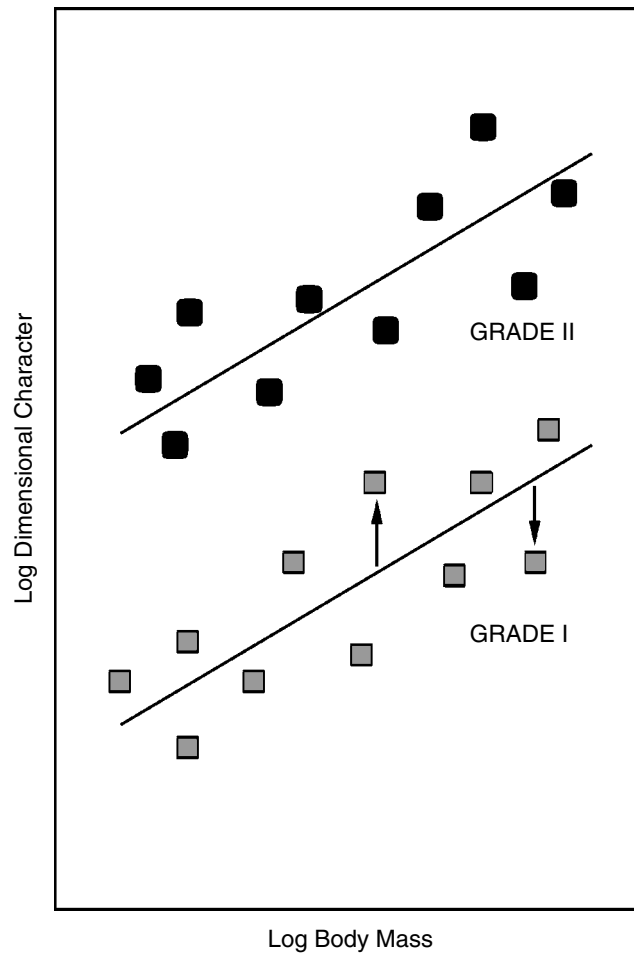


**Figure 1.1** Outline phylogenetic tree of primates. Euprimates are represented by the six 'natural groups' of modern primates and various fossil relatives dating back to the beginning of the Eocene (55 mya). Note the initial subdivision between strepsirrhines and haplorhines in the evolution of euprimates. The tree also includes 'archaic primates' (Plesiadapiformes), which are of uncertain affinities. Original illustration by Lukrezia Bieler-Beerli. Reprinted by permission from Nature (Martin, R.D., vol. 363, pp. 223–234) copyright © (1993) Macmillan Journals Limited (<http://www.nature.com/>)

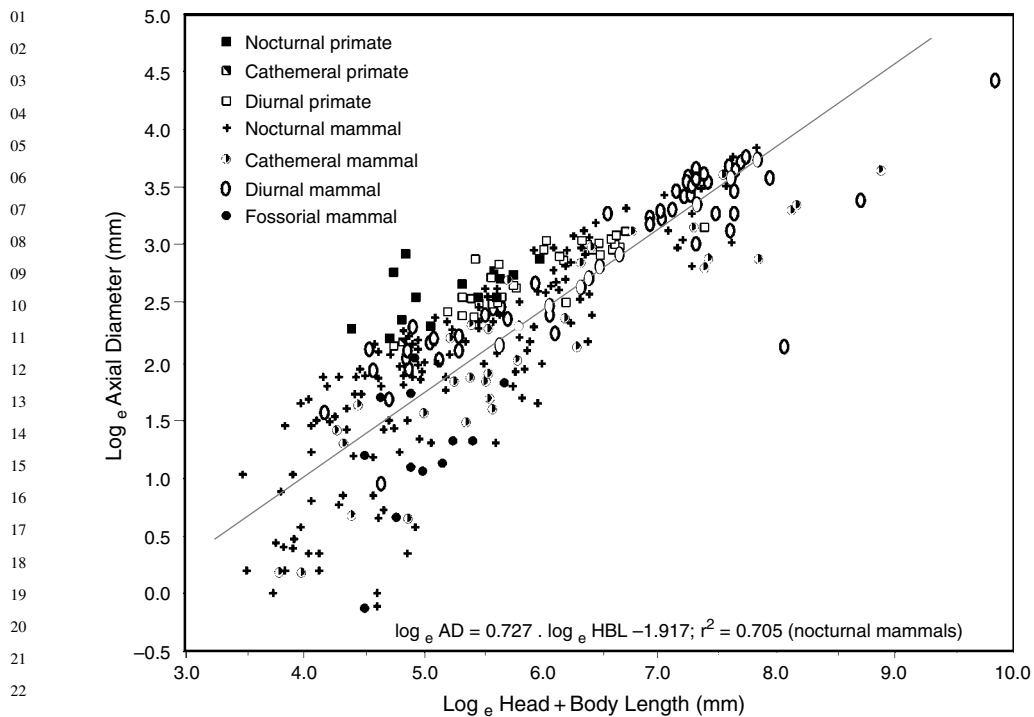
01 interpretation of results obtained from highly focussed studies of individual species.  
02 Furthermore, comparisons between species permit formulation of hypotheses and some  
03 degree of testing thereof. Indeed, a comparative approach is essential for the inclusion  
04 of fossil evidence and hence for any comprehensive phylogenetic interpretation, as is  
05 exemplified in this review. At the same time, it should be emphasized that comparisons  
06 can yield no more than correlations and indirect inferences. Although it is possible, given  
07 appropriate caution, to make certain functional inferences on the basis of interspecific  
08 comparative studies, causal analysis ideally requires additional inputs from testing of  
09 individual species. In an ideal world, interspecific comparisons and detailed investigation  
10 of individual species should be mutually enriching.

11 The comparative approach can be particularly informative when quantitative data are  
12 available, but it is then essential to take the scaling effects of body size into account. One  
13 relatively simple approach is to conduct bivariate allometric analysis, which requires the  
14 examination of trends in logarithmically transformed data (Martin, 1980, 1989, 1990).  
15 A basic model for allometric scaling is shown in Figure 1.2. Even with this relatively  
16 simple approach, however, there are several complex issues involved in analysis and  
17 interpretation. Bivariate allometric analyses are confronted by at least four fundamental  
18 problems: (1) choice of an appropriate best-fit line (Harvey and Mace, 1982; Martin  
19 and Barbour, 1989; Isler *et al.*, 2002); (2) successful recognition of grades in a dataset  
20 (Martin and MacLarnon, 1985; Martin, 1998; Isler *et al.*, 2002); (3) potential bias arising  
21 from patterns of phylogenetic relatedness among species in a sample (Felsenstein, 1985;  
22 Harvey and Pagel, 1991; Purvis and Rambaut, 1995; Purvis and Webster, 1999); and  
23 (4) questionable extrapolation from correlation to causation (Martin, 1998). Proper dis-  
24 cussion of the complexities involved is beyond the scope of this review, so a pragmatic  
25 approach has been adopted here. As the primary aim is to identify general trends and  
26 principles, rather than to draw statistical conclusions from the data, bivariate plots with  
27 least-square regression lines are used essentially for description, and potential problems  
28 of interpretation are discussed where necessary.

29 In assessing the evolution of primate vision, the value of comparisons is evident even  
30 at a very superficial level. For example, comparison of primates with other mammals  
31 immediately reveals that the visual sense is of particular importance in primates. The  
32 eyes of primates tend to be relatively larger than in other mammals (Ross *et al.*, in press;  
33 Figure 1.3). Moreover, the eyes are rotated forward at least to some extent in all primates,  
34 thus enlarging the binocular field in which an object can be seen simultaneously with  
35 both eyes (Figure 1.4). The existence of a binocular field is an essential precondition  
36 for the emergence of three-dimensional vision, which also requires the development of  
37 appropriate processing centers in the brain. In all primates, there is an approximate balance  
38 between the ipsilateral and contralateral optic fibers passing to each side of the brain,  
39 such that inputs from the two eyes can be directly matched (Martin, 1990). Furthermore,  
40 it is a universal feature of primates that the lateral geniculate nucleus (an intermediate  
41 relay station in the visual system) shows clear lamination corresponding to these balanced  
42 inputs from the two eyes (Chapter 6). In fact, primates show an unusual condition that  
43 differentiates them from most or all other mammals with enhanced binocular vision. In  
44 other mammals, the entire binocular field is typically represented in the visual cortex  
45 on each side of the brain, whereas in primates only one half of the binocular field is  
46 represented on each side (Allman, 1982, 1999).

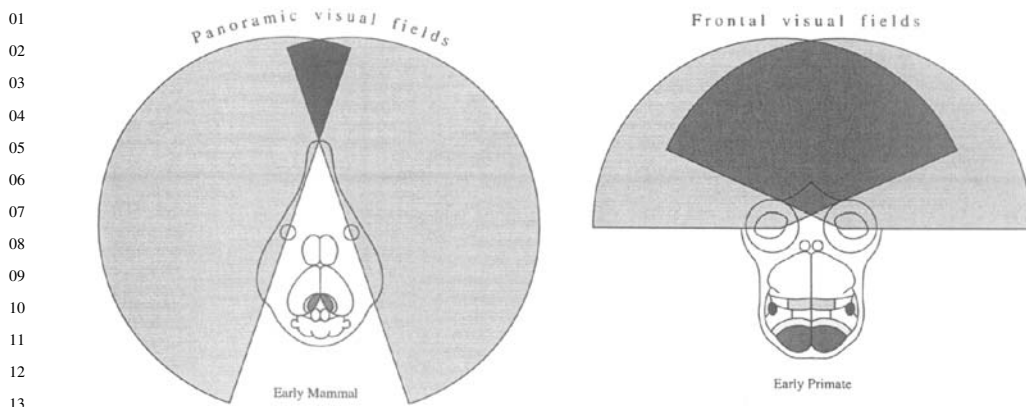


**Figure 1.2** Illustration of basic principles of interspecific allometric scaling (after Martin, 1989). The standard allometric formula is  $Y = k \cdot X^\alpha$ , where  $X$  is some measure of body size,  $Y$  a dimensional character of interest,  $\alpha$  the allometric exponent, and  $k$  the allometric coefficient. This potentially curvilinear relationship can be transformed into linear form by logarithmic conversion:  $\log Y = \alpha \cdot \log X + \log k$ . The allometric exponent ( $\alpha$ ) is indicated by the slope of the line, while the intercept ( $\log k$ ) indicates the value of the allometric coefficient. For a given group of species (squares, representing average values for each species), a best-fit line can be determined as shown. The best-fit line indicates the idealized *scaling principle*, while positive or negative vertical deviations of individual species from the best-fit line (see arrows) – that is, their *residual values* – indicate special adaptations. In many cases, when a second group of species is taken (circles), a best-fit line of similar slope is obtained, but it is displaced vertically relative to the line determined for the first set. The two groups of species are then said to belong to distinct *allometric grades* (grade I; grade II). The vertical distance between the lines indicates the magnitude of the *grade shift* involved



**Figure 1.3** Bivariate plot of the axial diameter of the eye against head-and-body length for primates and other mammals, showing that both nocturnal primates and (to a lesser extent) diurnal primates tend to have relatively larger eyes in comparison to other mammals. (Adapted from Ross, 2000, incorporating data from Ritland, 1982.) Among non-primates, nocturnal species show a wide range of relative eye sizes. Some show comparatively large eyes, overlapping with values for primates, while others have very small eyes. Overall, in contrast to primates, among non-primates nocturnal species generally tend to have smaller eyes than diurnal species

The function of increased orbital convergence in euprimates has traditionally been linked to arboreality (Wood Jones, 1916; Elliot Smith, 1924; Le Gros Clark, 1959), but comparisons with other animals by Cartmill suggested that convergent orbits facilitate visual predation on insects on the fine branches of the shrub layer of tropical rainforests (Cartmill, 1970, 1972). ‘Stereoptic integration of the two visual fields improves the accuracy of the final strike; increase in visual-field overlap facilitates compensation for evasive movements of the prey’ (Cartmill, 1972, p. 113). Subsequent work by Pettigrew (cited by Allman, 1977, p. 29; Pettigrew, 1978) and Allman (1977) demonstrated that the dioptric benefits of orbital convergence are primarily obtained in nocturnal animals. The Allman–Pettigrew model posits that orbital convergence improves image quality by converging the optic axis (the axis of the dioptric apparatus of the eye; i.e. lens and cornea) with the visual axis, or ‘physiological line of fixation’ (Walls, 1942, p. 292). Another way to enhance retinal image quality is to decrease pupil diameter so as to restrict incoming images to the paraxial region of the dioptric apparatus. However, this option

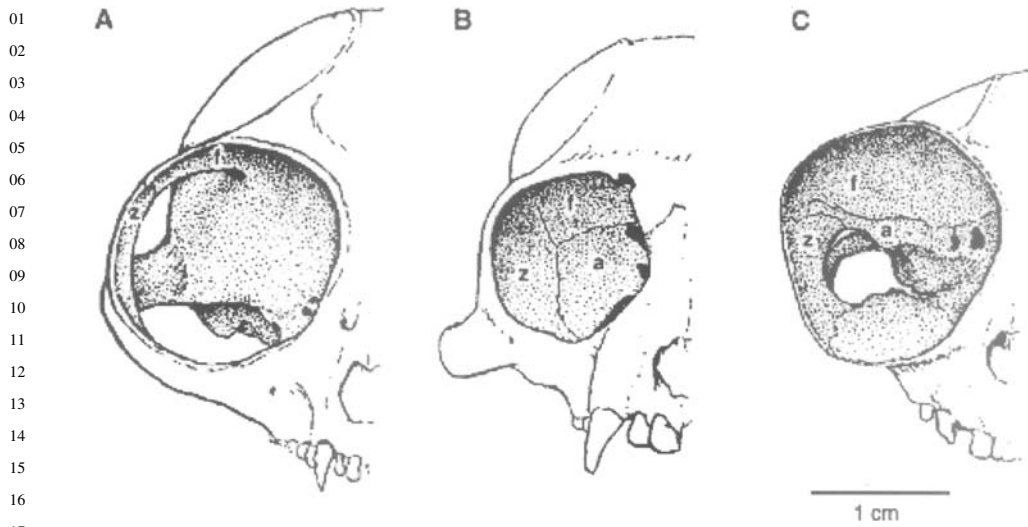


**Figure 1.4** The primitive condition for mammals is to have relatively small, laterally oriented eyes that show very little convergence and hence only a small area of binocular overlap. In all euprimates (but not in plesiadapiforms), the eyes are relatively large and rotated forward at least to a moderate degree, such that there is a relatively large binocular field (adapted from Allman, 1999)

is not available to nocturnal animals, which must operate with enlarged pupils in order to maintain image brightness. Consequently, nocturnal animals improve image quality in the area of visual field overlap by increasing optic convergence. Nocturnal animals also benefit from increased visual field overlap because their eyes receive twice as many photons from any point in the binocular visual field as from points in the monocular visual fields, increasing their sensitivity to low-light levels.

Further significant characteristics of the primate visual system are revealed by comparative studies of the skull, notably with respect to the eye socket (orbit). One obvious feature that has long been seen as a defining feature of euprimates is that all of them possess at least a bony strut (postorbital bar) around the outer margin of the orbit (Figure 1.5). A simple bar is characteristic of all modern strepsirrhine primates and is also uniformly present in fossil adapiforms and omomyiforms. In modern haplorhine primates, by contrast, there is a bony partition (postorbital septum) closing the gap between the postorbital bar and the skull wall and effectively isolating the orbit from the temporal jaw musculature. This is one case in which tarsiers share an advanced feature with simian primates. Although it has been suggested that tarsiers and simians may have acquired the postorbital septum independently (Simons and Rasmussen, 1989), the fact that this feature is unique among mammals suggests that there was some basis in the common ancestor of haplorhine primates even if there may be differences in detail in the subsequent evolution of the postorbital partition (Cartmill, 1980; Ross, 1994).

Noble *et al.* (2000) reviewed three main hypotheses that have been proposed to explain the formation of the postorbital bar in primates: (1) resisting masticatory stresses (Greaves, 1985, 1995); (2) protecting the eye from injury (Prince, 1953; Simons, 1962); and (3) augmenting rigidity of the orbital margin to enhance visual acuity (Collins, 1921; Cartmill, 1970, 1972). A direct experimental test of the first hypothesis with the bush baby *Otolemur crassicaudatus* showed that strains arising from mastication are too low to account for development of the postorbital bar (Ravosa *et al.*, 2000). As the second



**Figure 1.5** Illustration of the postorbital bar and the postorbital septum in primates. All strepsirrhine primates, such as *Nycticebus coucang* (A), possess a postorbital bar formed by contact between processes of the frontal (f) and zygomatic (z) bones. Uniquely among mammals, all haplorhine primates possess a postorbital septum formed from the frontal, alisphenoid (a), and zygomatic bones. This is illustrated for the New World simian *Saguinus* (B) and for *Tarsius* (C). Reproduced with permission from R.F. Kay *et al.*, *Science* **275**, 797–804 (1997). Copyright 1997 AAAS

27 hypothesis was effectively discounted by Cartmill, only enhancement of visual acuity  
28 remains as a promising hypothesis. It should be noted that the postorbital ligament, from  
29 which the bar arises, itself forms from the anteriormost free edge of the fascia of the  
30 temporal musculature, underscoring the close proximity between the eye and the main  
31 jaw muscles. This proximity means that any alterations in skull morphology that move  
32 the temporal fossa and the orbit out of the same plane put the eye in danger of disruption  
33 from movements in the temporal fossa (Heesy, 2003). These alterations might be due  
34 to increased orbital convergence, increased brain size, or some combination of the two  
35 (Cartmill, 1972; Noble *et al.*, 2000). Although most mammals do not possess a postorbital  
36 bar, this feature is by no means exclusive to primates. Tree-shrews possess a postorbital  
37 bar, and this has commonly been cited as a feature linking them to primates. However,  
38 postorbital bars are found in several carnivores and fruit-bats (Noble *et al.*, 2000), in  
39 horses and several artiodactyls, in some hyraxes, in a sea-cow and in some marsupials  
40 (Martin, 1990). Hence, possession of a postorbital bar is clearly not in itself sufficient to  
41 link tree-shrews to primates. Moreover, the presence of this feature in horses, artiodactyls,  
42 and a sea-cow reveals that it is not even linked to arboreal life as had been supposed  
43 by some authors. By contrast, given that possession of a postorbital bar (at least) is  
44 universally characteristic of all living and fossil euprimates, it is noteworthy that this  
45 feature is uniformly lacking in Plesiadapiformes. This is just one indication of the fact  
46 that any link between the Plesiadapiformes and euprimates is tenuous.



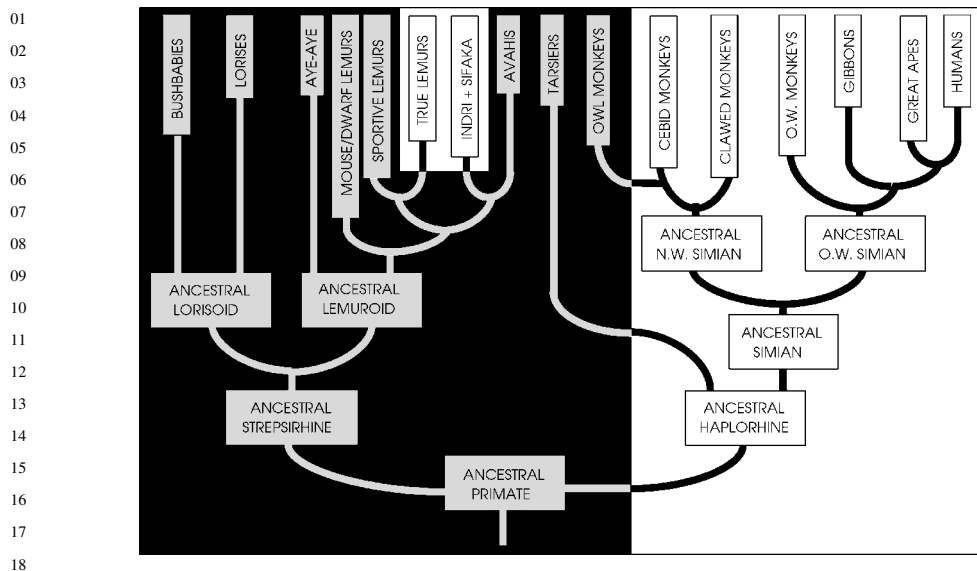
01 Ross (1995a, 2000) assesses possible functional reasons for the development of the  
02 postorbital septum in haplorhines, comparing the relative merits of two main hypotheses:  
03 (1) Cachel's (1979) proposal that the septum evolved to increase muscle attachment  
04 area in the anterior temporal fossa and (2) Cartmill's (1980) proposal that the septum  
05 evolved to insulate the eye from masticatory movements of muscles in the temporal  
06 fossa. Dissections of 55 primate species revealed that in all anthropoids the temporal  
07 muscles have their origins on the portion of the septum formed by the frontal bone and  
08 actually follow a curving path, thus indicating that the second hypothesis is more likely.  
09 Other alternative hypotheses (e.g. dissipation of masticatory stresses) have been falsified  
10 (Ross 1995a; Ross and Hylander, 1996). Thus, it would seem that both the develop-  
11 ment of the postorbital bar in ancestral euprimates and the subsequent development of a  
12 postorbital septum in haplorhines served to isolate the eye from the temporal jaw mus-  
13 culature. Such insulation is of particular importance in animals, like anthropoids, that  
14 have high visual acuity which they employ to search for prey or predators while chewing  
15 (Cartmill, 1980).

## 18 **1.2 The phylogenetic background** 19 **to primate vision**

### 21 **1.2.1 The nocturnal/diurnal divide**

22  
23 A key factor with respect to vision in primates is the distinction between nocturnal and  
24 diurnal species (Figure 1.6). Most primates are either clearly nocturnal (i.e. active between  
25 dusk and dawn) or clearly diurnal (i.e. active between dawn and dusk). A few lemurs  
26 (species of the genera *Eulemur* and *Haplemur*) exhibit an unusual pattern involving a  
27 combination of nocturnality and diurnality that has been labeled 'cathemeral activity'  
28 (Tattersall, 1988). Most strepsirrhine primates are nocturnal. Lorisiforms are uniformly  
29 nocturnal, while among the Madagascar lemurs fully diurnal behavior is limited to certain  
30 members of two of the six families: Lemuridae (*Lemur* and *Varecia*) and Indridae (*Indri*  
31 and *Propithecus*). By contrast, the vast majority of haplorhine primates are diurnal. The  
32 only exceptions are species belonging to the two genera *Tarsius* and *Aotus*, which are  
33 typically nocturnal. It would seem that some populations of owl monkeys (*Aotus*) may also  
34 exhibit cathemeral rather than exclusively nocturnal activity. The basic division between  
35 nocturnal and diurnal primates is, of course, directly relevant to fundamental visual  
36 processes, as the former are adapted for activity in dim light intensities, whereas the latter  
37 are adapted for activity in relatively bright light (i.e. for scotopic and photopic conditions,  
38 respectively, using the terminology proposed by Walls, 1942; see also Chapters 5 and 6).  
39 Cathemeral primates are faced with the problem that they must cope with both scotopic  
40 and photopic conditions.

41 In connection with the nocturnal/diurnal divide, there is a pervasive distinction between  
42 strepsirrhines and haplorhines in that the former typically possess a reflecting tapetum  
43 lucidum, generally interpreted as an adaptation for vision under dim light conditions,  
44 whereas the latter do not. It is noteworthy that a well-developed tapetum is present not  
45 only in all nocturnal lorisiforms and lemurs but also in all diurnal lemurs (*Indri*, *Lemur*,  
46 *Propithecus*, and *Varecia*), whereas it is not well developed in lemurs with cathemeral



**Figure 1.6** Outline phylogenetic tree of primates showing the distribution of nocturnal and diurnal habits among living representatives and inferred ancestral conditions. Note that some true lemurs (*Eulemur* and *Hapalemur*) show an unusual cathemeral pattern, involving both diurnal and nocturnal activity. Fossil forms have not been considered in this reconstruction, which is based exclusively on the characteristics of living primates. (Reproduced from the chapter by R.D. Martin in *Creatures of the Dark: The Nocturnal Prosimians* (1995), with permission from Kluwer Academic Publishers/Plenum Publishers.)

habits (*Eulemur* and *Hapalemur*). A notable feature of the tapetum in strepsirrhine primates is that, as far as is known, the active principle is a layer of plate-like riboflavin crystals (Pirie, 1959; Martin, 1990), which generates a conspicuous golden yellow eyeshine. Riboflavin, which belongs to the general class of flavins, is best known as the water-soluble vitamin B<sub>2</sub>, which serves a variety of biological roles (reviewed by Massey, 2000). Among other things, it plays a major part in aerobic metabolism, in photosynthesis, in light-dependent repair of DNA damage, in fetal development, and in regulation of biological clocks. However, the role of riboflavin as the active principle of a tapetum lucidum seems to be unique to strepsirrhine primates.

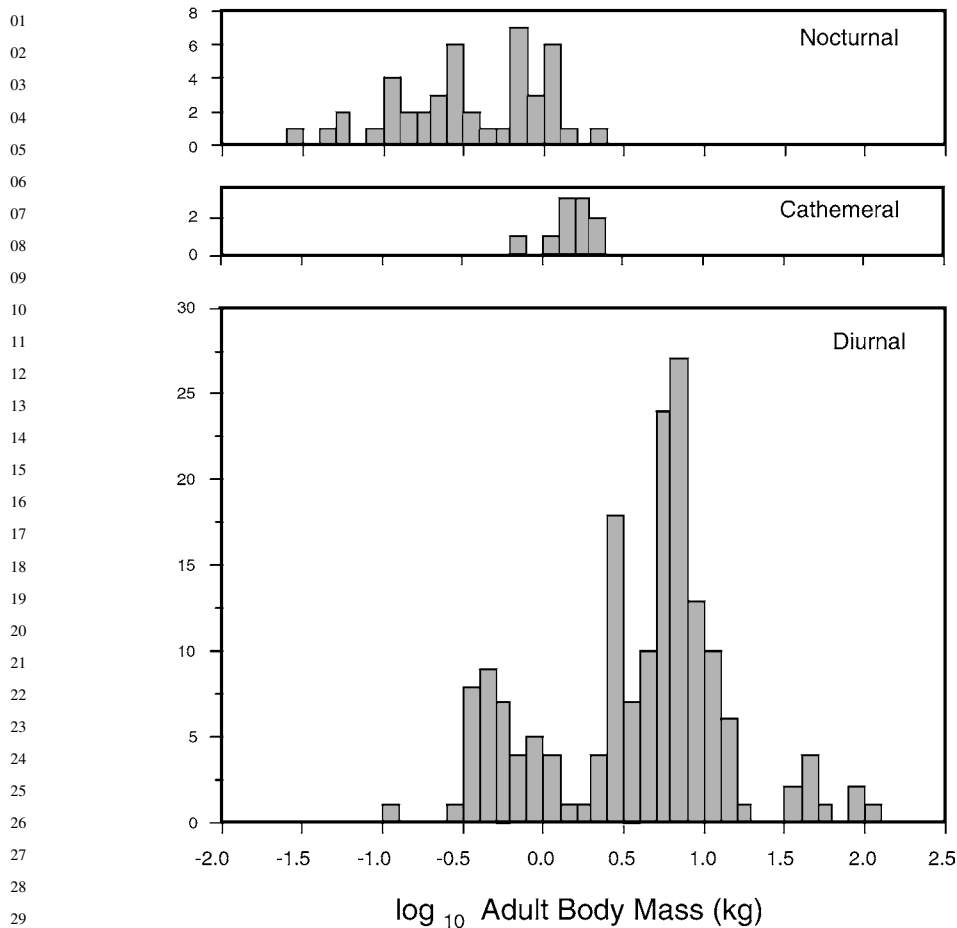
In fact, there are major differences between mammalian groups in the structure of the tapetum and in the active principle responsible for reflective properties (Schwab *et al.*, 2002). As a general rule, a tapetum serves to increase the amount of light absorbed by the photoreceptors, reflecting photons that were not initially absorbed on their first pass. It is always located behind the photoreceptors, but may occur either in the choroid (choroidal tapetum) or, more rarely, in the deep retina (retinal tapetum). Furthermore, two different kinds of choroidal tapeta can be recognized: (1) the tapetum fibrosum, which is the simplest type with stacks of densely packed collagen fibrils, and (2) the tapetum celluloseum, with reflecting cells stacked in a tile-like array. Strepsirrhine primates possess a tapetum celluloseum and therefore differ from several other mammal

01 groups that have either a tapetum fibrosum (e.g. elephants, horses, artiodactyls, cetaceans,  
02 some marsupials, and at least one rodent) or a retinal tapetum (e.g. some marsupials and  
03 megachiropteran bats). Certain mammals, such as carnivores and pinnipeds, superficially  
04 resemble strepsirrhine primates in possessing a tapetum cellulosum, but the active prin-  
05 ciple is different. The eyeshine of carnivores, for example, has a distinctive greenish  
06 hue, while it has been reported that the pen-tailed tree-shrew (*Ptilocercus*) – the only  
07 nocturnal scandentian – has a silvery eyeshine (Emmons, 2000). This wide variation in  
08 constitution indicates that tapeta have evolved several times independently in different  
09 mammalian lineages. This is, for instance, the most likely explanation for the fact that  
10 marsupials can possess either a tapetum fibrosum or a retinal tapetum. The development  
11 of a tapetum cellulosum with riboflavin as the active principle therefore seems to be  
12 a shared derived feature characterizing the common ancestor of strepsirrhine primates.  
13 This, in turn, strongly indicates that the common ancestor of strepsirrhines was nocturnal  
14 in habits. It is possible that a tapetum of some kind was already present in ancestral  
15 primates and was then lost in the common ancestry of haplorhines, as was suggested by  
16 Ross (2000); but it is also possible that ancestral primates did not possess a tapetum, or  
17 at least did not possess a tapetum with riboflavin as the active principle, and that this  
18 was first developed in the lineage leading to strepsirrhine primates (Martin, 1990).

19 The distinction between nocturnal, cathemeral, and diurnal habits among primates  
20 shows an obvious association with body mass (Figure 1.7). Nocturnal primates tend to be  
21 quite small, with a modal body mass of only 315 g, whereas diurnal primates are generally  
22 much larger, with a modal body mass that is more than 17 times greater (5.45 kg). The  
23 modal body mass of cathemeral primates (1.66 kg) is intermediate between these two  
24 main categories. The generalization that nocturnal species tend to be smaller than diurnal  
25 species applies across mammals, and Charles-Dominique (1975) proposed that this could  
26 be an outcome of competition with birds. Using data from tropical forest ecosystems  
27 in Africa and South America, he argued that mammals are typically nocturnal within  
28 the body size range covered by flying birds (up to about 5 kg). Diurnality is common  
29 only among mammals that exceed a body mass of 5 kg. In reasonable agreement with  
30 this, no nocturnal primate has a body mass greater than 2.5 kg, while 91 of 171 diurnal  
31 primate species have a body mass exceeding 5 kg. This is of crucial importance with  
32 respect to the overall phylogenetic tree of mammals (Figure 1.8). The precursors of  
33 mammals, the mammal-like reptiles (synapsids), were generally of moderate to large  
34 body size. By contrast, the first mammals, which appeared near the Jurassic/Triassic  
35 boundary some 200 mya, were relatively small, comparable in size to modern shrews  
36 or mice. This remained true for the next 135 my up until the end of the Cretaceous,  
37 about 65 mya (i.e. for the first two-thirds of mammalian evolutionary history). Partly for  
38 this reason, it has been generally accepted that early mammals were nocturnal and that  
39 diurnal habits did not emerge until the Tertiary, when a general trend toward increasing  
40 body size is seen in many lineages (Alroy, 1998). Accordingly, the late Jurassic/early  
41 Cretaceous common ancestors of marsupials and placentals were presumably both small  
42 and nocturnal. Against this background, it is most parsimonious to assume that, following  
43 their divergence from ancestral placental mammals, the ancestral primates had remained  
44 nocturnal (see Figure 1.6).

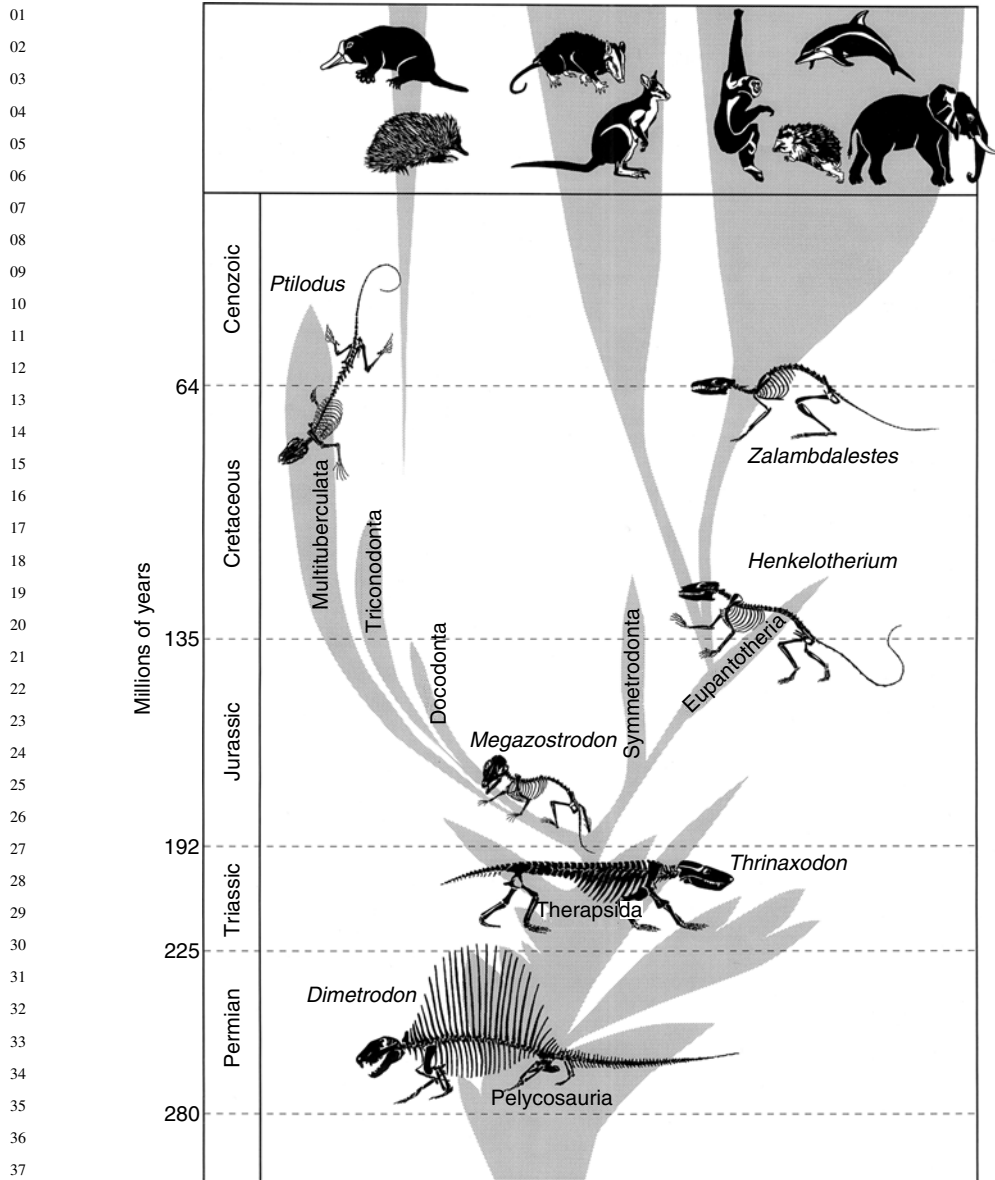
45 Whereas ancestral primates were seemingly nocturnal, there are several indications  
46 that the common ancestor of haplorhines was diurnal (Martin, 1990; Heesy and Ross,

12 The Evolutionary and Ecological Context of Primate Vision



**Figure 1.7** Histograms showing body mass distributions for nocturnal, cathemeral, and diurnal primates (data from Smith and Jungers, 1997). Nocturnal primates (mean value: 545 g; modal value: 315 g) are generally smaller than diurnal primates (mean value: 8.07 kg; modal value: 5.45 kg), with cathemeral primates being intermediate (mean value: 1.61 kg; modal value: 1.66 kg). However, there is considerable overlap, particularly because marmosets and tamarins are all diurnal despite their small body sizes

2001). In the only nocturnal haplorhines, *Tarsius* and *Aotus*, the retina shows a number of features indicative of a diurnal ancestry. In the first place, both *Tarsius* and *Aotus* lack a tapetum lucidum and have developed particularly large eyes that may compensate for this. More strikingly, a fovea (a pit with a higher density of receptors) is present in the central area of the retina of *Tarsius* (Polyak, 1957; Wolin and Massopust, 1970; Castenholz, 1984; Ross, 2000, 2004). Curiously, the presence of a fovea is variable in the nocturnal simian *Aotus* (Provis *et al.*, 1998), but there is definitely a foveal pit in some individuals. Haplorhine primates are the only mammals that consistently possess a



**Figure 1.8** Outline phylogenetic tree for mammals. Modern mammals are divided into three groups: monotremes, marsupials, and placentals. Fossil mammals first appear in the record at the Triassic/Jurassic boundary, about 195 mya. They are derived from mammal-like reptiles (synapsids), which diverged from the diapsid reptiles leading to modern reptiles and birds at least 310 mya. For approximately two-thirds of their evolutionary history, between the Triassic/Jurassic boundary and the Cretaceous/Tertiary boundary 65 mya, the mammals remained very small and are widely presumed to have been nocturnal in habits. Original illustration by Lukrezia Bieler-Beerli

01 histologically identifiable retinal fovea, so this is another unique feature that characterizes  
02 this group. The fovea is interpreted as an adaptation for high visual acuity and it is  
03 typically associated with a high density of cones and hence with diurnal habits and  
04 some degree of color vision (see Chapter 5). Although a fovea is unique to haplorhine  
05 primates among mammals, it is a common feature in diurnal birds and lizards with well-  
06 developed visual acuity and color vision (Ross, 2004). In diurnal haplorhines, the fovea  
07 is consistently associated with a yellow spot (macula lutea) that has been interpreted as  
08 promoting high visual acuity (Kirk and Kay, 2004). Interestingly, in *Tarsius* (although  
09 not in *Aotus*) the fovea is surrounded by a faint yellow macular pigment (Hendrickson  
10 *et al.*, 2000). Overall, it is reasonable to conclude that both *Tarsius* and *Aotus* are derived  
11 from a diurnal ancestral haplorhine possessing both color vision and a fovea, and that  
12 there has been some subsequent reduction in the fovea that has for some reason progressed  
13 further in *Aotus* than in *Tarsius*.

14 Diurnal anthropoids also have a distinctive eye shape in comparison with other  
15 mammals, having a large axial diameter relative to cornea diameter (Ross, 2000). A larger  
16 axial diameter increases the focal length of the eye, thereby increasing image size and –  
17 all other things being equal – visual acuity as well. Just as other diurnal mammals do  
18 not share a retinal fovea and postorbital septum with anthropoids, they also lack the  
19 enlarged axial diameters relative to cornea size seen in anthropoids, along with their high  
20 visual acuity (Ross, 2000). Anthropoid primates are unusual among mammals in their  
21 adaptations for high visual acuity.

## 22 23 **1.3 Comparative analyses of cranial dimensions**

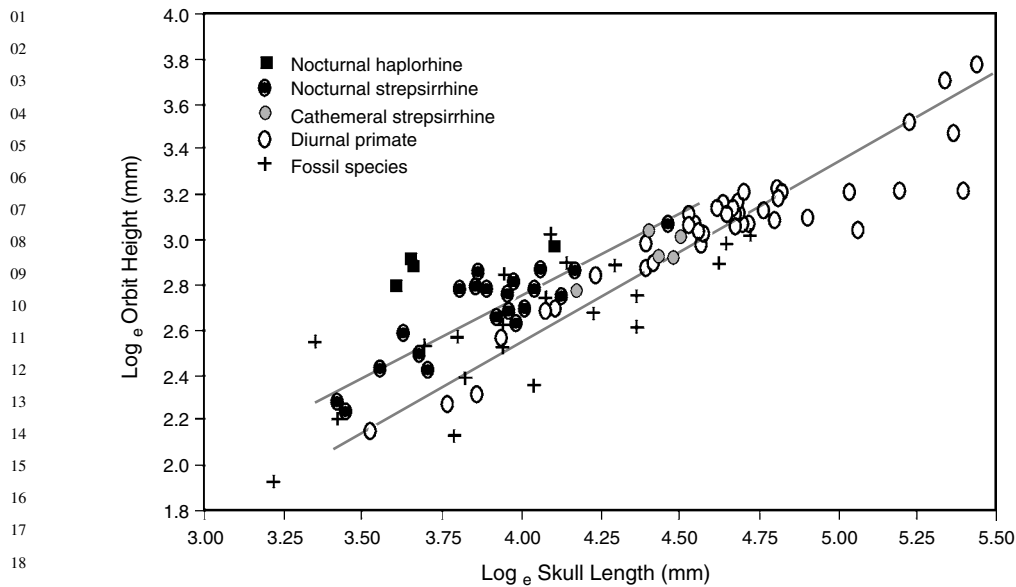
### 24 25 **1.3.1 Allometric analysis of the eye and orbit**

26  
27 A basic guide to visual adaptations in primates and other mammals can be obtained by  
28 simply examining dimensions of the eyeball or of the bony socket (orbit) in which it  
29 resides. As has already been noted, a bivariate plot of eyeball diameter against head-and-  
30 body length for a representative sample of mammals (Figure 1.3) confirms the expectation  
31 that primates tend to have relatively large eyes (Ross, 2000). However, there is consider-  
32 able overlap between primates and certain other mammals, and it is noteworthy that only  
33 some nocturnal primates (especially tarsiers) have exceptionally large eyes in comparison  
34 to all other mammals. Nevertheless, it should also be noted that most non-primate mam-  
35 mals are nocturnal, so diurnal primates overlap with many mammals that are nocturnal,  
36 while nocturnal primates commonly have larger eyes than other nocturnal mammals.  
37 Given that a larger retina can potentially accommodate more photoreceptors, it would  
38 seem that in nocturnal primates (but not in most other nocturnal mammals) the number  
39 of photoreceptors has generally increased markedly as an adaptation to high-acuity  
40 vision under scotopic conditions (Ross *et al.*, in press; see also Chapter 2 for differences  
41 between diurnal and nocturnal primates in the ontogenetic development of the retinae).

42 Data on the size of the eyeball are relatively scarce (Schultz, 1940; Rohen, 1962;  
43 Ritland, 1982) and are, of course, completely lacking for fossil species. It is therefore  
44 useful to have a substitute dimension on the skull that can be used as an indicator of  
45 eye size, and the size of the orbit has been widely used for this purpose (Kay and  
46 Cartmill, 1977; Martin, 1990; Kay and Kirk, 2000; Ross, 2000; Heesy and Ross, 2001).

01 It should at once be noted that there is a pervasive problem involved in taking the size  
 02 of the orbit as an indicator of eye size. Although the size of the eye generally increases  
 03 progressively with body size, the former does not keep pace with the latter (i.e. there is  
 04 a negatively allometric relationship). This generalization, labeled ‘Haller’s Law’, applies  
 05 not only to primates and other mammals (Ritland, 1982; Martin, 1990; Kay and Kirk,  
 06 2000) but also to other terrestrial vertebrates such as birds (Brooke *et al.*, 1999). As a  
 07 result, the ratio of eye size to skull size progressively declines as body size increases.  
 08 One outcome of this is that the eye does not completely fill the orbit in large-bodied  
 09 mammals, even in the relatively large-eyed primates (Martin, 1990; Kay and Kirk, 2000).  
 10 Particular caution must therefore be exercised in inferring the size of the eye from the size  
 11 of the orbit in large-bodied mammals. There is an additional problem in that body size  
 12 must be indirectly inferred for fossil species, so a substitute measure must also be taken.  
 13 A common approach is to take the maximum length of the skull (prosthion–inion length)  
 14 as an indicator of overall body size. This has the advantage that a relatively complete  
 15 skull will yield data indirectly indicating both eye size and body size. On the other hand,  
 16 it is important to note that skull length itself can vary relative to body size and may  
 17 hence be misleading as an indicator of overall body size. This applies particularly to the  
 18 long-snouted baboons, which have undergone a secondary increase in muzzle length.

19 Despite the inherent limitations, a bivariate plot of orbit height against skull length for  
 20 living and fossil primates (Figure 1.9) yields a number of valuable conclusions. In the first  
 21 place, among living primates there is a fairly clear grade distinction between nocturnal  
 22 and diurnal species. Tarsiers have the largest orbits relative to skull size, while nocturnal  
 23 strepsirrhines (most lemurs and all lorises) and owl monkeys come next, generally having  
 24 relatively larger orbits than diurnal primates (some lemurs and all simian primates except  
 25 owl monkeys). However, although there is an overall grade separation between nocturnal  
 26 strepsirrhines and diurnal primates, there is a considerable amount of overlap. As might  
 27 be expected, cathemeral lemur species fall in this zone of overlap between nocturnal and  
 28 diurnal species. For comparative purposes, especially for interpretation of data from fossil  
 29 species, it is useful to examine positive and negative deviations (residual values) relative  
 30 to some overall best-fit line. Unfortunately, because of the considerable scatter of data in  
 31 Figure 1.9, the choice of an appropriate best-fit line to use as a standard for comparison is  
 32 not immediately obvious. Following the pragmatic approach taken by Martin (1990), the  
 33 least-squares regression line fitted to extant diurnal primates (excluding the long-snouted  
 34 baboons) in Figure 1.9 can be taken as one option for calculation of residual values.  
 35 The distributions of residual values (Figure 1.10) confirm the main conclusions from  
 36 visual inspection of the bivariate plot. Nocturnal primates generally have relatively larger  
 37 orbits than diurnal primates, with the nocturnal haplorhines (especially tarsiers) having  
 38 conspicuously enlarged orbits. The distribution of residual values for relative orbit size  
 39 in cathemeral primates is intermediate between those for nocturnal and diurnal primates.  
 40 However, the histograms in Figure 1.10 also reveal that, despite the wide range of values  
 41 for relative orbit size shown by each category, there is only partial overlap. The maximum  
 42 logarithmic residual value for a diurnal primate is 0.123, found in the Old World leaf  
 43 monkey *Trachypithecus cristatus*. This value in fact exceeds or equals those found in  
 44 four nocturnal strepsirrhines (*Arctocebus calabarensis*, 0.080; *Perodicticus potto*, 0.090;  
 45 *Cheirogaleus medius*, 0.095; *Microcebus murinus*, 0.123); but all other nocturnal primates  
 46 show values exceeding that for *Trachypithecus*.



**Figure 1.9** Scaling of orbit height ( $H$ ) against maximal skull length ( $S$ ) for 71 extant and 21 fossil primate species (data from Kay and Kirk, 2000, supplemented with data for 11 additional extant primate species measured by the first author). The two least-squares regression lines, for orientation only, are for nocturnal strepsirrhine primates (upper line;  $n = 21$ ;  $\log_e H = 0.736 \cdot \log_e S - 0.182$ ;  $r^2 = 0.788$ ) and for diurnal primates, excluding the long-snouted baboons (lower line;  $n = 37$ ;  $\log_e H = 0.793 \cdot \log_e S - 0.616$ ;  $r^2 = 0.948$ ). The lines are approximately parallel, indicating a grade distinction between these two categories of primates: extant nocturnal primates generally tend to have relatively larger orbits than extant diurnal primates. However, there is considerable overlap between members of the two grades. The scaling exponent is less than 1 for both lines, reflecting the fact that the size of the orbit does not keep pace with increasing skull size ('Haller's Law'). Fossil primates show considerable scatter for the relationship between orbit height and skull length. Note that the point for *Teilhardina asiatica* (minimal values for both skull length and orbit height) lies below the range of values for modern primates

In fossil primates, residual values indicating relative orbit height cover a wide range, extensively overlapping those for both nocturnal and diurnal species among extant primates. Relatively large orbits, indicated by residual values greater than for *Trachypithecus*, are found in some Eocene omomyiforms (*Microchoerus*, *Necrolemur*, *Shoshonius*), a few Eocene adapiforms (*Mahgarita*, *Pronycticebus*), an enigmatic Oligocene strepsirrhine (*Plesiopithecus*), and the Miocene loriform *Mioeoticus*. The Eocene omomyiform *Tetonius* has a value of 0.123, matching that of *Trachypithecus*, while all other fossil primates examined have smaller residual values lying within the range of extant diurnal primates. This applies to the Eocene omomyiform *Teilhardina*, several Eocene adapiforms (*Smilodectes*, *Leptadapis*, *Notharctus*, *Adapis*), the Oligocene prosimian *Rooneyia*, late Eocene/early Oligocene stem simians (*Catopithecus*, *Aegyptopithecus*, *Apidium* and *Proteopithecus*), and Miocene New World monkeys (*Tremacebus*, *Dolichocebus*). In fact,

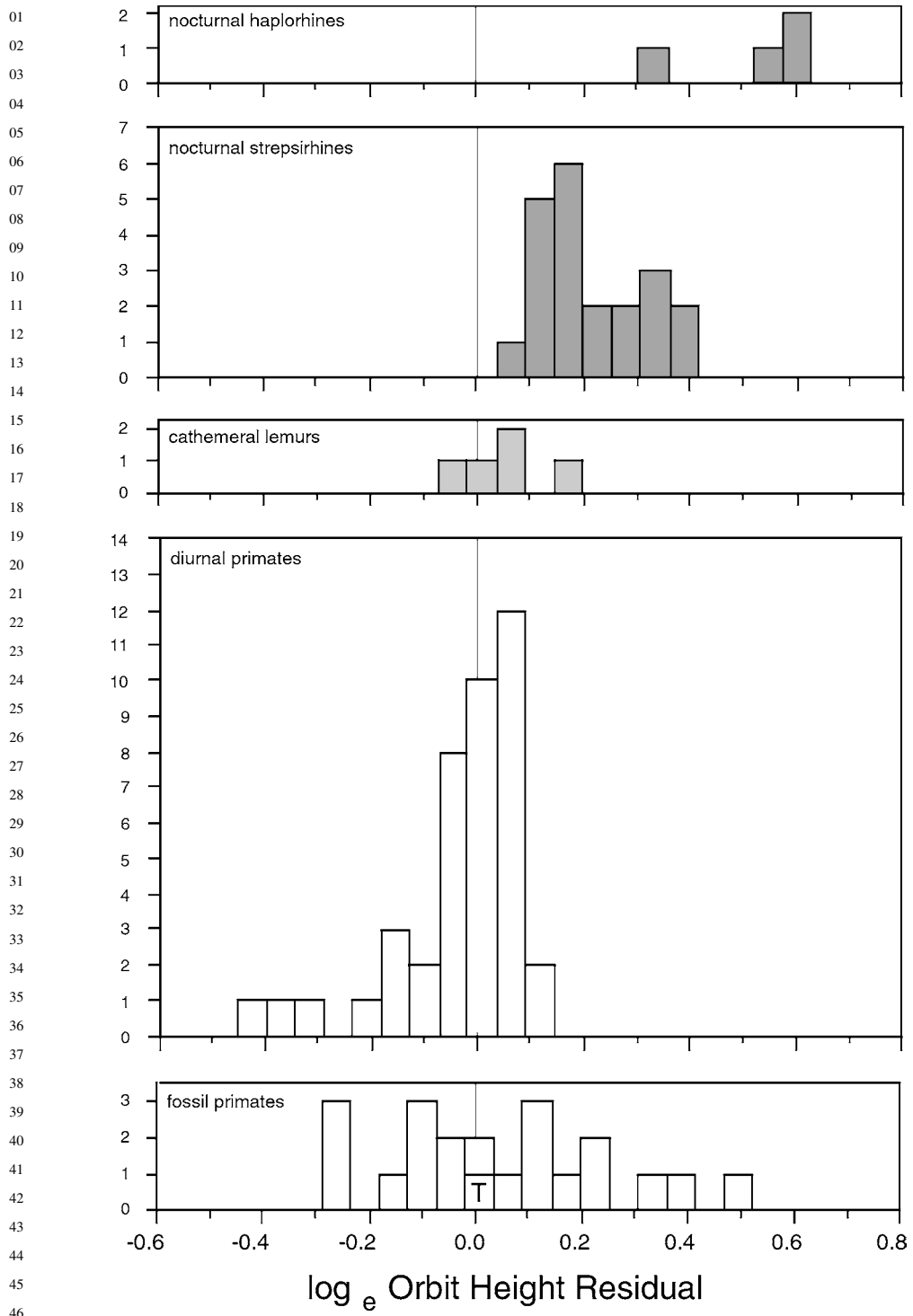


01 *Apidium*, *Adapis*, and *Proteopithecus* all have strikingly small orbits. Among living pri-  
 02 mates, only the long-snouted baboons (*Mandrillus*, *Papio*, and *Theropithecus*) and the  
 03 patas monkey (*Erythrocebus*) have comparably small orbits relative to skull length.

04 Because early fossil euprimates include species with both large and small orbits relative  
 05 to skull size, it is not immediately apparent from this source of evidence whether ancestral  
 06 euprimates would have been nocturnal or diurnal. However, a phylogenetic analysis  
 07 conducted by Heesy and Ross (2001) yielded as the most parsimonious solution the  
 08 conclusion that ancestral euprimates were probably both nocturnal and dichromatic. This  
 09 inference was subsequently challenged by Ni *et al.* (2004) on the basis of the small relative  
 10 size of the orbits in a newly discovered skull of the early omomyiform *Teilhardina*  
 11 *asiatica*. It is, indeed, true that for *Teilhardina* the residual value for orbit size in relation to  
 12 skull length falls among values for extant diurnal primates. Probably because *Teilhardina*  
 13 *asiatica* seems to occupy a very basal position in the phylogenetic tree for primates, when  
 14 Ni *et al.* (2004) repeated the phylogenetic analysis conducted by Heesy and Ross (2001),  
 15 they came to the opposing conclusion that the ancestral primates were diurnal. Thus,  
 16 this new analysis seemingly challenges the long-standing interpretation that ancestral  
 17 primates had retained nocturnal habits from their mammalian heritage. Before abandoning  
 18 this well-established view, however, it is necessary to consider a number of special  
 19 factors in the interpretation of relative orbit size of *Teilhardina asiatica* (Martin, 2004).  
 20 In the first place, it should be noted that the inferred body mass of this early fossil  
 21 primate is less than 30 g, which is smaller than that of any extant primate species. Hence,  
 22 calculation of the residual value for the size of the orbit relative to skull length requires  
 23 extrapolation below the range of variation found among modern primates (Figure 1.9).  
 24 On statistical grounds alone, such extrapolation is questionable. In addition, as is evident  
 25 from Figure 1.3, the relationship between eye and body size is clearly curvilinear, being  
 26 positively allometric at small body size and becoming negatively allometric at large  
 27 body size. Ni and coworker's extension of the relationship seen in extant primates to the  
 28 smaller fossil does not take this curvilinearity into account. More importantly, caution  
 29 is necessary in another kind of extrapolation, namely in interpreting the relative size of  
 30 the orbit in fossil primates directly on the basis of relationships determined for modern  
 31 primates. Given the very wide range of variation in relative size of the orbit found among  
 32 fossil primates, it seems likely that both nocturnal and diurnal habits were represented.  
 33 In particular, it would seem likely that species with very large orbits (e.g. the Eocene  
 34 omomyiforms *Microchoerus*, *Necrolemur*, and *Shoshonius*) were nocturnal, while those  
 35 with very small orbits (e.g. the adapiform *Adapis* and the early simians *Apidium* and  
 36 *Proteopithecus*) were diurnal. But for species with orbits of intermediate size (including  
 37 *Teilhardina*, which lies close to the borderline between modern diurnal and nocturnal  
 38 species; see Figure 1.10), it would be unwise to draw any firm conclusions in the absence  
 39 of additional evidence.

40 It should also be noted that there is a marked phylogenetic influence on the relationship  
 41 between orbit size and body size in primates. In a plot of orbit diameter against body mass  
 42 for prosimians (Figure 1.11), it can be seen that lorisiforms tend to have relatively larger  
 43 orbits than lemuriforms, while the largest orbits of all are found in tarsiers. Furthermore,  
 44 all lemur species conform closely to a single best-fit line despite the fact that they may  
 45 exhibit nocturnal, cathemeral, or diurnal habits. Hence, for lemurs the scaling of orbital  
 46 diameter to body size reveals no clear separation according to activity pattern. It is

18 *The Evolutionary and Ecological Context of Primate Vision*



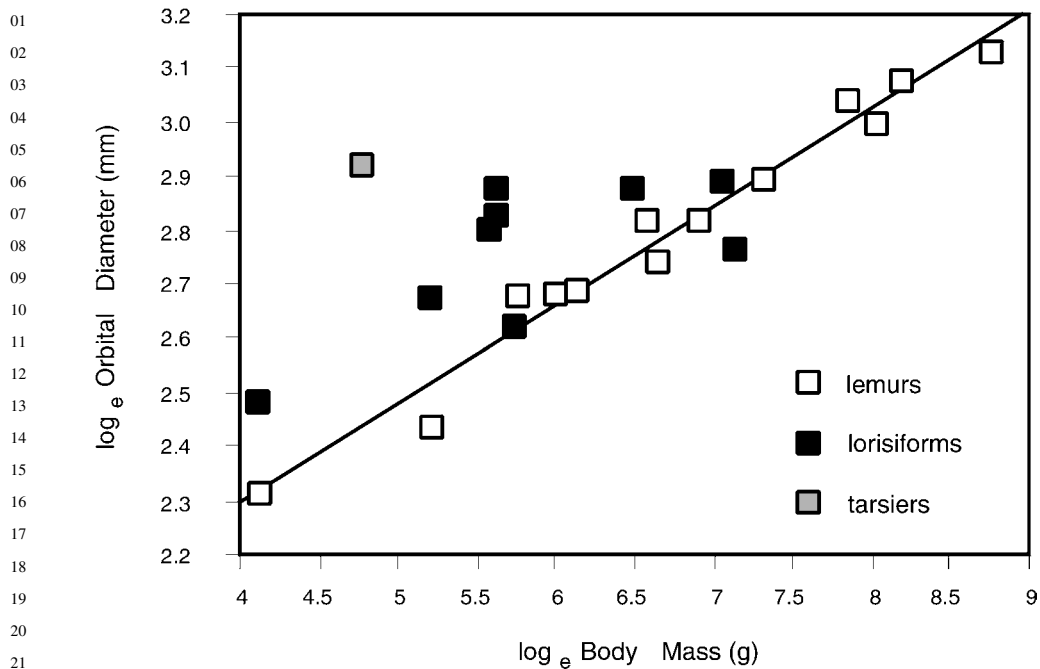
01 also noteworthy that the two African lorid genera (*Arctocebus* and *Perodicticus*) both  
 02 possess relatively small orbits in comparison with other loridiforms. Given this apparent  
 03 phylogenetic influence, the interpretation of relative orbit size in isolation should be  
 04 treated with appropriate caution. A reconstruction of nocturnal habits in basal primates  
 05 is also more parsimonious when the appropriate outgroups are added to the primate  
 06 phylogeny of Ni *et al.* (2004). Most importantly, the pen-tailed tree-shrew (*Ptilocercus*)  
 07 and the flying lemurs are all nocturnal, firmly fixing nocturnality at the basal primate  
 08 node, regardless of the activity pattern inferred for *Teilhardina asiatica*.

09 Measurements conducted on the skull can also yield valuable information on the  
 10 orientation of the orbit and, by inference, of the eyes themselves. Orientation of the  
 11 orbit includes both convergence and frontation (Figure 1.12). Orbital convergence is  
 12 the degree of forward rotation of the orbit, measured as the dihedral angle between  
 13 the mid-sagittal plane and the plane of the orbital margin (Cartmill, 1972). Forward  
 14 rotation of the orbit directly influences the angular magnitude of the binocular field and  
 15 hence the extent of three-dimensional vision. The primitive condition in mammals is  
 16 for the orbits to be oriented almost entirely laterally (degree of convergence not much  
 17 above 0°), such that there is only a relatively small binocular field (Figure 1.4; Ross,  
 18 2000; Heesy, 2004). Accordingly, progressive increase in the level of orbital convergence  
 19 to approach the maximum value of 90° (orbits facing directly forwards) is an advanced  
 20 feature corresponding to an increase in the magnitude of the binocular field. Frontation  
 21 is the degree of verticality of the orbital margin, measured as the plane angle between  
 22 the nasion-inion line and the chord along which the orbital and mid-sagittal planes  
 23 intersect (Cartmill, 1972). Primitively, the plane of the orbital margin is oriented obliquely  
 24 upwards in primates and the degree of frontation can be as low as 40° in some extant  
 25 prosimian primates. As an advanced feature among primates, the orbital plane becomes  
 26 more vertical in orientation and can in fact overshoot the vertical (i.e. 90°) to reach a  
 27 value of up to 110°.

28 Convergence and frontation of the orbits in primates were originally studied in detail  
 29 by Cartmill (1970, 1972), with an emphasis on prosimians. In a later study using the same  
 30 methods, Ross (1995b) examined a larger sample of primate species and focussed more  
 31 on the particularly advanced condition found in simian primates. Simians differ quite  
 32 markedly from prosimians in the range of values for both convergence and frontation,  
 33 which are generally higher in simians and show relatively little overlap with the values  
 34 for prosimians. Thus, in simians the orbits are generally not only more forward-oriented

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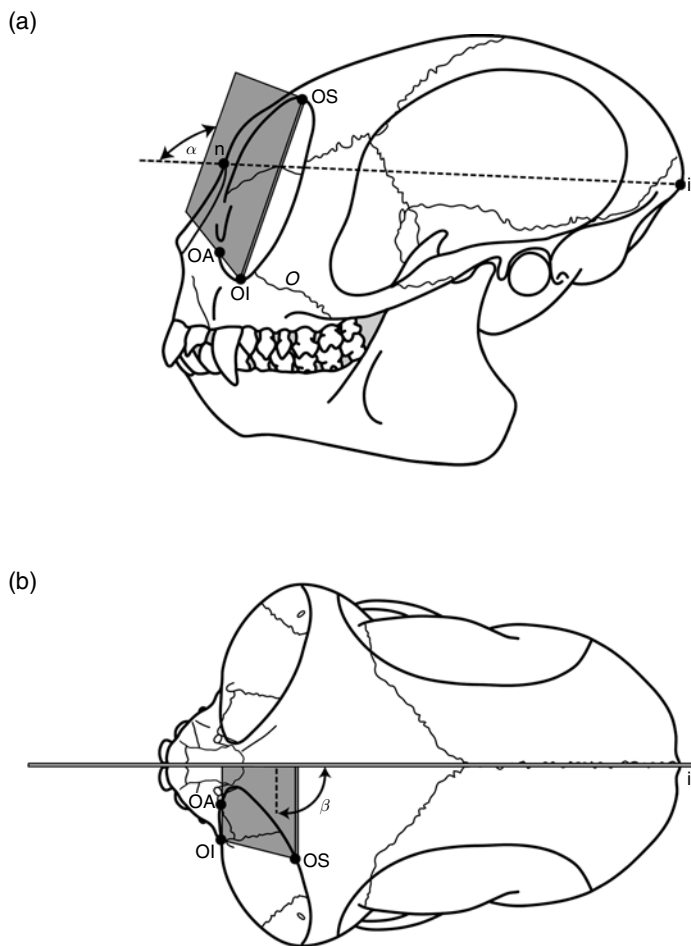
36  
 37 **Figure 1.10** Histograms showing residual values for orbit height for modern and  
 38 fossil primates, derived from the bivariate plot in Figure 1.9. The least-squares regres-  
 39 sion line for diurnal primates (excluding the long-snouted baboons) was taken as  
 40 the baseline for calculations. Modern nocturnal species (dark bars) generally have  
 41 relatively larger orbits than modern diurnal species (white bars), while cathemeral  
 42 species (hatched bars) are intermediate. However, there is some overlap between  
 43 the three categories. Fossil primates cover almost the entire range of relative orbit  
 44 sizes found among modern primates and presumably included nocturnal, diur-  
 45 nal, and perhaps cathemeral species. The value for the early fossil omomyiform  
 46 *Teilhardina* (T) falls very close to the boundary between modern nocturnal and diur-  
 nal species



**Figure 1.11** Scaling of orbit diameter ( $D$ ) against body mass ( $M$ ) for prosimian primates. The least-squares regression line, for orientation only, is for lemurs alone ( $n = 13$ ;  $\log_e H = 0.182 \cdot \log_e M + 1.569$ ;  $r^2 = 0.973$ ). Although different lemur species exhibit nocturnal, cathemeral, or diurnal habits, they all conform closely to a single best-fit line. Lorisiforms, all of which are nocturnal, tend to have larger orbits than lemurs, although the African lorisids *Arctocebus* and *Perodicticus* are exceptional in possessing relatively small orbits

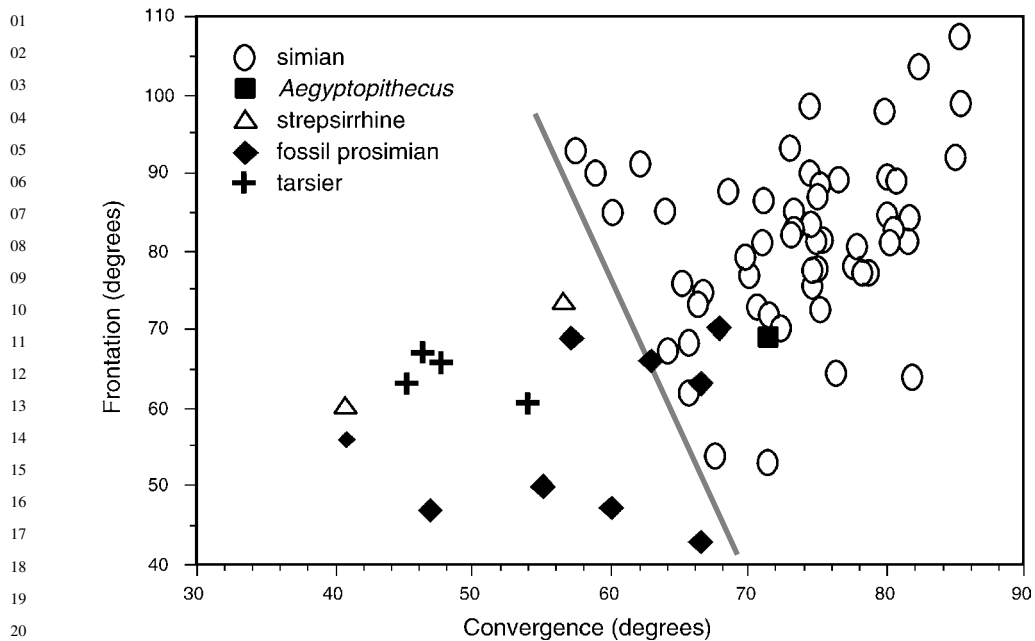
but also more vertical. The results are best summarized by a combined plot of frontation against convergence, which reveals a clear separation between modern prosimians and simians (Figure 1.13). Among simian primates, increases in convergence are accompanied by increases in frontation, whereas in prosimians increases in convergence are accompanied by decreases in frontation. Simians converge their orbits to the fronts of the heads, prosimians to the top. It is noteworthy that the tarsiers in this case lie firmly within the distribution for strepsirrhine primates and do not show the more advanced condition that typifies the skull of simians. Most fossil primates in the sample examined by Ross (1995b) also fall within the strepsirrhine range, although there are a few exceptions. In addition to a number of Eocene fossil prosimians (*Adapis*, *Leptadapis*, and *Microchoerus*), two large-bodied subfossil lemurs (*Megaladapis* and *Palaeopropithecus*) fall within the distribution for modern prosimian primates. The Oligocene 'omomyiform' *Rooneyia* falls on the boundary between modern prosimians and simians, while two medium-sized subfossil lemurs (*Archaeolemur* and *Mesopropithecus*) and the early Oligocene simian *Aegyptopithecus* clearly fall among the simians. In this context, it should be noted that one implication of 'Haller's Law' is that a high degree of convergence may be easier

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**Figure 1.12** Illustrations of degrees of convergence and frontation in the primate skull, taking the example of *Aotus*. (A) Frontation (lateral view): the sagittal plane is shown with light shading, while the plane of the orbital margin is heavily shaded. The sagittal plane passes through nasion (n) and inion (i). The plane of the orbital margin passes through orbitale inferius (OI), orbitale superius (OS), and orbitale anterius (OA). The angle of frontation is equal to  $180^\circ - \alpha$ . (B) Convergence (superior view): the sagittal plane is indicated by the shaded line. The angle of convergence is equal to  $\beta$ . Reproduced from Ross (1995b), with kind permission from Elsevier, Inc.

to acquire in larger-bodied species because the eyes are smaller in relation to skull size. Hence, it is conceivable that the generally greater degrees of convergence found in simian primates are attributable, at least in part, to the fact that the average body size of simians is considerably greater than that of prosimians. However, this does not fit well with the observation that large-bodied subfossil lemurs fall into the prosimian range with respect to orbital convergence whereas medium-sized subfossil lemurs overlap



**Figure 1.13** Plot of frontation against convergence for modern and fossil primates (data from Ross, 1995b). Modern prosimians (strepsirrhines and tarsiers) show moderate degrees of convergence and frontation, while modern simians generally show higher values for both measures. It is possible to define a boundary that separates all prosimians from all simians (oblique dashed line). Whereas most fossil primates in the sample fall into the distribution for modern prosimians, the enigmatic Oligocene prosimian *Rooneyia* falls onto the boundary, while two subfossil lemurs (*Archaeolemur* and *Mesopropithecus*) fall at the lower end of the simian range

with simians. Cartmill (1970, 1972) proposed that convergence is primarily influenced by relative orbit diameter and relative interorbital breadth. However, comparisons with other mammals (carnivores and fruit-bats) throw some doubt on this conclusion. Noble *et al.* (2000) found that data from felid carnivores and fruit-bats provided limited support for Cartmill's hypothesis, while data from herpestid carnivores provided no support at all. Hence, it would seem that additional factors might be involved in the evolution of orbital convergence in primates. Noble and coworkers found evidence that brain size (which tends to be larger in primates than in other mammals and is reflected in a relatively larger braincase) may be an important contributory factor.

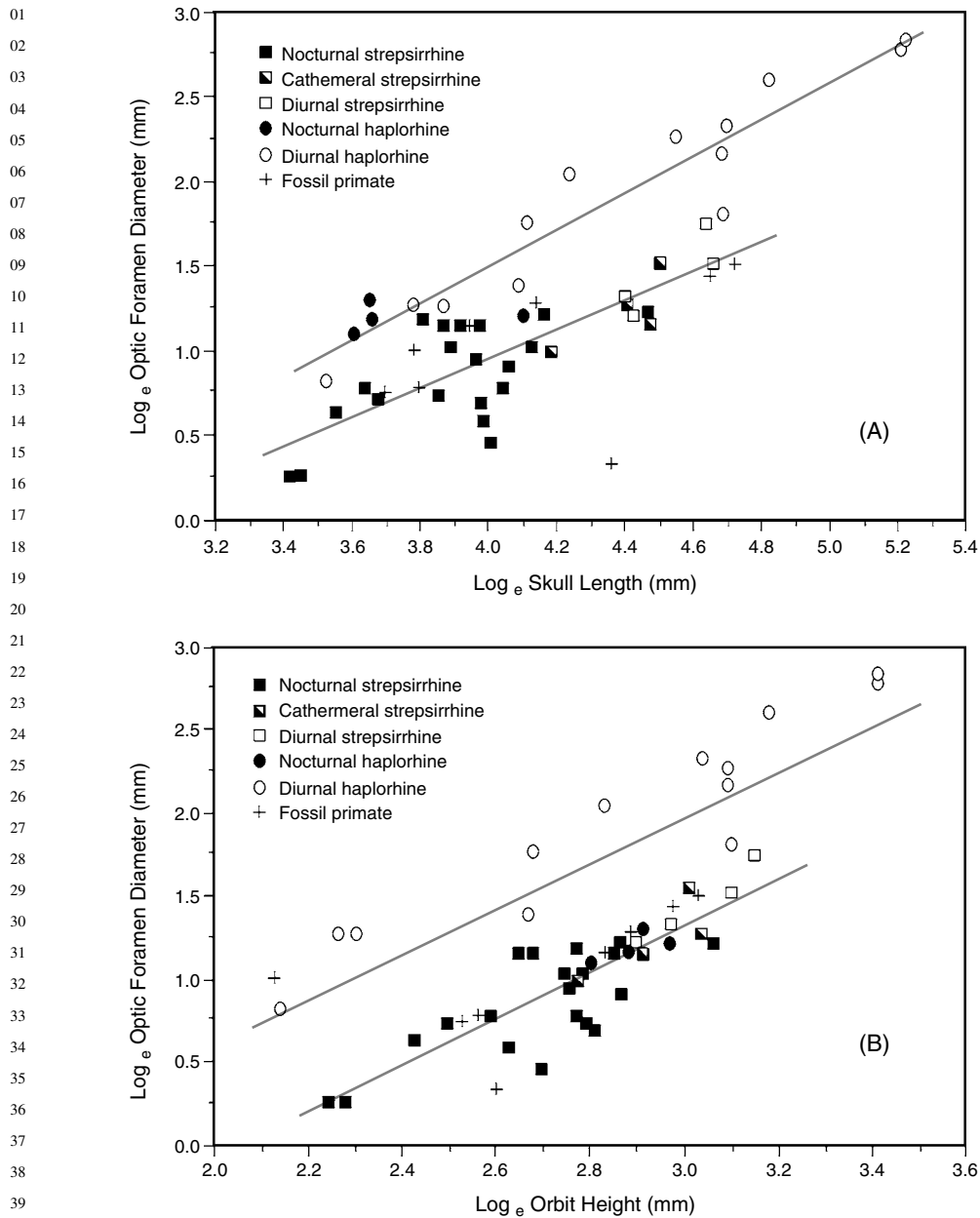
### 1.3.2 Allometric analysis of optic canal size

Valuable additional information for interpreting visual adaptations can be obtained from the skull of living and fossil primates by examining the relative size of the optic foramen, through which the optic nerve passes on its way to the brain. A key factor in the processing of photoreceptor signals is the trade-off between sensitivity and visual acuity. In dim light, increased sensitivity can be achieved through summation of the inputs from

01 photoreceptors, but this necessarily entails a reduction in visual acuity, which is enhanced  
 02 by maximizing inputs from small numbers of photoreceptors (Chapters 4–6). In line with  
 03 this, it is a general rule that rods show more summation than cones. Hence, it is only to  
 04 be expected that nocturnal primate species should show a greater degree of summation  
 05 than diurnal species, and it was indeed demonstrated by Hassler (1967) and Stephan  
 06 *et al.* (1984) that nocturnal primates typically have much smaller optic nerves than diurnal  
 07 primates. This was further confirmed by a study conducted by Kay and Kirk (2000), who  
 08 also reviewed data confirming that diurnal haplorhines perform considerably better on  
 09 tests of visual acuity than all other mammals. After demonstrating with a sample of living  
 10 primates that data for the size of the optic foramen yield very similar results to those  
 11 provided by information on the size of the optic nerve itself, Kay and Kirk proceeded  
 12 to investigate scaling of the optic foramen in extant and fossil primates. In accordance  
 13 with expectation, it was found that nocturnal primates showed the smallest values for  
 14 relative size of the optic foramen, whereas diurnal simians showed the largest values.  
 15 Interestingly, although the relative size of the optic foramen was found to be significantly  
 16 larger in diurnal lemurs than in nocturnal primates, the difference was relatively small  
 17 and far more limited than for diurnal simians. Thus, it would seem that in diurnal lemurs  
 18 visual sensitivity is only slightly decreased in comparison with nocturnal primates, while  
 19 visual acuity is only marginally greater. This fits well with the observation that there is  
 20 very little distinction between nocturnal and diurnal lemurs with respect to the relative  
 21 size of the orbit (Figure 1.11).

22 In fact, re-analysis of some of the data collected by Kay and Kirk (2000) provides an  
 23 additional perspective on scaling of the optic foramen (Figure 1.14). When the diameter  
 24 of the foramen is plotted against orbit height (Figure 1.14A), there is a relatively clear  
 25 grade separation between modern strepsirrhine primates and modern diurnal simians.  
 26 However, *Tarsius* species are found to lie very close to the line for diurnal simians,  
 27 whereas *Aotus* lies among the modern strepsirrhines. When optic foramen diameter is  
 28 plotted against skull length (Figure 1.14B), an even clearer grade separation between  
 29 modern strepsirrhines and modern diurnal simians is found. In this case, however, both  
 30 *Tarsius* species and *Aotus* lie clearly within the distribution for modern strepsirrhines.  
 31 The interpretation of this would seem to be that in *Tarsius* (but not in *Aotus*) the very  
 32 large size of the eyes is associated with a relatively large diameter of the optic nerve,  
 33 matching that in diurnal simians. In other words, it seems that *Tarsius* may be able to  
 34 combine a high degree of visual sensitivity with a relatively high level of visual acuity  
 35 simply by possessing a particularly large number of photoreceptors for its body size.  
 36 The difference between *Tarsius* and *Aotus* in this respect may explain why *Tarsius* has  
 37 consistently retained a clearly developed fovea whereas *Aotus* has not. It should also be  
 38 noted that there is no obvious distinction between diurnal lemurs and other strepsirrhines  
 39 in either Figure 1.14A or B, once again emphasizing the fact that there is no strong  
 40 indication of diurnal habits in lemurs from scaling of orbital dimensions.

41 As noted by Kay and Kirk (2000), the presence of a relatively small optic foramen  
 42 in the Eocene omomyiforms *Microchoerus* and *Necrolemur*, in the Eocene adapiform  
 43 *Pronycticebus*, and in the Oligocene strepsirrhine *Plesiopithecus* indicates that their eyes  
 44 were similar to those of modern nocturnal primates, with rod-dominated retinas showing  
 45 a marked degree of summation. By contrast, it can be inferred that the Eocene adapiform  
 46 *Leptadapis* and the enigmatic Oligocene prosimian *Rooneyia* resembled diurnal lemurs,



**Figure 1.14** (A) Scaling of optic foramen diameter ( $D$ ) against maximal skull length ( $S$ ) for extant and fossil primates (data from Kay and Kirk, 2000). The two least-squares regression lines, for orientation only, are for modern haplorhine primates (upper line;  $n = 17$ ;  $\log_e D = 1.089 \cdot \log_e S - 2.865$ ;  $r^2 = 0.900$ ) and for modern strepsirrhine primates (lower line;  $n = 28$ ;  $\log_e D = 0.866 \cdot \log_e S - 2.516$ ;  $r^2 = 0.665$ ). In this plot, modern tarsiers and diurnal simians together represent a distinct grade in relation to other



probably possessing moderate retinal summation and a larger cone:rod ratio than in nocturnal primates. In these cases, information from the relative size of the optic foramen reinforces inferences from the relative size of the orbit in indicating nocturnal or diurnal habits for those particular fossil primates. On one hand, it should be noted that the optic foramen is unusually small relative to skull length in the Eocene adapiform *Adapis*, suggesting a particularly high degree of summation (Figure 1.14A). On the other hand, when the size of the optic foramen in *Adapis* is considered in relation to orbital height, the deviation from other prosimian primates is far less marked (Figure 1.14B). In other words, the very small orbits of *Adapis* are matched by a very small size of the optic foramen. However, the comparatively high degree of summation that is indicated even by Figure 1.14B does not fit well with the common inference based on the small size of its orbits that *Adapis* was diurnal. This provides one very good example in which inference of the activity pattern through direct comparison with modern primates can be problematic.

## 1.4 Evolution of color vision

### 1.4.1 Occurrence of color vision among mammals

Very useful general reviews of the evolutionary background to color vision in mammals are provided by Jacobs (1993) and Ahnelt and Kolb (2000). Light-sensitive cells (photoreceptors) in the vertebrate retina can typically be divided into rods, adapted for monochromatic (black-and-white) vision under scotopic conditions, and cones, adapted for color vision under photopic (normal daylight) conditions. No mammal is known to have more than one kind of rod receptor, but most mammals have two types of cones, in principle providing a basis for dichromatic color vision. Rods are more sensitive to light than cones, so in dim light only the rods are functional. Conversely, signals from rods are saturated at the higher light intensities at which color vision operates well, so a fairly clear functional separation between rods and cones is to be expected. It is generally accepted that cones provide the basis for color vision and that two cone types are the minimal requirement. However, there are several indications (e.g. from work with humans) that rod signals can influence color vision. In fact, it has been shown that apparent behavioral evidence for trichromatic color vision in certain lemur species (*Eulemur fulvus* and *Lemur catta*) is attributable to a combination of signals from two cone types

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#### Figure 1.14 (continued)

modern primates. (B) Scaling of optic foramen diameter ( $D$ ) against orbital height ( $H$ ) for extant and fossil primates (data from Kay and Kirk, 2000). The two least-squares regression lines, for orientation only, are for modern haplorhine primates (upper line;  $n = 17$ ;  $\log_e D = 1.367 \cdot \log_e H - 2.143$ ;  $r^2 = 0.629$ ) and for modern strepsirrhine primates (lower line;  $n = 28$ ;  $\log_e D = 1.392 \cdot \log_e S - 2.864$ ;  $r^2 = 0.734$ ). In this plot, modern diurnal simians together represent a distinct grade in relation to all other modern primates. Note the extreme negative outlier among fossil primates in both plots is the Eocene adapiform *Adapis*, in which the foramen is strikingly small in relation to skull length and also quite small in relation to orbit height

01 with signals from rods (Jacobs and Deegan, 1993). However, some primates – notably  
02 the Old World simians – have three types of cones, which is unique among mammals  
03 (Jacobs, 1993; Kremers *et al.*, 1999; Dominy *et al.*, 2003; see Chapters 3 and 4).

04 The original distinction between rods and cones was based on morphological differ-  
05 ences, with rods being typically long and thin and cones being short and squat. Because  
06 no clear morphological distinction was evident between different classes of photorecep-  
07 tors, several investigators (notably Walls, 1942) concluded that cones were completely  
08 lacking from the retina of many nocturnal mammals. As it was also widely believed that  
09 the ancestral mammals were nocturnal, it was only logical to infer that cones had been  
10 completely lost in the ancestral stock, leaving an all-rod retina, and that they had to be  
11 redeveloped in those mammals that subsequently became diurnal in habits. Conversely, a  
12 comparable absence of any clear morphological distinction between photoreceptors led to  
13 the view that some diurnal mammals, especially squirrels and tree-shrews, have all-cone  
14 retinas. However, the distinction between rods and cones has been increasingly refined  
15 with additional criteria: cytological, neuroanatomical, physiological, immunological, and  
16 molecular. In the wake of this, it has emerged that nocturnal mammals – including  
17 monotremes, marsupials, and placentals – generally do not seem to have completely  
18 cone-free retinas. Furthermore, it is now known that diurnal mammals, including squirrels  
19 and tree-shrews, generally have at least some rods. In the retina of nocturnal mammals,  
20 cones are usually present, albeit at a relatively low frequency, and there are commonly  
21 two cone types with different photopigments. The retention of two cone classes (which  
22 presumably function only under photopic conditions) in the retina of nocturnal mammals  
23 is an enigma that requires some explanation. Be that as it may, it is now clear that the  
24 distinction between nocturnal and diurnal habits is reflected by a shift in the ratio between  
25 rods and cones, rather than by complete absence of one photoreceptor type. It should also  
26 be noted that even in fully diurnal mammals the rods often heavily outnumber the cones  
27 in the retina. In the human retina, for example, there are just 6 million cones compared  
28 with 120 million rods, a ratio of only 1:20. Tree-shrews and squirrels, originally thought  
29 to have pure cone retinas, are exceptional in having a high cone:rod ratio. In *Tupaia*, for  
30 instance, 95 percent of the photoreceptors are cones (Müller and Peichl, 1989).

31 Despite the fact that nocturnal mammals generally seem to have retained a small  
32 proportion of cones in the retina, there are several compelling reasons to accept Walls'  
33 hypothesis that ancestral mammals were nocturnal and had lost diurnal visual features  
34 found in other vertebrate groups. In the first place, most mammals (especially nocturnal  
35 species) lack vivid coloration of the pelage, indicating that color signals were generally  
36 not favored by selection. Further, as noted by Ahnelt and Kolb (2000, p. 715): 'Compared  
37 to the diversity of photoreceptors in groups such as teleost fish or reptilian families  
38 such as geckoes . . . mammalian photoreceptors are uninterestingly uniform and difficult  
39 to study.' This very uniformity, along with the associated difficulties in distinguishing  
40 rods from cones in many mammal species, suggests that in the course of their evolution  
41 mammals passed through an extended period of nocturnal adaptation. This interpretation  
42 is reinforced by the fact that mammalian cones are relatively simple compared with  
43 those of other vertebrates (fish, amphibians, birds, and reptiles). In the latter, a colored  
44 oil droplet (ellipsosome) is commonly present between the inner and outer segments of  
45 each cone (Kremers *et al.*, 1999). The droplets absorb light of particular wavelengths  
46 and hence narrow the spectral sensitivity of each of the four cone photopigments that

01 are present in the typical tetrachromatic visual system. In all placental mammals and  
02 some marsupials and monotremes oil droplets are completely lacking. Although certain  
03 marsupials and monotremes have retained oil droplets in some cones, they are colorless  
04 and their original function has presumably been diminished if not abolished. Walls (1942)  
05 proposed that colored oil droplets appeared at a very early stage of vertebrate evolution  
06 and that a shift to nocturnal habits in mammals was accompanied by loss of color  
07 from the droplets and eventually by their complete loss. This hypothesis was rejected as  
08 unparsimonious by some authors, but subsequent demonstration of colored oil droplets  
09 in the cones of lungfish has increased the probability that they were present, possibly  
10 in conjunction with tetrachromatic vision, in the common ancestor of lungfish and land  
11 vertebrates (Robinson, 1994).

12 In the vertebrate retina, the outer segment of each photoreceptor is composed of  
13 a stack of membranes in which the photosensitive visual pigments (photopigments)  
14 are embedded. Different photopigments are maximally sensitive to different parts of  
15 the spectrum (spectral tuning). The photon-capturing properties of vertebrate photopig-  
16 ments depend essentially on apoproteins known as opsins, each containing approximately  
17 350 amino acids, which are integral membrane proteins. Each photopigment is formed  
18 by the binding of an opsin with the chromophore retinal, derived from vitamin A. Each  
19 type of opsin corresponds to a different gene. Accordingly, differential spectral tuning of  
20 photopigments is determined by amino acid differences between the different opsin pro-  
21 teins, and those differences have turned out to be relatively few in number (Hunt, 2001;  
22 see Chapter 3). The amino acid substitutions responsible occur at particular sites in the  
23 transmembrane portion of the pigment molecule.

24 Recent evidence indicates that five opsin types are commonly present in the retina of  
25 vertebrates other than mammals, namely fish, amphibians, reptiles, and birds (Ahnelt and  
26 Kolb, 2000; Hunt, 2001; see Chapter 3). In addition to the rhodopsin present in rods, there  
27 are four cone opsins that are maximally sensitive to different regions of the spectrum:  
28 long-wave sensitive (L-) cones (peak sensitivity at 530–570 nm), medium-wave sensitive  
29 (M-) cones (peak sensitivity at 480–520 nm), short-wave sensitive I (S-I) cones (peak  
30 sensitivity at 440–460 nm), and short-wave sensitive II (S-II) violet to ultraviolet cones  
31 (peak sensitivity at 355–430 nm). Mammals typically have just three of these opsins –  
32 rod rhodopsin and two cone opsins (an M-/L-opsin and an S-I-opsin) – and it is now  
33 generally agreed that the basic conformation of the mammalian retina is dichromatic  
34 (Ahnelt and Kolb, 2000). The gene for long-wave sensitive red-opsin is located on the  
35 X-chromosome, while the gene for short-wave sensitive blue-opsin is located on an  
36 autosomal chromosome. Some primates are unique among mammals in having three kinds  
37 of cone opsins – L-opsin, M-opsin, and S-I-opsin – and in all cases the gene for M-opsin  
38 (which is also located on the X-chromosome) is secondarily derived in some way from  
39 the gene for L-opsin. Valuable information has been provided by molecular comparisons  
40 of opsin genes (Jacobs, 1993; Yokoyama, 2000). DNA sequence comparisons indicate  
41 that divergence between the ancestral rod gene and a common ancestor for the cone  
42 pigment genes occurred very early in vertebrate evolution. As cones typically develop  
43 before rods in the vertebrate retina, it is possible that the ancestral photoreceptor was  
44 adapted for photopic, rather than scotopic, conditions. This inference is reinforced by  
45 the fact that rod signals converge on the cone system prior to reaching the ganglion  
46 cells (Kremers *et al.*, 1999). In the evolution of cones, a divergence in the cone pigment

01 gene, probably at some time during the Permian or Triassic, yielded one gene producing  
02 a pigment with maximal sensitivity at short wavelengths (S) and another producing a  
03 pigment with maximal sensitivity at long wavelengths (L). This ancient divergence is  
04 reflected by the fact that there is now only about 40 percent sequence similarity between  
05 the S-opsin gene and the M-/L-opsin genes in primates (Chapter 3). Given that sequence  
06 comparisons suggest lineal continuity in the evolution of S and L genes in all mammals,  
07 it seems highly likely that ancestral mammals did, indeed, possess a duplex retina (one  
08 containing both rods and cones). Moreover, it would seem that two spectrally distinct  
09 types of cone photopigment were present and provided an ancestral basis for the typical  
10 condition of dichromacy in mammals.

11 In recent years, through a combination of new methods (e.g. electroretinography;  
12 labeling of photoreceptors with antibodies) and sequencing of opsin genes, a relatively  
13 clear picture of the evolutionary history of color vision in primates has emerged. It  
14 has been confirmed that nocturnal primates have heavily rod-dominated retinas and  
15 essentially monochromatic vision. Although it was originally thought that nocturnal  
16 primates possess cone-free retinas, this conclusion has proved to be erroneous across the  
17 board, as was anticipated by Martin (1990). For example, Dartnall *et al.* (1965) reported  
18 that *Galago crassicaudatus* has a pure rod retina, but labeling with a cone-specific  
19 antibody showed that *Galago garnettii* has a rod:cone ratio that varies from 100:1 to  
20 30:1 across the retina (Wikler and Rakic, 1990). It was subsequently confirmed that  
21 1–3 percent of the photoreceptors in the related species *Galago crassicaudatus* are cones  
22 (Jacobs *et al.*, 1995). The cones were all found to be of a single type, with an absorption  
23 peak corresponding to human L-cones. In fact, DNA sequencing revealed the presence  
24 of a gene for another cone type (corresponding to human S-cones), but is non-functional  
25 because of mutational modification (see also Zhou *et al.*, 1997). It therefore seems that  
26 *Galago crassicaudatus* and *Galago garnettii* lack color vision despite the possession of  
27 some cones. It was also originally believed that the retina of tarsiers exclusively contains  
28 closely packed rods (Castenholz, 1984), but it has now been clearly demonstrated that the  
29 retina of *Tarsius* does contain a small proportion of cones. Morphologically, the cones  
30 are not easily distinguishable from rods, but their outer segments are only half as long.  
31 Immunocytochemical labeling revealed the presence of two cone types in the retina of  
32 *Tarsius spectrum*, one with an M-/L-opsin and the other with an S-opsin (Hendrickson  
33 *et al.*, 2000). Thus, *Tarsius* does seem to possess a limited basis for dichromatic vision.  
34 A small proportion of cones have also been found in the retina of *Aotus*, which was  
35 originally believed to possess an all-rod retina (Jacobs, 1993). However, only one type  
36 of cone was found, with a sensitivity peak again corresponding to human L-cones.  
37 Furthermore, unlike many diurnal New World monkeys, *Aotus* shows no evidence of  
38 photopigment polymorphism in its L-cones. A limited degree of color discrimination  
39 that has been identified for this nocturnal species is probably attributable to interaction  
40 between signals from cones and rods (Jacobs, 1993).

41 Corresponding to behavioral evidence indicating limited powers of color discrimina-  
42 tion, the retina of diurnal lemurs generally possesses at least a basis for dichromacy. For  
43 example, both *Lemur catta* and *Eulemur fulvus* have two cone types corresponding to  
44 human S-cones and L-cones, respectively. Indeed, it is almost certain that these diurnal  
45 lemurs use rods in combination with the two cone types to achieve some degree  
46 of trichromatic vision (Jacobs, 1993). However, an analysis of opsin genes on the

01 X-chromosome revealed that there is a polymorphism involving M- and L-alleles in  
 02 *Propithecus verreauxi coquereli* and *Varecia variegata* (Tan and Li, 1999). The presence  
 03 of an M-/L-opsin polymorphism in *Propithecus verreauxi coquereli* was subsequently  
 04 confirmed with electroretinographic evidence (Jacobs *et al.*, 2002). It would there-  
 05 fore seem that female *Propithecus* and *Varecia* with different opsin alleles on their  
 06 X-chromosomes possess a basis for trichromacy.

07 It now seems likely that some basis for trichromacy was already present in ancestral  
 08 simians (Kremers *et al.*, 1999). At one time, all New World monkeys were generally  
 09 thought to possess dichromatic color vision, with an autosomal gene for an S-opsin  
 10 and a gene for an L-opsin on the X-chromosome. However, it then progressively  
 11 emerged that several platyrrhine species possess a polymorphism of the opsin gene on  
 12 the X-chromosome similar to that subsequently discovered in *Propithecus* and *Varecia*  
 13 (Jacobs, 1993). Here, too, females with different opsin alleles on their X-chromosomes  
 14 possess a basis for trichromacy. This condition increasingly seemed to be typical for di-  
 15 urnal New World monkeys, until it was discovered that the howler monkey (*Alouatta*) pos-  
 16 sesses three separate opsin genes, one autosomal and the other two on the X-chromosome.  
 17 Electroretinograms revealed that *Alouatta* possesses trichromatic color vision with three  
 18 photopigments in males as well as females (Jacobs *et al.*, 1996). This closely resembles  
 19 the system for trichromatic color vision that is universally found in catarrhine primates  
 20 (Old World monkeys, apes, and humans). The genetic basis is very similar to that  
 21 of catarrhines; the M- and L-opsins on the X-chromosome have comparable spectral  
 22 peaks.

23 Trichromatic color vision based on the presence of three opsin genes is a consistent  
 24 feature of all catarrhine primates, so it seems highly likely that this was an ancestral  
 25 feature of Old World simians. All catarrhines possess an autosomal gene coding for an  
 26 S-opsin and two genes on the X-chromosome that code for an M-opsin and an L-opsin  
 27 (Jacobs, 1993). The high degree of sequence similarity between the two opsin genes on the  
 28 X-chromosome (approximately 97 percent) indicates that they arose through duplication  
 29 of a single ancestral locus (Kremers *et al.*, 1999). The two genes lie very close to one  
 30 another on the X-chromosome in a head-to-tail array (Hunt, 2001; see Chapter 3).

31 It is accordingly reasonable to suggest that color vision in diurnal primates evolved  
 32 in stages. The first stage was development of a dichromatic system with an increased  
 33 proportion of cones with two photopigments, an S-opsin coded by an autosomal gene  
 34 and an M-/L-opsin coded by a gene on the X-chromosome. Such a dichromatic system  
 35 was undoubtedly present as a minimum in the common ancestor of simian primates  
 36 and it is possible that it was present in ancestral primates. It is a moot point whether  
 37 the dichromatic system of diurnal lemurs was retained from the ancestral primates or  
 38 whether it was redeveloped following derivation from an ancestral lemur that possessed  
 39 only one cone photopigment. In any event, polymorphism of the opsin gene on the  
 40 X-chromosome presumably developed separately in some diurnal lemurs and in numerous  
 41 New World monkeys (or perhaps in the common platyrrhine ancestor), yielding a basis  
 42 for trichromatic vision in heterozygous females. (It should be noted that trichromacy in  
 43 female New World monkeys is well established. On the other hand, no trichromatic lemurs  
 44 have been found. The data only showed the possibility of the presence of trichromacy.)  
 45 This was possibly an intermediate stage in the development of full trichromatic vision  
 46 in both sexes. The final stage in the evolution of trichromatic color vision in primates,

01 which was achieved independently by at least one New World monkey (*Alouatta*) and  
02 by the common ancestor of the catarrhine primates, was duplication of the opsin gene on  
03 the X-chromosome to produce an M-opsin in addition to the ancestral L-opsin.

04 This scenario was questioned by Tan and Li (1999), who examined X-linked opsin  
05 genes in 20 prosimian species. In addition to finding evidence for a polymorphism of the  
06 opsin gene on the X-chromosome in the diurnal lemurs *Propithecus* and *Varecia*, they  
07 also reported a similar polymorphism in *Cheirogaleus major*. Furthermore, they reported  
08 that in other prosimians examined the gene on the X-chromosome may code either for  
09 an M-opsin or for an L-opsin. The former was found most often among the species  
10 examined (despite the fact that it is presumably derived from an ancestral L-opsin), but  
11 the latter was found in nocturnal mouse lemurs (*Mirza coquereli* and *Microcebus muri-*  
12 *nus*) and in the cathemeral bamboo lemur (*Hapalemur griseus*). It was also reported that  
13 *Tarsius syrichta* has an L-opsin, whereas *Tarsius bancanus* has an M-opsin. On this basis,  
14 Tan and Li (1999) concluded that the common ancestor of tarsiers and strepsirrhines  
15 (i.e. the ancestral primate) might have been trichromatic, such that trichromacy originated  
16 much earlier than is commonly believed. However, this interpretation was challenged by  
17 Heesy and Ross (2001) because it conflicts with a large body of morphological, phylo-  
18 genetic, and behavioral data. In fact, in a footnote added in press, these authors reported  
19 a personal communication from Tan to the effect that the polymorphism attributed to  
20 *Cheirogaleus major* had proven to be unfounded. Hence, polymorphic trichromacy has  
21 so far been demonstrated only for two diurnal lemurs (*Propithecus* and *Varecia*), and  
22 this provides no convincing basis for inferring that ancestral primates were trichromatic.

23 Regardless of whether the ancestral primates were nocturnal or diurnal, the fact remains  
24 that the majority of modern prosimians are nocturnal. It now seems to be clearly estab-  
25 lished that all nocturnal primates have a small proportion of cones scattered among the  
26 rods in the retina. As far as is known, however, there is usually only one type of cone  
27 in the retina of any nocturnal strepsirrhine species. So far, no S-cones have ever been  
28 identified in the retina of a nocturnal strepsirrhine and the single cone type demonstrated  
29 has been found to belong to the M/L class (Jacobs, 1996; Tan and Li, 1999). It may  
30 initially seem surprising that nocturnal primates possess cones at all. However, it is per-  
31 fectly possible that some residual capacity for color discrimination may be advantageous  
32 (e.g. when a nocturnal primate is disturbed by a predator during the daytime). Further-  
33 more, it has been suggested that possession of some cones may facilitate detection of the  
34 transition from daytime (photopic) to night-time (scotopic) conditions. This suggestion  
35 was prompted by the observation that the onset of activity in various nocturnal strep-  
36 sirrhines typically coincides with the time at dusk when human cones cease to function  
37 (Martin, 1990).

38 The most likely hypothesis, given present evidence, seems to be that the ancestral  
39 primates were nocturnal and that the acquisition of diurnal habits represents a sec-  
40 ondary development in three lineages of diurnal primates (Ross *et al.*, unpublished data).  
41 However, there has been some support for the alternative suggestion that ancestral pri-  
42 mates were diurnal (Ni *et al.*, 2004). It certainly seems likely that the ancestral primate  
43 possessed two types of cone (S-cones and M-/L-cones), as sequence comparisons indicate  
44 lineal continuity for these two types of cone in terrestrial vertebrates including primates  
45 and other mammals (Yokoyama, 2000). Incidentally, such lineal continuity indicates that  
46 mammals retained S-cone and M-/L-cone opsins throughout the Jurassic and Cretaceous

01 periods (a total of 135 my) when they were presumably consistently nocturnal. It would  
02 therefore seem that inactivation of S-cones occurred in one or more nocturnal strepsir-  
03 rhine lineages, as diurnal lemurs are at least dichromatic and have both S-cones and  
04 M-/L-cones. Independent inactivation of S-cones has also occurred in the lineage leading  
05 to nocturnal *Aotus*. Retention of two types of cone in the retina throughout the first  
06 two-thirds of mammalian evolution and apparently in the ancestral primate is somewhat  
07 surprising and is not explicable on the basis of detection of the switch from photopic to  
08 scotopic conditions, as a single cone type would presumably suffice for this.

09 Among modern primates, diurnal behavior seems to be a prerequisite for effective  
10 color discrimination. Diurnal primates are at least dichromatic, but trichromacy has  
11 emerged a number of times, either through polymorphism of a single opsin gene on  
12 the X-chromosome (possibly some diurnal lemurs; many New World monkeys) or by  
13 duplication and sequence divergence of that gene (howler monkeys and all catarrhine  
14 primates). As dichromacy would seem to be the basic condition for mammals (Jacobs,  
15 1993; Ahnelt and Kolb, 2000), this does not require any special explanation within the  
16 context of primate evolution. However, trichromatic color vision is unique among mam-  
17 mals and does need some explanation. The primary hypothesis that has been considered  
18 is that trichromacy is particularly advantageous for detection of yellow or orange fruits  
19 against a background of green foliage (Osorio and Vorobyev, 1996; Regan *et al.*, 2001;  
20 see Chapter 4). This fits well with the fact that fruits typically constitute a significant  
21 part of the diet in primates. Furthermore, the two diurnal lemurs that have been found  
22 to have a polymorphic basis for trichromacy (*Propithecus*, *Varecia*) are predominantly  
23 frugivorous, and the same applies to New World monkeys that have been shown to have  
24 the same development of the visual system. However, it should be noted that in Old  
25 World monkeys and apes (catarrhine primates), which all possess full trichromacy in  
26 both sexes, folivory is quite common (which is not the case among the predominantly  
27 frugivorous New World monkeys). It is also noteworthy that *Alouatta*, the only New  
28 World monkey so far shown to possess full trichromacy paralleling that of catarrhines, is  
29 one of only two platyrrhines that includes a large proportion of leaves in its diet (the other  
30 being *Brachyteles*, whose visual adaptations have not yet been explored). In fact, a field  
31 study of four catarrhine species in Kibale Forest (Uganda) showed that they eat immature  
32 leaves which are discriminated from mature leaves only on the basis of red, as opposed  
33 to green, coloration. Red coloration of leaves correlated with high protein content and  
34 low toughness. By contrast, fruits are discriminated by a much broader range of visual  
35 cues (Dominy and Lucas, 2001). In a subsequent paper, Dominy *et al.* (2003) proposed  
36 a two-stage explanation of the evolution of primate color vision. Initially, historical bio-  
37 geography of figs and arborescent palms accounted for patterns of variation in primate  
38 color vision. With respect to polymorphic systems in which some females are trichromatic  
39 but other females and all males are dichromatic, it was suggested that foraging groups  
40 with mixed capabilities for chromatic distinction gained a selective advantage in relation  
41 to the abundance and inconspicuous coloration of figs and palms. In the second stage,  
42 following regional extinction of palms and probably figs because of climatic change,  
43 the evolution of routine trichromatic vision permitted primates to exploit protein-rich  
44 immature leaves as a substitute resource. Hence, it seems quite possible that the evolution  
45 of color vision was connected both with fruits and with leaves, but that full trichromacy  
46 is more strongly linked to folivory (see also Chapter 4).

01 As this brief survey illustrates, satisfactory explanations for the distribution of many  
 02 aspects of the primate visual system require that their points of origin be precisely  
 03 located on the primate evolutionary tree. Not only do primate visual systems differ, but  
 04 visual systems differ even among simian primates ('monkeys') and prosimians, often  
 05 quite radically. An evolutionary and comparative approach to the primate visual sys-  
 06 tem is therefore needed that invokes specific sequences of evolutionary events. This  
 07 must take into account not only the distribution of visual adaptations in extant primates,  
 08 but also the inferred visual adaptations of fossil primates. Fossils can exhibit combina-  
 09 tions of characteristics that are not seen in living primates, falsifying hypotheses based  
 10 on extant animals, and enriching our understanding of the diversity of primate visual  
 11 adaptations.

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36 *The Evolutionary and Ecological Context of Primate Vision*

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