Old World Monkeys

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Introductory article

Article Contents

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Old World monkeys, or cercopithecoids, are a diverse and widespread group of primates found throughout Africa and Asia. They are characterised by their specialised molar teeth, quadrupedal running behaviour, often spending more time on the ground than other primates, as well as their often large and complex social groups. They survive in the widest range of habitats of any nonhuman primates, with some species restricted to humid tropical forests whereas others are found in mountains and deserts. There are two main groups: the cercopithecines, which have cheek-pouches and include macaques, baboons, mangabeys, vervets and guenons; and the colobines, characterised by complex stomach anatomy that allows them to digest leaves and which include langurs, proboscis monkeys, doucs and snub-nosed monkeys and colobus monkeys. Although they are termed 'monkeys' they are more closely related to apes and humans (hominoids) than they are to the monkeys of Central and South America.

Introduction

Old World monkeys, technically termed cercopithecoids, are the most successful evolutionary radiation of nonhuman primates in the world (Grubb *et al*., 2003; Brandon-Jones *et al*., 2004). They live in the tropical and temperate regions of Africa and Asia along with many adjacent Islands. Relative to other primate groups they are geographically widespread, taxonomically diverse, and ecologically flexible. They have spread to occupy higher latitudes and altitudes than any other primate excluding humans. Scientists currently recognise 20 different living genera divided into two distinct adaptive radiations: the cercopithecines, who live in terrestrial and arboreal habitats and forage for a variety of foods, but mostly fruit; and the colobines, who live in arboreal habitats and rely upon leaves and seeds for major portions of their diet. Interestingly, cercopithecoids have achieved this diversity in spite of being less varied anatomically and in their social behaviour than other primate groups (Szalay and Delson, 1979; Di Fiore and Rendall, 1994; but see Fleagle *et al*., 2010). Cercopithecoids also have an extensive fossil record, especially in Africa, which shows that Old World monkeys are both a relatively recent adaptive radiation and that in the past they were even more diverse and occupied an even greater geographic, taxonomic and ecological range (Jablonski, 2002; Jablonski and Frost, 2010).

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Basic Biology

Old World monkeys are catarrhine primates, and as such share anatomical features with modern apes and humans (hominoids) but are distinct from the New World monkeys, which are a separate radiation of anthropoid (Szalay and Delson, 1979; Fleagle, 1999). These catarrhine features include narrow and downward-facing nostrils, two premolar teeth, a complete bony auditory tube (tympanic bone) extending from the middle ear to the external ear, trichromatic colour vision, and ischial callosities, or 'sitting pads'. Old World monkeys are further distinguished from other catarrhines by their specialised molar teeth, termed 'bilophodont' for the two parallel transverse ridges that cross the width of each crown and link the four cusps as paired sets. These lophs are not independent crests; rather, they are the effect of altering, or folding, the normally rounded surfaces of the inner sides of each cusp into ridges. Old World monkeys also have specialisations of their body for quadrupedal running. As primates, they are medium to large in size, ranging from the talapoin monkey, the smallest modern catarrhine at slightly more than 1 kg, to male mandrills and baboons at 30 kg (Delson *et al*., 2000). They are also often highly sexually dimorphic with males being much larger than females and

are further distinguished by having large projecting canine teeth. **See also**: Apes; New World Monkeys; Primates (Lemurs, Lorises, Tarsiers, Monkeys and Apes)

Diversity

In some measures, Old World monkeys are a very diverse radiation (**Figure 1**). In taxonomic terms, more than 20 genera and over 80 species are recognised (Grubb *et al*., 2003; Brandon-Jones *et al*., 2004), more genera than either the New World monkeys or the Malagasy strepsirhines. Recent surveys have added to their biodiversity, including the Arunachal Macaque in India and the Kipunji in Tanzania which were both only discovered in 2005 (Jones *et al*., 2005; Sinha *et al*., 2005). In ecological terms, Old World monkeys occupy a greater variety of habitats than do any other primate except humans (Campbell *et al*., 2010). Further, many species appear to hybridise readily with other close relatives, and some species may have arisen as a result of hybridisation among other species in the distant past (Tosi *et al*., 2003; Karanth, 2008; Jolly *et al*., 2011). Anatomically and behaviourally, however, they are more uniform than the South American and Madagascan groups. The adaptive diversity of Old World monkeys is due to the generalised nature of their anatomy and the flexibility of their behaviour, not to dietary or locomotor specialisation. **See also**: Adaptation and Natural Selection: Overview

Old World monkeys are classified into two subgroups: cercopithecines and colobines (**Figure 2**; **Table 1**). Cercopithecines include guenons, macaques, baboons, mangabeys and mandrills; colobines include colobus monkeys, langurs and odd-nosed monkeys. Cercopithecines are characterised by relatively generalised low-cusped molars, large specialised incisor teeth, cheek pouches for food storage, and arms and legs of similar length. By contrast, colobines are characterised by molars with taller cusps and sharper crests, small incisors, complex ruminating stomachs and long legs relative to arms.

Figure 1 Examples of a few of the more than 80 species of Old World Monkeys. Clockwise from upper left these are: male gelada baboon (*Theropithecus gelada*) (photo Naomi Levin), group of vervet monkeys (*Chlorocebus aethiops*), male black and white colobus monkey (*Colobus guereza*) (photo Grace Hunter), Zanzibar red colobus monkey (*Procolobus kirkii*), male and female olive baboon (*Papio hamadryas anubis*), a Samango monkey (*Cercopithecus mitis albogularis*).

Table 1 Genus level classification of living Old World monkeys

Family	Subfamily	Genus	Common name	Number of species
Cercopithecidae	Cercopithecinae	*Macaca*	Macaques	14
		Cercocebus	Mangabeys	3
		Lophocebus	Mangabeys	2
		Rungwecebus	Kipunji	1
		Papio	Baboons	1
		Theropithecus	Gelada baboons	1
		Mandrillus	Mandrills	2
		Cercopithecus	Guenons	16
		Chlorocebus	Vervets, Patas, l'Hoest's	5
		Allenopithecus	Allen's monkey	1
		Miopithecus	Talapoins	2
	Colobinae	*Colobus*	Colobus	4
		Procolobus	Red and Olive colobus	6
		Semnopithecus	Langurs	3
		Trachypithecus	Leaf monkeys	7
		Presbytis	Leaf monkeys	7
		Nasalis	Proboscis monkey	1
		Simias	Simakobu	1
		Pygathrix	Douc langur	1
		Rhinopithecus	Snub-nosed monkey	4

Habitats and Abundance

Cercopithecines live in a wide variety of habitats including tropical, temperate and swamp forests, woodlands, savannahs, deserts and high altitudes in both Africa and Asia. Most are African, but macaques range from Gibraltar to the Tibetan highlands, Japan and remote southeast Asian islands. Some species spend most of their time in the trees, whereas others spend much of their time on the ground, some even sleeping on cliffs and crags instead of trees. Ground dwellers live in both forested and open country environments. Although many species are abundant, and some even thrive in human-altered habitats, including cities, many others are highly threatened with extinction (IUCN, 2010).

Colobines are more restricted to arboreal habitats, which is consistent with their general dietary specialisation on leaves. They are found in the tropical and temperate woodlands of Africa and Asia, but are more diverse in Asia than in Africa. In addition to being more arboreal, they occupy almost every available forest habitat in southern and southeast Asia, including mangrove swamps and conifer forests. In general, all colobine groups are threatened with extinction and some species are believed to number only a few dozen individuals (IUCN, 2010).

Habits and Life Histories

Given their taxonomic and ecological diversity, some aspects of social behaviour in Old World monkeys are remarkably uniform. In most species, females remain in the social groups into which they were born, often surrounded by close female relatives throughout their lives. Males, on the other hand, typically emigrate from their natal group as juveniles or young adults, only later joining a new social group (Campbell *et al*., 2010). In other respects, the two subfamilies differ.

Cercopithecines tend to be omnivorous, with an emphasis on seasonally available fruit and specific preferences for the amount of leafy or seed material in the diet. Some baboon populations have been observed to consume small vertebrates and others to forage for shell fish in coastal areas. Sometimes their food resources are highly clustered into large patches that can support many individuals. In relationship to this the macaques, baboons and guenons tend to be highly social primates, with some troops of some species numbering more than 100 individuals. The cheek pouches of this subfamily serve to reduce the levels of aggression among individuals within these large groups, by allowing low ranking individuals to collect food items at the feeding source but then consume them at a safe distance (Hannibal, 2009). The high level of sexual dimorphism in, for example, baboons, is a consequence of the high level of competition among males for access to females (Plavcan and van Schaik, 1992, 1997). **See also**: Primates and the Origin of Culture; Sexual Selection

The specialised gut anatomy of colobines allows them to process plant foods, such as leaves, that contain a high portion of cellulose and other structural carbohydrates that make them difficult to digest, as well as toxins. Colobine stomachs are functionally similar to those of ruminant artiodactyls (such as sheep and cattle), and some of their

digestive enzymes have even converged on those of ruminants as well (Zhang, 2006). Given this, colobines tend to be folivorous with specific preferences for locally or seasonally available fruits or seeds, which tend to be more evenly distributed than the resources of cercopithecines. Colobine social behaviour is poorly studied by comparison to cercopithecines, but field data indicate that they often form single-male troops. One notable exception is the African red colobus monkey, which gathers in multimale groups of more than 70 individuals, feeds on fruits and shoots, and is subject to considerable predation by chimpanzees (Stanford, 1995).

Both groups of Old World monkeys typically give birth to one offspring at a time, and at a maximum rate of one per year after reaching reproductive maturity (Fleagle, 1999). Old World monkey offspring tend to be more precocial than those of apes, but still spend a considerable amount of time under parental care. Male parental investment in the offspring is low in most species. In some species with well-developed dominance hierarchies, such as the Hanuman langurs (*Semnopithecus entellus*), newly dominant males may kill existing offspring so that the now childless females quickly return to oestrus and enable the male to foster his own offspring sooner (Palombit, 1999). **See also**: Reproduction in Eutherian Mammals

Fossil History

Old Word monkeys have one of the best fossil records among primates, especially in Africa (Jablonski, 2002; Jablonski and Frost, 2010). In spite of this, the earliest part of their evolutionary history is not well documented, and some groups (such as the guenons) are nearly absent from the fossil record. The earliest extinct primates that resemble living Old World monkeys are 12–20 million-year-old fragmentary fossils from eastern and northern Africa. They are usually included in a separate family, Victoriapithecidae (Miller *et al*., 2009). Relatively complete fossils of one species of victoriapithecid, *Victoriapithecus macinnesi* from Maboko Island in Kenya, confirm that the earliest Old World monkeys already evolved terrestrial locomotion similar to extant species, and that their molar teeth were partially, but not completely, bilophodont. Several other species of victoriapithecid are known, but are represented only by very fragmentary remains. **See also**: Fossil Record; Fossil Record: Quality

Of the fully modern cercopithecoids, colobines appear in the fossil record first even though they are not the most primitive. Their earliest representatives in Africa are nearly 10 million years old, in Europe they are 8 million years old, and finally in Asia between 6 and 7 million years old. Cercopithecines are found across the same continents approximately 5–7 million years ago (Ma). From approximately 5 Ma until the present, Old World monkeys are common as fossils, over 50 species are represented, ranging in estimated size from less than 5 to almost 100 kg, and including all major groups. Some show rather interesting differences from their modern relatives. For example, the African fossil colobine *Cercopithecoides williamsi* was probably highly terrestrial in its locomotion and probably not as folivorous as modern leaf-eaters. *Theropithecus brumpti*, a large baboon from East Africa, has uniquely flaring cheek bones that are difficult to interpret functionally. In many cases the fossils are larger than are their modern relatives, and in other cases distinguishing the fossils as a separate species from the moderns is based more on the age of the fossil than on a compelling anatomical difference. The fossil record, corroborated by estimates from modern genetic studies, seems to indicate that the adaptive radiation of living Old World monkeys is the youngest of the major extant primate

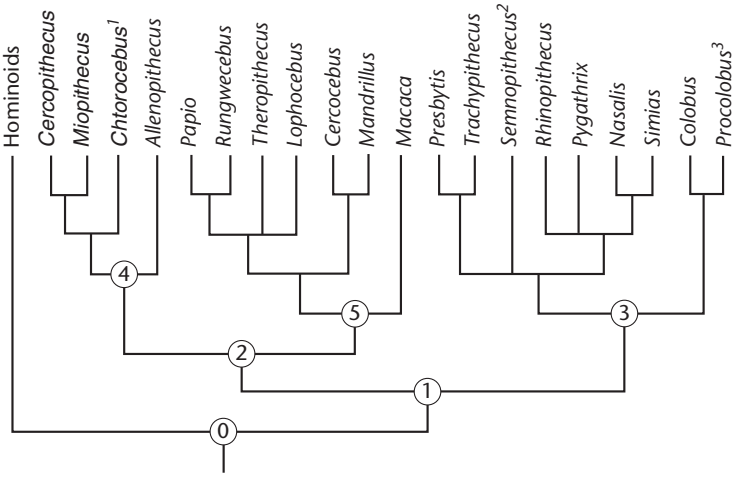

Figure 2 Phylogeny of living Old World monkeys showing the evolutionary relationships among genera. (0) catarrhines, (1) cercopithecids, (2) cercopithecines, (3) colobines, (4) cercopithecins (guenons) and (5) papionins. Old World monkeys are African except for most species of *Macaca* and all of the colobines except for *Colobus* and *Procolobus*. [1] *Chlorocebus* includes *Erythrocebus* and *Allochrocebus*; [2] *Semnopithecus* includes *Kasi*; [3] *Procolobus* includes *Piliocolobus*.

radiations, and that they probably had their origin in Africa (Raaum *et al*., 2005). **See also**: Adaptive Radiation

The geologically recent expansion of Old World monkeys is consistent with a radical contraction in the radiation of apes and other nonmonkey catarrhines, the fossil record of which is abundant in the period from 23 to 10 Ma. This suggests that over the last 10 million years global climate has shifted such that the amount of land supporting 'ape-friendly' tropical habitat has declined considerably. Opportunistic Old World monkeys capable of moving and foraging both on the ground and in trees then increased to replace them.

Phylogeny

Compared to other groups of primates, Old World monkey phylogeny is less problematic, with anatomical, behavioural and molecular data converging on a consistent interpretation (e.g. Tosi *et al*., 2003; Xing *et al*., 2005; Ting, 2008; Gilbert *et al*., 2009; **Figure 2**). The living cercopithecoids are clearly a monophyletic group (share a recent direct common ancestor exclusive of other species), and they clearly are exclusively linked more closely with hominoids than any other group. The colobines and cercopithecines are also clearly monophyletic groups. Within the cercopithecines, the African guenons form a monophyletic group relative to all of the other cercopithecines; and the colobines are clearly divided into African and Asian forms. **See also**: Molecular Phylogeny Reconstruction

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