

Old World monkey

Although Old World monkey, as a word, corresponds to New World monkey, its taxonomic rank is much lower than that of the New World Monkey. Therefore, it is speculated that the last common ancestor of Old World monkeys is newer compared to that of New World monkeys.

While New World monkey is the vernacular name for infraorder *Platyrrhini*, Old World Monkey is the vernacular name for superfamily *Cercopithecoidea* (family *Cercopithecidae* is limited to living species). As a side note, the taxon including Old World Monkey at the same taxonomic level as New World Monkey is infraorder *Catarrhini*. *Catarrhini* includes *Hominoidea* (humans and apes), as well as *Cercopithecoidea*.

Cercopithecoidea comprises the families *Victoriapithecidae* and *Cercopithecidae*.

Victoriapithecidae is fossil primates from the early to middle Miocene (15-20 Ma; Ma = megannum = 1 million years ago), with known genera *Prohylobates* and *Victoriapithecus*. The characteristic that defines the Old World Monkey (as synapomorphy – a derived character shared by two or more groups – defines a monophyletic taxon), is the bilophodonty of the molars, but the development of biphilodonty in *Victoriapithecidae* is still imperfect, and crista obliqua is observed in many maxillary molars (as well as primary molars). (Benefit, 1999; Fleagle, 1999)

Recently, there is an opinion that *Prohylobates* should be combined with *Victoriapithecus*.

Living Old World Monkeys are all classified in the family *Cercopithecidae*.

Cercopithecidae comprises the subfamilies *Cercopithecinae* and *Colobinae*. *Cercopithecinae* has a buccal pouch, and *Colobinae* has a complex, or sacculated, stomach. It is thought that the buccal pouch is an adaptation for quickly putting rare food like fruit into the mouth, and the complex stomach is an adaptation for eating leaves. This difference in dietary adaptations is related to differences between the subfamilies in morphology (such as the height of molar cusp, the proportion of upper and lower limbs, atrophy of the pollex, or thumb), behavior (foraging, allomothering), society (tendency of females to gather together), habitat (arboreality or terrestriality) and locomotion (frequency of leaping).

The subfamily *Cercopithecinae* comprises tribes *Cercopithecini* and *Papionini*, and *Papionini* is further classified into subtribes *Macacina* and *Papionina*.

Cercopithecini includes genera *Cercopithecus* (guenon), *Allenopithecus*, *Miopithecus* (talapoin), *Erythrocebus*, and *Chlorocebus*. Sometimes these are all placed in *Cercopithecus*.

Subtribe *Macacina* in the tribe *Papionini* comprises only the genus *Macaca*, and subtribe *Papionina* includes genera *Cercocebus*, *Theropithecus*, *Papio*, and *Mandrillus*. *Mandrillus* is also sometimes considered a subgenus of *Papio*, *Papio* (*Mandrillus*). In recent years, researchers often isolate the *albigena* group in *Cercocebus* as *Lophocebus*.

Subfamily *Colobinae* is normally divided into African colobines (subtribe *Colobina*) and Asian colobines (subtribe *Presbytina*). However, there is an opinion that it should be divided into the genus *Nasalis* (in the broad sense including *Simias concolor*) and all other colobines.

Included in African colobines are genera *Colobus* (Black-and-white Colobus monkey, Guereza), *Procolobus*, and *Piliocolobus*. *Piliocolobus* is often considered a subgenus of *Procolobus*, *Procolobus*

(*Piliocolobus*). Also, there are cases when all African colobines are placed in the genus *Colobus*.

Included in Asian colobines are the genera *Pygathrix*, *Rhinopithecus* (Golden monkey), *Nasalis*, *Simias* (Pig-tailed Snub-nosed monkey), *Presbytis* (Leaf monkey), *Trachypithecus* (Langur), *Kasi* (Purple-faced Langur), and *Semnopithecus* (Hanuman Langur). Among these, some are often placed as subgenera of others, such as *Rhinopithecus* below *Pygathrix*, *Simias* below *Nasalis*, *Kasi* below *Semnopithecus* or *Trachypithecus*, and *Semnopithecus* below *Presbytis*. *Trachypithecus* is also sometimes considered a subgenus of *Semnopithecus*.

Among major phylogenetic problems regarding the ancestry of Living Old World Monkeys are the following issues:

Regarding the tribe *Cercopithecini*, there is an issue about the positioning of genera *Allenopithecus* and *Miopithecus* (which one diverged first) and the monophyly of *Cercopithecini* (the origin of *Erythrocebus* and *Chlorocebus*). Because of these unknowns, some assert that all of these groups should be placed in the genus *Cercopithecus* for convenience.

Regarding the tribe *Papionini*, problems include the genealogical relationship of species within genus *Macaca* (the origin of three types of derivative glans penis morphologies), the relationship between *Mandrillus* and *Papio*, the monophyly of *Cercocebus* (whether we should recognize *Lophocebus*), the positioning of *Theropithecus* (conflict regarding morphology, eating habits, and society between the phenotype perspective and the molecular perspective – Disotell, 1994).

There are still many things unknown about the subfamily Colobinae, and there is not even agreement on the deepest divergence (whether to split between African and Asian or a broad category of *Nasalis* and other colobines). Another problem is the monophyly of genera such as odd-nosed monkeys (relationship between *Nasalis*, *Simias concolor*, *Pygathrix* and *Rhinopithecus*; Jablonski, 1998), *Nasalis* (its relationship with *Simias concolor*; Jablonski, 1998), *Rhinopithecus* (its relationship with *Pygathrix*) and *Presbytis* (classification of genus and subgenus).

Comments regarding a few genera and species.

The genus *Cercopithecus* includes many different species and is rich in different fur colors and numbers of chromosomes. The diversity of the species within this genus is suggested to be related with the cycle of contraction-division and expansion-fusion of tropical rainforests during the ice age. (Refugia theory of speciation; Gautier-Hion, 1988) A similar speciation structure is suspected in the macaque monkeys of Southeast Asia.

Miopithecus talapoin is the smallest Old World monkey. It is said that the female is more dominant than the male.

Erythrocebus patas can run at a speed of 55 KPH, and it is said to be the fastest primate.

Since genus *Macaca* has many species and is widely distributed, it is said to be the most successful non-human primate genus. Because *Macaca mulatta* has historically been used often as a subject for experiments, it is widely researched. For example, even in recent years, the possibility of specific parapatry in *M. mulatta* and *M. assamensis* (a difference between maternal inheritance and bisexual inheritance) has been revealed through mitochondrial DNA (mtDNA) research.

The genus *Papio*, although it looks as if there is a distinct regional difference (between morphological species), because there is mixture of blood near the edges of these regions, there have long been problems regarding the definition and recognition of species. (Jolly, 1993) Interspecific breeding in the natural environment has been observed as well among *Macaca* and *Cercopithecus*.

Papio hamadryas and *Theropithecus gelada* are famous for having a multi-level social structure.

However, there seem to be basic differences the multi-level societies of the two species, such as while *Papio hamadryas*' one-male unit is formed through kidnapping by the male and supported by his behaviors such as neck-biting, the *Theropithecus gelada* one-male unit is a matrilineal group. *Rhinopithecus* and *Pygathrix* also appear to have a two-tiered social organization comprising a one-male unit and larger groups.

Cercopithecus, under the broad definition, has either no pollex, or a very short one. It is thought that this is an adaptation so they can hook their hands and hang from thick branches. The platyrrhine *Ateles* and *Brachyteles* also have no thumb (convergence phenomenon). *Hylobates* also has very short thumbs.

Ptilocolobus (depending on the region) have a patrilineal society structure, where females leave the group in which they were born. This is in contrast to the matrilineal unit group maintained by most Old World monkeys.

Simias concolor is monogamous – a very rare feature for Old World monkeys. Also, their tails are a short – diverging from the norm for *Colobinae*.

Infanticide in *Semnopithecus entellus* is well known.

Fossil Old World monkeys

Many Old World monkey fossils have been excavated in Africa and Europe. The Oligocene *Parapithecidae* (such as *Parapithecus*, *Apidium*) was once thought to be of the same ancestry as the Old World Monkey, but now this has been contradicted.

Presently, the fossils of the oldest Old World monkey are of the family *Victoriapithecidae* (also often considered a subfamily) from 20-15 Ma. These are of a genealogical line that split off before the divergence of the two subfamilies of living Old World monkey. In the 1980's, many *Victoriapithecus* fossils were excavated on Maboko Island in Lake Victoria, changing our image of the ancestors of living Old World monkeys. For instance, it was thought that the subfamily *Colobinae*, with strong arboreality, a short facemask and wide distance between eye sockets, was closer to the state of Old World monkey ancestors than the subfamily *Cercopithecinae*, but since *Victoriapithecus* is more similar to *Cercopithecinae* on these points, this assessment is in the process of being reversed. (Benefit, 1999)

After *Victoriapithecus*, fossil records disappear until the late Miocene.

Cercopithecinae fossils begin to appear approximately following the end of the Miocene. The oldest fossils are teeth and jawbone fragments resembling Macaque from around 5 Ma excavated near the Mediterranean Sea. These are recorded as multiple species within genus *Macaca*. However, since there are few divergent characteristics in Macaque teeth, classification in *Macaca* is supported only passively. Macaque fossils have also appeared in countries such as England, India, Pakistan, Vietnam, China, Korea and Japan. Fossils related closely to the Macaque include *Procynocephalus* and *Paradolicopithecus* (2.5 Ma, from Spain to central Asia).

Fossils of baboons and geladas have been discovered from around the end of the Miocene in eastern and southern Africa. Because the *Parapapio* teeth and skull are primitive, they are considered possibly to be close to the ancestors of living baboons and geladas. Baboon and gelada fossils are also being excavated in Eurasia.

Today there is only one species related to gelada baboons living in the highlands of Ethiopia, but in the past they were flourishing. Fossils are varied in type (with the largest at 100 kg) and broad in distribution (Africa, India and Spain) following 3.5 Ma.

Mangabey fossils have been found from eastern and southern Africa following the end of the

Pliocene, but they are fragmental and do not provide a lot of information.

Guenon fossils are scarce. Isolated teeth have been found from around 3 Ma. It is speculated that the diversity of present species (adaptive radiation) is a relatively new phenomenon since 1 Ma.

Colobinae fossils have been discovered older than *Cercopithecinae* fossils. Most of *Cercopithecinae* fossils are deeply related to living genera, but there are many among *Colobinae* fossils whose relationship with living genera is unclear. Also, there are many arboreal species within the *Colobinae* subfamily, but among the fossils there are ones that display some terrestriality (especially *Mesopithecus* and *Cercopithecoides*).

The oldest *Colobinae* fossil in Eurasia is that of *Mesopithecus* (8.5-2.5 Ma). *Mesopithecus* has been excavated in many areas, ranging from England, southern and central Europe to Iran, and almost its entire body has been found. Its teeth, skull and pollex are similar to those of living *Colobinae*, but the bones of its limbs are sturdy, and it seems that it was at least partially terrestrial.

Dolicopithecus fossils are known as similar to those of *Mesopithecus*. The oldest primate fossil in Japan, a skull fossil (2.5 Ma) from the Nakatsu stratum in Atsugi city, Kanagawa prefecture, is classified as *Dolichopithecus eohanuman* by Delson (1994) (?).

There is no decisive way to say whether *Mesopithecus* and *Dolicopithecus* are more similar to Asian colobines or African colobines. From their distribution it is speculated that they might be closer to Asian colobines.

Fossils from the end of the Miocene in India and the Siwalik Hills are placed in the genus *Presbytis* (*Presbytis sivalensis*), but this is not conclusive because they are only fragmental fossils.

Several Pleistocene fossils have been discovered in China and placed within living genera. The lower jaw of a large *Rhinopithecus* (Golden Monkey) was previously recorded as *Megacolobus*.

The oldest *Colobinae* fossil in Africa is the *Microcolobus* from eastern Africa (9 Ma). As its name suggests, it is small (estimated body weight around 4 kg). Its relationship with living *Colobinae* is unknown. *Libypithecus* (a skull) has been discovered from late Miocene Egypt.

There have been multiple fragmental fossils said to be *Colobinae* (*sensu lato*) from around 7 Ma excavated in eastern and southern Africa. However, information these fossils provide is scarce.

Multiple large colobines are known in eastern Africa ranging from the Pliocene until the early Pleistocene. They are *Cercopithecoides*, *Paracolobus* and *Rhinocolobus*. Among these it is speculated that *Cercopithecoides* was especially well suited for living on the ground.

Reference

General

- Fleagle, John G., 1999: Primate adaptation and evolution. 2nd ed. Academic Press.
- Napier, J. R. & P. H. Napier, 1985: The natural history of the primates. MIT Press.
- Macdonald, D. W., 1986: Encyclopedia of Mammals. Vol. 3. "Primates." Heibonsha.
- Sugiyama, Yukimaru (ed.), 1996: Saru no Hyakka. Datahouse.
- Disotell, Todd R., 1996: The phylogeny of Old World monkeys. *Evolutionary Anthropology* 5: 18-24.

Old World monkeys

Whitehead, Paul F. & C. J. Jolly (eds), 2000: Old World monkeys. Cambridge University Press.

Guenons

Gautier-Hion, Annie (ed.), 1988: A primate radiation: evolutionary biology of African guenons. Cambridge University Press.

Glenn, Mary E. & Marina Cords (eds.), 2002: The guenons: diversity and adaptation in African monkeys. Kluwer Academic/Prenum Publishers.

Macaques

Lindburg, Donald G. (ed.), 1980: The macaques: studies in ecology, behavior and evolution. Van Nostrand Reinhold.

Fa, John E. & D. G. Lindburg (eds.), 1996: Evolution and ecology of macaque societies. Cambridge University Press.

Mangabeys

Cronin, J. E. & V. M. Sarich, 1976: Molecular evidence for dual origin of mangabeys among Old World monkeys. *Nature* 260: 700-702.

Baboons and Geladas

Jolly, Clifford J, 1993: Species, subspecies and baboon systematics. In Kimbel, William H. & L. B. Martin (eds.) *Species, species concepts, and primate evolution*. Plenum. pp. 67-107.

Jablonski, Nina G. (ed.), 1993: *Theropithecus: the rise and fall of a primate genus*. Cambridge University Press.

Disotell, Todd R., 1994: Generic level relationships of the Papionini (Cercopithecoidea). *American Journal of Physical Anthropology* 94: 47-57.

Colobines

Davies, A. Glyn & John F. Oates, 1994: Colobine monkeys: the ecology, behaviour and evolution. Cambridge University Press.

Jablonski, Nina G. (ed.), 1998: *The natural history of the doucs and snub-nosed monkeys*. World Scientific.

Victoriapithecus

Benefit, Brenda R. 1999: *Victoriapithecus*: the key to Old World monkeys and catarrhine origins. *Evolutionary Anthropology* 7 (5): 155-174.