PRIMATE EVOLUTION

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Summary

Living primates include the Strepsirrhini (lemurs, lorises, and galagos) and the Haplorhini (tarsiers, monkeys, and apes). The order arose 80 MYBP (million years before present) to 90 MYBP, and the two major groups are likely to have diverged before 65 MYBP. The Plesiadapiformes, an extinct Paleocene group, may have been related to true primates, but were not their direct ancestors. The earliest true primate radiations occurred in the Paleocene and earliest Eocene, about 60 MYBP. These were the Omomyiformes (haplorhines, chiefly in North America), the Adapiforms (strepsirrhines, mainly in Eurasia), and the simians (haplorhines, in North Africa). The origins of modern strepsirrhines are obscure, because of a scarcity of fossils. Between 45 MYBP and 37 MYBP the simians diverged into the two major groups recognized today: the Catarrhini (Old World monkeys) and the Platyrrhini (New World monkeys). The oldest fossil from the New World is only 29 MY old, suggesting the group probably emigrated from the Old World. Apes diversified in Africa during the Miocene (23 MYBP to 5 MYBP), and spread to Eurasia about 16 MYBP. Cercopithecoid monkeys radiated later than the apes, and may have descended from ape-like ancestors. The earliest putative hominin fossil is between 7 MY old and 6 MY old. The early hominin

radiations were extensive, with about a dozen australopithecine species known from Africa between 4.5 MYBP and 1.5 MYBP. They moved bipedally on the ground, but had adaptations to facilitate climbing in the trees. They were highly sexually dimorphic, and fed on fruit and hard nuts and seeds. The genus *Homo* arose in Africa about 2 MYBP. The first obligate biped capable of long-range bipedalism (*H. ergaster*) emigrated to Eurasia shortly after its appearance in the fossil record. The same course was followed by at least two descendant species, *H. heidelbergensis* and *H. sapiens.*

1. Introduction

Living primates can be grouped relatively easily into two (or sometimes three) suborders. The Strepsirrhini, named for their twisted nares or nostrils, have noses that resemble those of most nonprimate mammals; the skin (called the rhinarium) is hairless and moist, and the upper lip has a deep median groove that tethers it to the gum tissue of the upper jaw. Living members of this suborder, the lemurs of Madagascar and the lorises and galagos of Africa and Asia, are also known as the tooth-combed primates, as the six anterior teeth in their lower jaws are long, thin, and orientated horizontally, forming an effective comb structure used in grooming the fur and gathering food. In most members of this group, the left and right halves of the lower jaw are joined in front by a ligament, which permits some degree of independent movement by the two jawbones during chewing. The Haplorhini, by contrast, have simple or round nostrils, and mobile upper lips that are not fixed securely to the gum. The external skin on the nose is dry and covered with hair, and the two halves of the lower jaw are generally fused together to form a single element. In haplorhine primates, the eye socket (orbit) is walled off posteriorly, insulating the eye from the movements of the chewing muscles—a condition known as postorbital closure. Haplorhines include the monkeys, apes, and humans, and the enigmatic Southeast Asian tarsier. The tarsier shares many characteristics with the other haplorhines, including partial postorbital closure, but also shares superficial similarities with the strepsirrhines: it is nocturnal, it has elongated hind limbs that allow it to move by leaping between the vertical stems of trees, the two lower jawbones are unfused, and the animal is small-bodied and faunivorous. Because of this strange mix of primitive and derived characteristics, some primatologists prefer to place this animal in its own suborder, the Tarsiiformes.

This neat pigeonholing system breaks down, however, as soon as the fossil primates are included, and the picture of primate history and relationships becomes rather confused. Part of the reason for this lack of clarity lies in the fact that the major divergences in the primate lineage occurred a long time ago. The Order Primates evolved relatively early in mammalian history from primitive insectivore-like ancestors, alongside the Scandentia (tree shrews), the Dermoptera (colugos or flying lemurs), and the Chiroptera (bats), and the subdivisions within the order appear to have occurred shortly after the initial radiation (Figure 1).

2. Archaic Primates

Fossil evidence indicates that primates evolved during the late Cretaceous period (perhaps 80 MYBP to 90 MYBP), when dinosaurs roamed the earth. Deposits from the Paleocene Epoch, 65 MYBP to 57 MYBP, have yielded evidence of a highly successful group of small mammals, the extinct Suborder Plesiadapiformes, that disappeared in the early Eocene after they had diversified into more than 25 genera and 75 species. Plesiadapiforms were widely distributed over North America and Europe. Many of them had a large, procumbent lower central incisor, and most were apparently arboreal. They have been associated with the primates primarily because of the structure of their cheek teeth; although it is likely that these animals were at least partially insectivorous like their ancestors, the more extensive crushing surfaces of their teeth and more rounded tooth cusps indicate that their diet was broadening to include a wider range of foodstuffs, specifically vegetable matter.

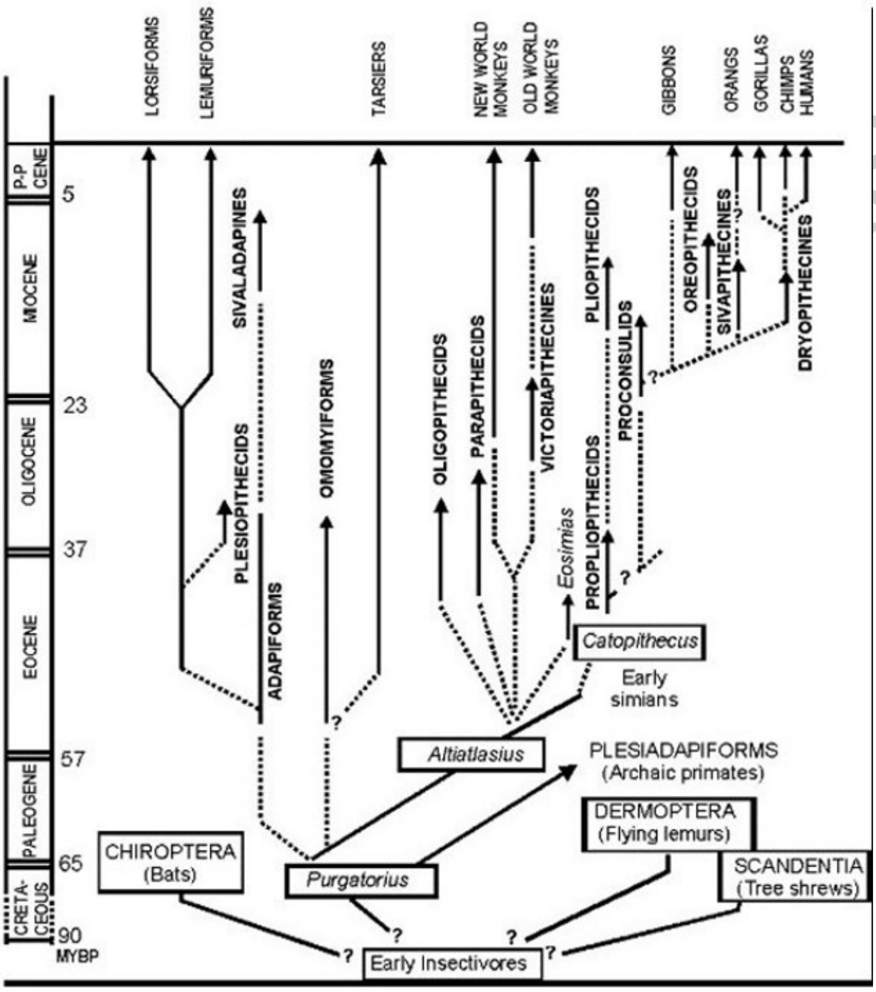

Figure 1. A possible hypothesis of relationships among living and extinct primates. “PP CENE” refers to the Plio-Pleistocene epoch. Dotted lines are inferred relationships; question marks indicate uncertainties.

Within the plesiadapiforms, the lineage most commonly accorded the position of earliest primate is called *Purgatorius,* after Purgatory Hill, Montana, where some of the fossils were found. These animals are known only from a few lower jaws and isolated teeth. An obvious structural trend that has marked the course of primate evolution is the reduction of the snout, and a concomitant reduction in the number of teeth. This is best represented by a dental formula, which describes the number of different kinds of teeth

occurring in one quadrant of the mouth, as follows:
incisors.# canines.# premolars.# molars

While all other known living and fossil primates (including the other plesiadapiforms) are considered to have a maximum of two incisors in each quadrant, *Purgatorius* had three. Similarly, the maximum number of premolars known in living primates and most known fossils is three, while *Purgatorius* had four. This means *Purgatorius* had a dental formula of 3.1.4.3, while the primitive dental formula of living primates (and indeed of the remaining plesiadapiforms) is 2.1.3.3.

The concept of the plesiadapiforms as the basal group that gave rise to all the descendant primate groups, both living and fossil, has been challenged by fossil discoveries indicating that the living primate suborders, the Strepsirrhini and Haplorhini, had already begun to diverge from one another in the Paleocene, during the time that the plesiadapiforms were undergoing their own radiation. The plesiadapiforms other than *Purgatorius* were rather specialized animals that lived contemporaneously with the ancestors of the modern primates. If they were primates at all, their evolutionary diversification had little to do with later developments in primate history.

3. Early Euprimates—“Primates of Modern Aspect”

Euprimates (true primates) are characterized by several shared features, the most obvious of which include orbits that face forward, and grasping hands and feet. In most mammals, including the plesiadapiforms described above, the eye sockets are situated laterally on the skull, and the visual fields of the two eyes do not overlap much. The lateral margin of the orbit is formed by a fibrous ligament. In euprimates, however, the orbits are directed forward so that there is substantial overlap of the two visual fields, and a great improvement in depth perception. The lateral margin of the orbit is made of bone (called the postorbital bar) so that the orbit is surrounded by a complete bony ring.

In all euprimates with the exception of humans, the big toe (called the hallux) is opposable to some degree; that is it is positioned at an angle to the remaining digits and can be rotated in opposition to them to enable a strong gripping action by the foot. The first digit of the hand (called the pollex) is also opposable to some extent in most euprimates. The palms and soles of the hands and feet of living primates are covered with highly sensitive pressure pads, and the skin is folded into papillary ridges that house sweat glands, all of which help the animals to maintain a firm grip on tree branches during locomotion. In addition, euprimates have replaced the claws of their insectivore-like ancestors with flattened nails—although in a few cases, the nails have reverted back to claws. The Aye-aye of Madagascar has claws on all digits except the hallux, a condition that is also found among the marmosets and tamarins of South and Central America. In all living strepsirrhines, the second digit of the foot has a sharp-pointed grooming claw used for dislodging foreign matter that has become stuck in the fur, and the tarsier has similar grooming claws on both the second and third digits.

Earlier theories of primate evolution saw these changes to the orientation of the orbits and the development of grasping hands and feet as adaptations to life in the trees. However, other arboreal mammals such as squirrels manage well without them. What then was the driving force behind the evolution of these distinctly primate characteristics? Some researchers think that they represent the adaptations of a small-bodied predator that used its hands to capture insects on the wing while moving around in an environment made up of small branches. Once the adaptations had been acquired, it became possible for primates to increase greatly in body size and occupy higher levels of the forest canopy in safety, using their grasping hands and feet.

3.1. Adapiforms and Omomyiforms

The earliest well-documented euprimate radiations date from the Eocene epoch (57 MYBP to 37 MYBP). This was a time of global warming, when moist tropical forests spread across Europe, Asia, and North America. During the Paleocene epoch, there had been intermittent connections between the landmasses of Europe and North America; in the Eocene, these contacts ceased, and the faunas on the two continents became progressively more distinct (see *Geology; Paleoclimatology*). The vast majority of fossil primates recovered from this time have been classified into two distinct, but highly diverse, infraorders: the Adapiformes and the Omomyiformes. Paleontologists have identified between 78 and 81 different species of adapiform primates making up 30 genera, and ranging in body size from about 100 g to 4 kg. Judging from the size of their orbits and the form of their teeth, many of the adapiforms were diurnal, and fed on leaves and fruit like modern-day lemurs. Many species, including some that appeared relatively late in the radiation, had retained the primitive number of four premolars. They were distributed widely in North America and Europe. By contrast, the omomyiforms tended to be nocturnal like their ancestors, and lived predominantly in North America. The teeth of early omomyiforms resembled those of adapiforms closely (some of the earliest forms even retained the fourth premolar), and it is difficult to avoid the conclusion that the two groups were fairly closely related. Approximately 70 species comprising 34 genera of omomyiforms have been distinguished, spanning a size range from 30 g to 2.5 kg. The few skeletal elements that have been found indicate that they moved by leaping, in a similar (if less efficient) manner to that used by modern-day bushbabies and tarsiers. While many of the earlier, smaller species were probably insectivores, later, larger species are likely to have been frugivores, and one genus (*Macrotarsius*) may even have contained leaf-eaters. Despite the wide adaptive diversity found among the adapiforms and omomyiforms, both groups went extinct in North America and Europe in the early Oligocene, 33 MYBP, during an event known to paleontologists as the Grande Coupure. This event signaled a major drop in temperature, and was followed by a dry period during which forested regions would have been dramatically reduced. A few adapiform species (referred to as the sivaladapines) lingered on in India, Pakistan, and China until the late Miocene, where they coexisted alongside various ape species.

The majority view among primate paleontologists is that adapiforms were close relatives of the ancestor of the modern-day tooth-combed primates, while at least some omomyiforms show similarities to tarsiers (e.g., *Shoshonius*). Although adapiforms did not have tooth-combs, they shared with the living strepsirrhines several details of their wrist and ankle morphology. The issue as to whether the similarities observed between tarsiers and omomyiforms are indicative of a close evolutionary relationship is the subject of some debate, but most modern classifications would agree that omomyiforms fall on the haplorhine side of the subordinal divide, while adapiforms fall with the strepsirrhines.

3.2. Early Simians

Prior to the 1990s it was common for theories reconstructing the history of the simian or anthropoid primates (i.e. the monkeys and apes) to involve either the adapiforms or the omomyiforms directly in their origins. Since then there have been several important fossil discoveries that have demanded a major rethinking. The fossil *Altiatlasius* was recovered from Paleocene deposits approximately 58 MY old to 56 MY old, in the Atlas Mountains of Morocco. Although this animal is only known from isolated teeth, the structure of these teeth suggests a relationship with later simians. If this relationship is valid, it indicates that the living suborders Strepsirrhini and Haplorhini diverged prior to that date.

A slightly later simian fossil, *Algeripithecus*, recovered from early Eocene (50 MYBP to 46 MYBP) beds at Glib Zegdou, Algeria, paints a similar picture. Both *Altiatlasius* and *Algeripithecus* were small-bodied animals (*Algeripithecus* is estimated to have had a body weight of 150 g to 300 g), and they had teeth with cusps that were lower and more rounded that those of similarly sized omomyiforms and adapiforms. This suggests that early simians had different dietary habits from their nonsimian contemporaries, including more fruit and perhaps a larger proportion of hard food in their diets. This dietary shift may have led to the evolution of the skull characteristics that differentiate the strepsirrhine and haplorhine primates (e.g., complete closure of the bony orbits, fusion of the lower jawbones).

Simian primates have also been recovered from middle Eocene deposits in Burma (40 MYBP) and in eastern China (45 MYBP), indicating that these animals were distributed across a large portion of the Old World. Several species of a genus called *Eosimias* have been found in fissure-fillings in karstic rocks near Shanghuang village in southern Jiangsu Province, China. Like the North African early simians, these animals were of diminutive size, weighing about 100 g. An *Eosimias* lower jaw found subsequently has a dental formula of 2.1.3.3. The cheek teeth are low-crowned with blunt crests, suggesting that the animals subsisted primarily on a diet of fruit supplemented with insects. Eosimiids moved a little like the mouse lemurs of Madagascar—some quadrupedal scurrying with leaping between vertical supports.

What makes the *Eosimias* fossils particularly interesting to students of primate evolution is the company in which they were discovered. Also preserved in the fissure-fillings were some isolated cheek teeth that once belonged to an extinct species of tarsier (*Tarsius eocaenus*). The teeth were identical in structure to, but smaller than, those of living tarsier species. If tarsiers and simians did indeed share a common ancestor, and relatives of modern tarsiers were already present in the middle Eocene, then the date of origin of the haplorhine suborder must have been much earlier, and the euprimates may have originated as far back as the Cretaceous (> 65 MYBP).

Also present in the fissure-fillings were the fragmentary remains of an omomyiform genus previously known only from western North America, and two adapiform species.

One of the adapiforms is a primitive version of other species found in Europe, suggesting that the European representatives may have descended from Asian immigrants. It is difficult to assess from the evidence whether simians are more likely to have arisen in Africa or Asia, but certainly the role of Asia in early primate evolution has been underestimated. Certainly, too, anthropoids did not evolve from either Eocene adapiforms or omomyids.

4. Later Simian Radiations

4.1. Early Monkeys

Prior to the discovery of the Asian fossils in the early 1990s, all evidence pointed to Africa as the stage for early simian (and indeed early primate) evolution. Over the course of the twentieth century, excavations of the Fayum Depression in Egypt contributed considerably to the picture of primate diversity in North Africa from the end of the Eocene to the beginning of the Oligocene (about 30 MYBP to 36 MYBP). The fragmentary fossils recovered include *Afromonius*, an adapiform, and *Afrotarsius*, thought by some to be an extinct relative of the tarsiers, and suggesting that tarsiers once had a much wider distribution than they do today. However, the affinities of the latter fossil are controversial, and a fused tibia and fibula attributed to it have been identified as those of a rodent. Other nonsimian primate fossils have been assigned to the family Plesiopithecidae. *Plesiopithecus* apparently had no incisors whatsoever in the lower jaw, but had a compressed, projecting lower canine. This, together with its robust, loris-like skull, has led some authors to suggest that the plesiopithecids might have been early relatives of the strepsirrhines. But the true fossil wealth of the Fayum lies in its simians. No fewer than three families of simian primates have been discovered, recognizable by the fact that they have orbits that are completely enclosed by bone: the Parapithecidae, the Propliopithecidae, and the Oligopithecidae.

The Fayum simians tell us that, by the late Eocene, anthropoid primates had diverged into the two major subgroups that we identify today: the Platyrrhini (or New World monkeys), restricted today to Central and South America, and the Catarrhini (Old World monkeys and apes), which have a much wider distribution through Africa, the Middle East, and Asia. Of the two, the platyrrhines are more primitive in their organization. Postcranially they are more like the strepsirrhines than the catarrhines are, and they have a dental formula of 2.1.3.3. Catarrhines have lost a premolar, giving a dental formula of 2.1.2.3.

Catopithecus is a genus recovered from late Eocene deposits in the Fayum. It shows postorbital closure, and relatively small orbits that suggest a diurnal life style, defining it quite clearly as an anthropoid. It also has only two premolars, indicating that it falls with the Catarrhini; hence the Platyrrhini and Catarrhini must have diverged well before the appearance of this species, 37 MYBP. Members of the Fayum families Parapithecidae and Oligopithecidae had skeletons that looked a lot like those of platyrrhines, and parapithecids are known to have had a dental formula of 2.1.3.3. They were of small body size (200 g to 300 g), and lived on insects, gum, and fruit. *Apidium*, one of the best known parapithecids, probably moved quadrupedally, and by means of frequent leaping from a quadrupedal posture.

The propliopithecids were of a much larger body size, weighing 1 kg to 6 kg, and have been interpreted by some scientists as early apes. They had a catarrhine dental formula, and lived on fruits and leaves. Nevertheless, their limb bones, too, resembled those of platyrrhines. *Aegyptopithecus*, known from skull and postcranial material, was an arboreal quadruped with a strong, grasping hallux and a long tail.

Despite the presence of highly productive fossiliferous deposits of Paleocene and Eocene age in South America, the oldest simian fossils to have been discovered so far in the New World are of late Oligocene age (29 MYBP). The remains of this oldest New World taxon have been assigned to the genus *Branisella*, and represent a short-faced monkey weighing about 1 kg, and of uncertain affinities to the modern platyrrhines. *Branisella* was followed by a fauna of early simians that contained at least four additional genera that cannot be aligned with certainty with any of the living platyrrhines.

Considering the platyrrhine-like nature of early Old World simians, and the relatively late appearance of simians in the New World, it is likely that the ancestors of the living platyrrhines migrated to Central and South America from Africa or Asia at some time during the Eocene. The Asian *Eosimias* (45 MYBP) and the African catarrhine *Catopithecus* (37 MYBP) set the limits for the divergence time of the Platyrrhini and Catarrhini.

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Biographical Sketch

Judith Masters obtained her Ph.D. in evolutionary biology from the University of the Witwatersrand in 1985. Her specialization is in evolutionary mechanisms, chiefly those leading to the origination and extinction of species. The group that has been the focus of her research for the past twenty years is the primates, particularly the Strepsirrhini. She currently occupies the post of Assistant Director at the Natal Museum, Pietermaritzburg, South Africa.