Primate Evolution

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Lecture on the primate fossil record from the late Cretaceous to the end of the Miocene for the Human Origins course

Introduction

The Primates are the order of mammals that includes ourselves along with other well known creatures such as chimpanzees, baboons and lemurs. The non-human members of the orders show many similarities to us in areas of social behaviour, language, tool-use and anatomy; and study of these animals gives us important insights into the origins of these features in ourselves. This lecture will briefly summarise the various primate groups found alive today and then will talk in more detail about the fossil history of the primates in the Tertiary Period up to the start of the Pliocene Epoch. In addition the biogeographical factors that have influenced the migration and speciation patterns of the primates will also be covered.

Living Primates

There are approximately 300 species of living primates. These are grouped in a variety of ways depending on which textbook you read but the classification used here follows that given by Fleagle [5]. This is almost certainly not the taxonomy that best reflects the evolutionary history of the order but it is probably the one that is most commonly used and it is certainly easier to remember (and spell) than some. Figure 1 shows the part of this classification that includes humans. Side-branches have been pruned to keep the diagram simple and examples of the common names of the groups are given. I shall use the scientific and common names largely interchangeably.

If the classification accurately reflected evolutionary history then the vertical axis would represent time and the higher up the branching point between the taxa the further back in evolutionary time it occurred. This is sadly an oversimplification although it is quite helpful when trying to remember what is going on in the fossil record. The evolutionary bush (Figure 2) is much more true to life showing how at any particular time all we can see is a slice through a much more complicated structure where branches intertwine and terminate at all levels. What we are trying to do when we study primate evolution is reconstruct this historical structure.

FIGURE 1. **Traditional Primate Taxonomy [7]**

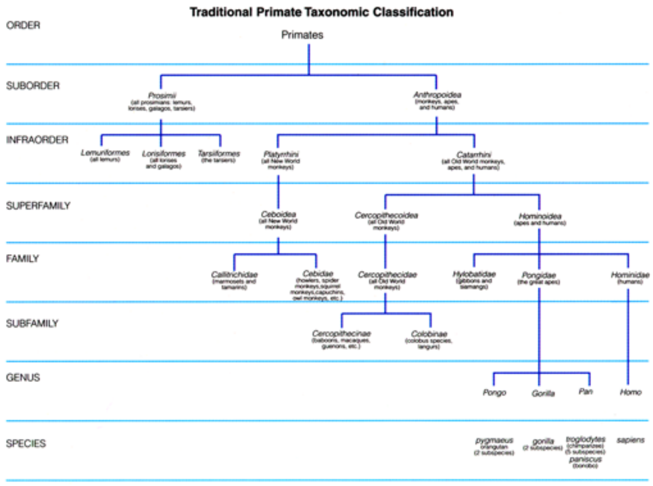
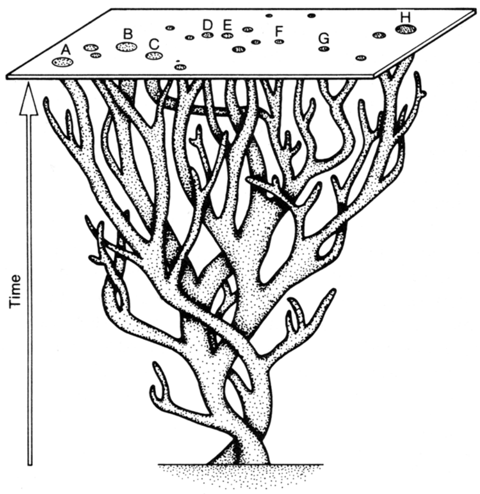


FIGURE 2. **The Evolutionary Bush [15]**



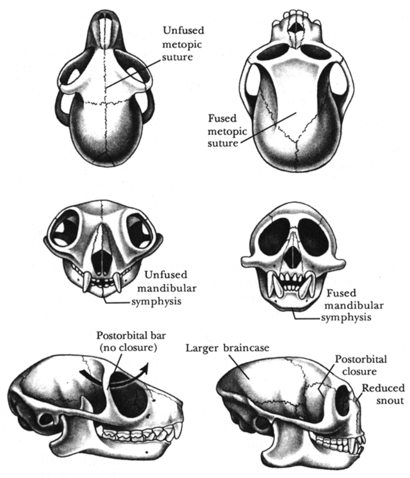
PROSIMIANS AND ANTHROPOIDS

The first major branch of the Order Primates is into the two Suborders: Prosimii and Anthropoidea.[1] This distinction is made on a number of anatomical and behavioural features however the most obvious are found in the skull as shown in Figure 3. There is a greater degree of midline fusion of skull bones in anthropoids: both the mandible and the frontal bone is a single bone in anthropoids and separate left and right bones in prosimians. The joint between the left and right frontal bones is a

1. This is the first major disagreement point too. Many authors (e.g. [3][17]) would split the Order into Strepsirhini and Haplorhini with the Tarsiiformes moved from the other prosimians and grouped with the anthropoids.

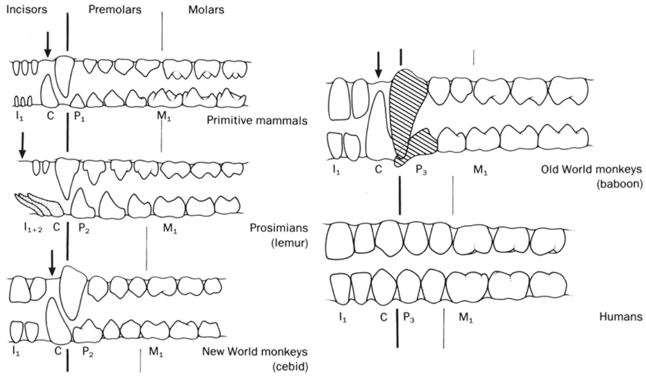
standard skull suture and immobile but the joint between the left and right mandibles is a fibrous joint that will allow a limited amount of movement. It is likely that this will affect the chewing mechanics of prosimians. Indeed the mandibular symphysis in some anthropoids is further reinforced by additional bony ridges (the so-called simian-shelf) suggesting that the mechanical stresses on the bone in this area are large. Post-orbital closure and post-orbital closure can be clearly seen. This may also be an adaptation for increased stresses on the skull during chewing. It is unlikely that protection of the eye is the sole reason since so many other mammals who would benefit from increased eye protection do not have this bony adaptation.

FIGURE 3. Diagram clearly showing the skull differences between prosimians and anthropoids [3]



In addition there are important dental differences. Figure 4 shows the basic tooth arrangements found in the major primate groups compared with that of a primitive mammal. Prosimians possess a unique procumbent tooth comb in the lower jaw whereas anthropoids possess larger, flattened incisors. Simply counting the teeth is a very good way of identifying broad groups of primates since the number is characteristic of many groups although not at the sub-order level.

FIGURE 4. Diagram showing the generalised dental morphology of the major primate groups [4]



There is a great range of living prosimians as illustrated in Figure 5. Although they are often described as primitive and indeed they have smaller brains and retain a number of cranial features more in common with early mammals, they have very specialised locomotor anatomy, dentitions and digestive systems, and the nocturnal varieties are widespread in the Old World although diurnal prosimians are restricted to the island of Madagascar.

FIGURE 5. Examples of extant prosimians[1] [14]

TARSIIFORMES

Tarsier, a rather strange animals need to be mentioned at this point. They are small, nocturnal primates that are found in several areas in South East Asia (Figure 6). They are interesting for us because they are very difficult to classify. At first sight they look a lot like other prosimians but some of their morphology would group them with the anthropoids. You can blame the tarsiers many of the alternative classification schemes! However this intermediate position makes them very interesting since it gives us clues to the evolutionary history of the order. Sadly modern tarsiers are clearly highly specialised animals: they have extremely large eyes which probably distort their cranial morphology; they have a greatly reduced dentition (2.1.3.3/1.1.3.3); and they have a uniquely fused tibia and fibula and a highly elongated tarsus. This makes it much more difficult to try and work out what the ancestral form would have been like. My feeling is that they should be grouped with the anthropoids but because the jury is still out I have left them with the prosimians since this is traditionally how they have been classified.

1. Top left, *Indri indri*; top right, *Daubentonia madagascariensis*; bottom left, *Mirza coquereli*; bottom right, *Loris tardigradus.*

FIGURE 6. Philippine Tarsier (*Tarsius syrichta*) [14]

NEW WORLD MONKEYS

The next major split in the human lineage is between the infraorders Platyrrhini and Catarrhini. The platyrrhine monkeys are also known as New World Monkeys since their geographical distribution is exclusively in Central and South America where they are the only primates found. The Catarrhines include the Old World Monkeys (monkeys found in Africa and Asia), Apes and Humans. Morphologically and behaviourally New World Monkeys are quite variable. They have a general dental formula of 2.1.3.3/2.1.3.3 (Figure 4) but about half of them have lost a molar. They also include the only clawed primates (primate generally have flattened nails like humans), the only nocturnal anthropoid and the only primates with prehensile tails. Figure 7 shows several examples.

FIGURE 7. Examples of extant New World Monkeys[1] [14]

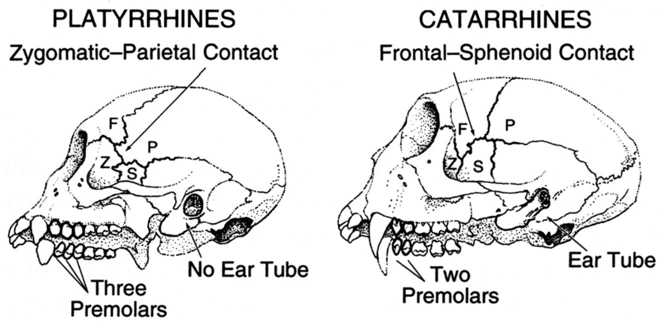
1. Top left, *Cebus apella*; top right, *Leontopithecus rosalia*; bottom left, *Ateles chamek*; bottom right, *Pithecia pithecia*.

OLD WORLD MONKEYS

The infraorder Catarrhini is split into two superfamilies corresponding to the Old World Monkeys (Cercopithecoidea) and the Apes and Humans (Hominoidea). There is a great deal of morphological uniformity within these two groups. The dental formula is always 2.1.2.3/2.1.2.3 (Figure 4) although the shape of the individual teeth is variable (dentition is one area where humans are very distinctive). The faces and pelage of living Old World Monkeys are also easy to recognise (Figure 8) but in terms of features that fossilize (apart from teeth) you need to look at details of the cranium such as the bones of pterion and morphology of the ear (Figure 9).

FIGURE 8. Examples of extant Old World Monkeys[1] [14]

FIGURE 9. Skull differences between Catarrhines and Platyrrhines [5]



APES

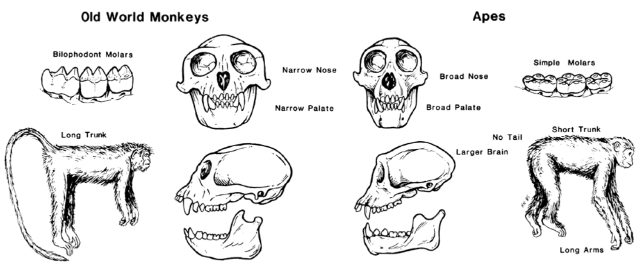
The traditional split at the family level is between lesser apes (gibbons and siamangs), great apes (orang-utans, gorillas and chimpanzees) and humans. Molecular evidence does not support this: chimpazees are more similar to humans than they are to the other great apes and orang-utans are more distant still. This conflicts with the morphological evidence and has not yet been resolved. It would probably be more accurate to reserve the Hominidae family for African great apes and human and keep

1. Top left: *Presbytis thomasi*; top right: *Procolobus badius*; bottom left: *Macaca nigra*; bottom right: *Cercopithecus neglectus*.

Pongidae for the Asian great ape, but since one of the goals of classification is reliable communication I shall once again stick with the traditional groupings. In any case, the sub-family name reserved for the human taxa is Homininae (hominin as an anglicized form) which is far trickier to say than Hominidae (hominid).

There are a number of cranial, postcranial and dental features that distinguish cercopithecoids and hominoids. The key features are illustrated in Figure 10. The term bilophodont refers to the two parallel ridges that run across cercopithecoid cheek teeth. This is thought to be an adaptation to an increasingly folivorous diet. The most obvious feature is that apes and humans lack a tail. This is why *Macaca sylvanus*, the tailless monkeys that live on Gibraltar used to be mistakenly referred to as Barbary Apes.

FIGURE 10. Morphological differences between Old World Monkeys and Great Apes & Humans [5]



The lesser apes are much smaller than the great apes and have a unique mode of locomotion called brachiation. This involves swinging under branches using only their arms. As can be seen from Figure 11 these animals have greatly elongated arms to aid this movement. Interestingly, because of these enormously long arms, gibbons are forced to walk bipedally on the rare occasions they find themselves on the ground.

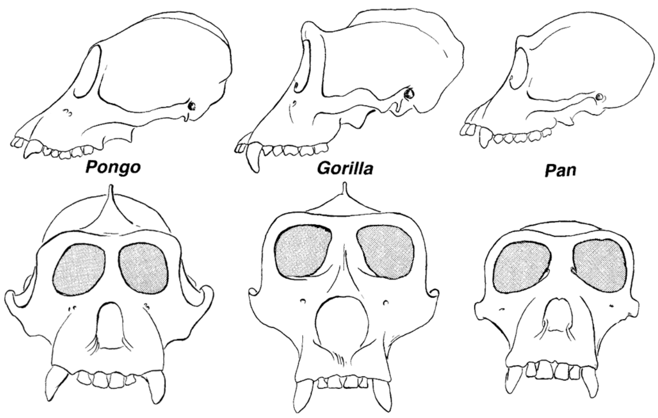
FIGURE 11. White-handed Gibbon (*Hylobates lar*) [7]

Great apes include 3 groups of animals: orang-utans found in Southeast Asia; and Gorillas and Chimpanzees found in equatorial Africa. There used to be a total of 4 species (common and pygmy chimps, gorillas and orang-utans) but there are moves afoot to more than double that number by elevating the various isolated population to species level. The reasons for this are as much political as morphological or genetic (it is easier to campaign to save a unique species than a unique sub-species) so I will stick to these 4 as illustrated in Figure 12.

FIGURE 12. Great Apes[1] [14]

At a skeletal level the morphological differences between these animals are by definition fairly small (they are after all closely related). They can be distinguished by their dentition and by the shapes of their crania and indeed details of almost every bone in their bodies. The skull differences are illustrate in Figure 13.

FIGURE 13. Extant Hominoid Skulls [1]



1. Top left: *Gorilla gorilla*; top right: *Pongo pygmaeus*; bottom left: *Pan troglodytes*; bottom right: *Pan paniscus*.

Fossil Primates

GEOLOGICAL TIMESCALE

In the days before radioactive dating, rocks were to great extent dated by their fossil contents. This is why changes in fossil faunas correspond do well to the named geological time units (Figure 14). The epochs in the Tertiary were defined variously by Charles Lyell, August von Beyrich and Wilhelm Schimper in the 1800 s and are defined by the percentages of modern day taxa present (mostly invertebrates). The names are thus independent of the absolute dates and the dates given here are not universally accepted. The age of mammals can be thought of as the Cenozoic Era from about 65 million years ago until the present day. Mammals first appeared in the Cretaceous Period, towards the end of the Mesozoic Era but it was after the demise of the dinosaurs at the boundary between the Cenozoic and the Mesozoic that great adaptive radiations of mammals took place. Most of the modern mammalian orders date back to the early Tertiary and Primates are no exception.

FIGURE 14. **Geological Timescale [9]**

Era	Period	Epoch
Cenozoic (65–present)	Quaternary (2–present)	Holocene (0.01–present)
		Pleistocene (2–0.01)
	Tertiary (65–2)	Pliocene (7–2)
		Miocene (26–7)
		Oligocene (38–26)
		Eocene (54–38)
		Palaeocene (65–54)
Mesozoic (225–65)	Cretaceous (136–65)	
	Jurassic (193–136)	
	Triassic (225-193)	
Palaeozoic (600–225)	Permian (280–225)	
	Carboniferous (345–280)	
	Devonian (395–345)	
	Silurian (440–395)	
	Ordovician (500–440)	
	Cambrian (600–500)	
Proterozoic (before 600)		

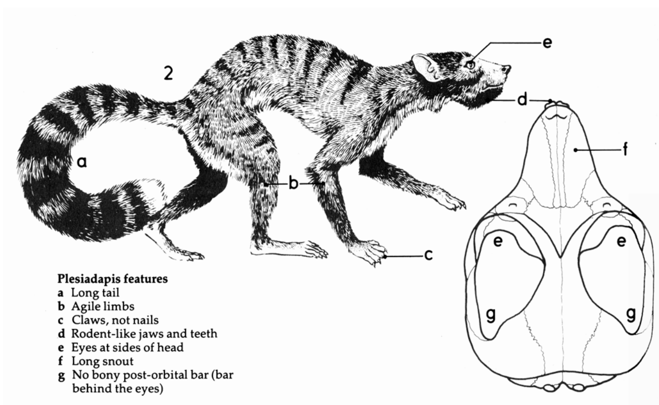
PALAEOCENE PRIMATES

The earliest mammalian group that have been attributed to the order Primates are the Plesiadapiformes. There is a single lower molar tooth that has been attributed to *Purgatorius ceratops* that was found in a late Cretaceous deposit [18]. However since the taxonomic position of the whole suborder (Plesiadapiformes) to which this belongs (there are later, more complete fossils) is under dispute [11][6], the evidence for Mesozoic primates is not especially good!

Once we get to the Palaeocene, we find quite a large number different plesiadapiform fossils in both Europe and North America and a few in Asia [5]. Plesiadapiformes have few recognisably primate features other than a general body shape that indicates an arboreal lifestyle and somewhat similar molar morphology. Plesiadapis itself (a rather spectacular fossil with relatively complete post-crania) possessed claws, rodent-like jaws and teeth, eyes at the side of the head, a long snout and a primitive orbital form (Figure 15). Szalay [16] has suggested that it might have possessed a divergent hallux but this is based on details of the shape of the calcaneus since the hallux has not been preserved. Overall, plesiadapiforms can certainly not be classified as primates of modern aspect but could be ancestral to the rest of the primate order. The problem with statements like this is that most plesiadapiforms are actually highly derived animals especially in terms of their anterior dentition [3]. The suborder Plesiadapiformes is traditionally distinct from Prosimii and Anthropoidea and it can be argued that plesiadapiforms are not ancestral to primates of modern aspect but an early offshoot from the primate family tree that does not lead to modern primates. Indeed the morphological similarity between plesiadapiforms and modern primates is no greater than the similarity between tree-shrews and flying lemurs and modern primates and yet neither of these two groups are considered primates which has led to some authors producing a separate order Plesiadapiformes [5]. It is entirely possible that we will never be able to work out conclusively the evolutionary relationships between these Palaeocene mammals and modern primates. They represent an early adaptive radiation and, as is always the case, most of these species became extinct and were not ancestral to any modern forms. The mammalian fossil record is patchy and it is quite possible that we have not yet discovered the actual species that were directly ancestral to modern primates.

Recent genetic work has suggested that the primate order may well be older than we think. The general approach to working out when a mammalian order appears is to look for the oldest fossils and add on 10 million years or so to allow for the fact that the oldest fossil we find is always an underestimate of the actual age. This would produce a date of 65 million years old for primates since the oldest unequivocal fossils are about 55 million years old [12]. However the genetic evidence based on the time taken for genetic differences to accumulate suggest a much earlier date of about 90 mya. It has been suggested that this may be due to a particularly poor early primate fossil record. The justification for this is that most of the earliest fossil primates have been found in Europe and North America. Modern primates are an essentially tropical group and there is no reason to believe that this was not the case in the past. The lack of fossil site of a suitable age in Africa and Asia for this period may have produced this bias since primates may well have evolved there earlier in the Cretaceous but we have yet to find any fossils.

FIGURE 15. Reconstruction of Plesiadapis [10]



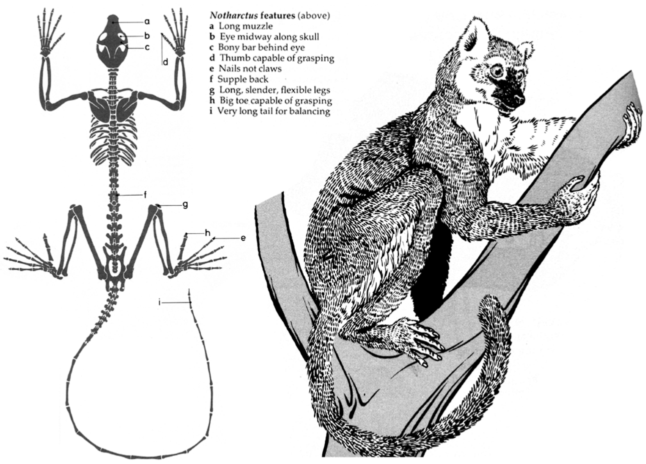
EOCENE PRIMATES

By the time we reach the Eocene the situation becomes much clearer. During this period we find a large number of fossils that can clearly be described as primates of modern aspect or euprimates. There are two main groups that are generally agreed to be two distinct families: the Adapidae and the Omomyidae. Fleagle [5] considers both these groups to be Prosimii and each is contained within its own infraorder: Adapiformes and Omomyiformes. Those who prefer the Haplorhini and Strepsirhini groupings find it more difficult since although superficially adapids look very much like lemurs and omomyids look very much like tarsiers and hence put Adapiformes as a infraorder within Strepsirhini and Omomyidae as a family within Tarsiiformes [17], the detailed anatomy is much more equivocal and any number of different taxonomic interpretations can be supported [3].

There are a number of good primate features found in these animals such as a bony bar behind the eyes similar to modern haplorhines. They also possess flattened nails instead of the claws found in most mammals and have large, forward facing eyes characteristic of stereoscopic vision. Eocene primates are quite widespread, being found in North America, Europe, Asia and Africa and adapid and omomyid species were in existence until the Grand Coupure , a mass extinction event triggered by rapid global cooling at the end of the Eocene.

Adapids tend to be larger animals (above 500g average body mass). Reconstructions of *Notharctus* (see Figure 16) show an animal very much like a modern lemur, and we have a good deal of confidence in these reconstruction since they are based on several extremely good fossils (*Notharctus* can be found in the American Museum of Natural History). This is a good moment to put in a warning about fossil reconstructions. Many of them are not based on very good fossils. We just do not have good fossils for many species and reconstructions are often based on a few teeth, a jawbone and fragments of skull. Postcranial elements (everything from the neck backwards) just do not get fossilised as often, and when we do find them it can be difficult to assign them to a particular species because they are very similar apart from size in many primates. As you might expect, a reconstruction of a whole animal based on just a few teeth has a rather large margin for error.

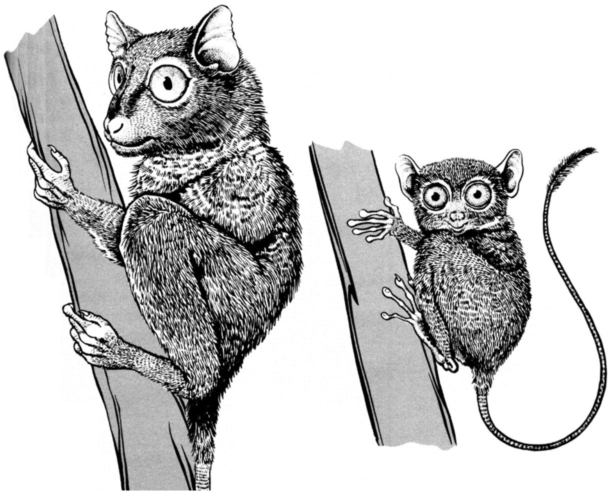
FIGURE 16. Reconstruction of *Notharctus* [10]



Other adapids, for example *Adapis* itself (see Figure 17) are much bulkier, slower moving animals that have been likened to modern lorises. Omomyids are smaller animals (less than 500g average body weight) and although the omomyid fossils are not as impressive as some of the adapids, reconstructions of *Necrolemur* (see figure 5) show an animal that looks a lot like a modern tariser.

FIGURE 17. **Reconstruction of *Adapis* [5]**

FIGURE 18. **Reconstruction of *Necrolemur* (left) and drawing of *Tarsius* (right) showing striking similarity [10]**

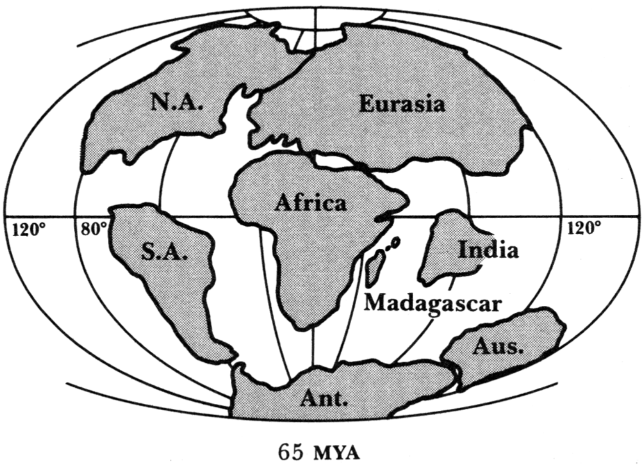


The evolutionary relationships between plesiadapiformes, adapids, omomyids and the extant primate groups are by no means certain. The plesiadapid relationship to primates at all is inconclusive, and whilst it is certain that adapids and omomyids are primates how they lie within the primate evolutionary tree is not clear. Unfortunately both groups share what are thought to be derived features with various groups of modern primates and both retain primitive features and the patterning of these shared features does not tell an obvious story. Thus some adapids have a fused mandibular symphysis which is a feature of anthropoids whilst all omomyids have the unfused mandibular symphysis found in prosimians. Omomyids have a tubular ectotympanic bone like many anthropoids and adapids have the ring-shaped ectotympanic of prosimians. And so the list continues. Indeed barring the striking similarity in overall shape between on the one hand adapids and lemurs, and on the other hand omomyids and tarsiers there is relatively little linking these fossil forms with modern species and there is nothing among the Eocene primates that is indicative of a common ancestor for platyrrhines and catarrhines.

MADAGASCAN PRIMATES

One of the unanswered questions of this period is the origin of primates in Madagascar. The modern lemur population is entirely restricted to this island off the East coast of Africa and genetic evidence suggests that these animals have been isolated from other primate groups for approximate 50 million years. It is clear that a small number of primates must have arrived from another continent and evolved independently on Madagascar.

FIGURE 19. Positions of the continents at the beginning of the Tertiary[3]



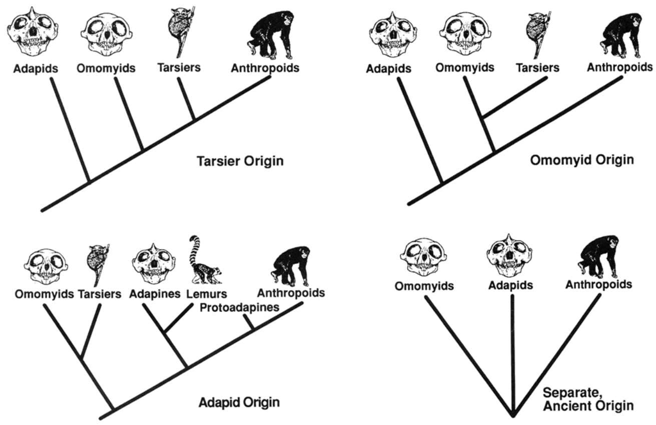
The traditional hypothesis is that one or more lemurs crossed the Mozambique channel from Africa on a raft of floating vegetation/ This is a 400 km distance which is within modern reported rafting distances. It is suggested that currents from rivers emptying into the channel helped push the raft. The second hypothesis is that the migration was actually from India. As you can see from the map (Figure 19) this is rather less implausible at the time due to the different position of India. The third hypothesis is that land bridges may have appeared between Madagascar and Africa sometime during the late Cretaceous to mid Oligocene due to periods of very low sea level caused by increased glaciation. The last two hypotheses would explain why colonisation events did not continue (India becoming too far away or the sea level becoming to high) although one could simply suppose that rafting is sufficiently rare for it to be a unique occurrence.

There is also the question of the number of these colonisation events. Traditionally it is assumed that a single event occurred and that all the modern Madagascan primate fauna can be traced to a single common ancestral population. However some classifications suggest that the dwarf lemurs (Cheirogaleidae) are actually more closely related to the African and Asian prosimians (Lorisidae) than they are to the other Madagascan lemurs [17]. This would require a second colonisation event, either from Africa to Madagascar or in the other direction.

ORIGIN OF THE ANTHROPOIDS

One of the major difficulties is how to link up the Eocene prosimians with the Oligocene Anthropoids. There are 4 major current theories (Figure 20) which attempt to do this. There is anatomical and genetic evidence to support all the hypotheses (one might be forgiven for believing that people just put forward their favourite prosimian as a potential ancestor). I prefer the Tarsier Origin since the anatomical linkage between Tarsiers and the Anthropoids is quite strong — however the Ancient Origin theory is also appealing since it is the only one that really explain the disparate nature of the evidence. There is no consensus answer on this question yet.

FIGURE 20. Anthropoid Origins [5]

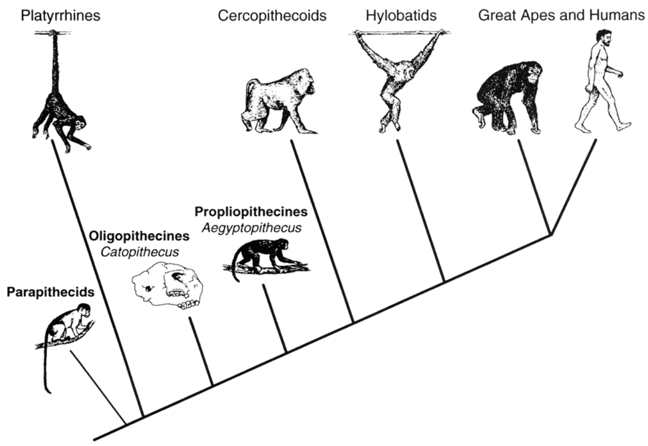


OLIGOCENE PRIMATES

Actually, we should really rename this section as Late Eocene because recent finds have pushed back the origin of the platyrrhines and catarrhines (anthropoid primates). Until recently there was very little anthropoid material except from the Fayum valley in Egypt. Some fossils from there have now been dated as Eocene and there have also been Eocene finds in Asia that have been described as anthropoid. Oligocene anthropoids have been found elsewhere in North Africa and in the Near East. Tarsioids have been found in China and Lorisoids have been found in North Africa. This puts an early limit on the lorisoid colonisation event in Madagascar although the lemuroid colonisation could have occurred earlier if they are indeed descended from adapids. A small number of Oligocene primates are found in South America although whether these originated from Africa or North America is unknown. Primates are very rarely found in North America or Europe as a result of the climate changes associated with the Grand Coupure . As mentioned before this presents a problem for the primate colonisation of South America since the continent was isolated at this period. There are implications of the colonisation route for the origin of platyrrhines. If they managed to raft from Africa then this is probably the location of the common ancestor for platyrrhines and catarrhines. If they island-hopped from North America then the platyrrhine origin is far less clear and it becomes more likely that the platyrrhines evolved independently from some Eocene primate ancestor. Sadly there is no obvious answer to this question.

The early Asian anthropoid fossils are still poorly classified. They are currently flagged as *Incertae sedis* at various taxonomic levels which means that people have not made up their minds where to put them. This is usually due to the fossils being only small fragments of jaws and teeth which is insufficient to make a complete classification. Fleagle [5] classifies them within Anthropoidea, superfamily *Incertae sedis* whereas Szalay and Delson [17] put them in infraorder Catarrhini (I suspect more due to their geographical location in the Old World rather than any morphological details). Early African anthropoid fossils are in the superfamily Parapithecoidea which again Fleagle classifies outside the catarrhines. The evolutionary position of the parapithecoids is interesting since there are a number of groups they could be considered ancestral to. Some of them could be ancestral to the platyrrhine/catarrhine split, or they could be catarrhine ancestors or indeed direct ancestors of the cercopithecoids (see Figure 21).

FIGURE 21. Diagram showing a possible phylogenetic tree of the early anthropoids [5]



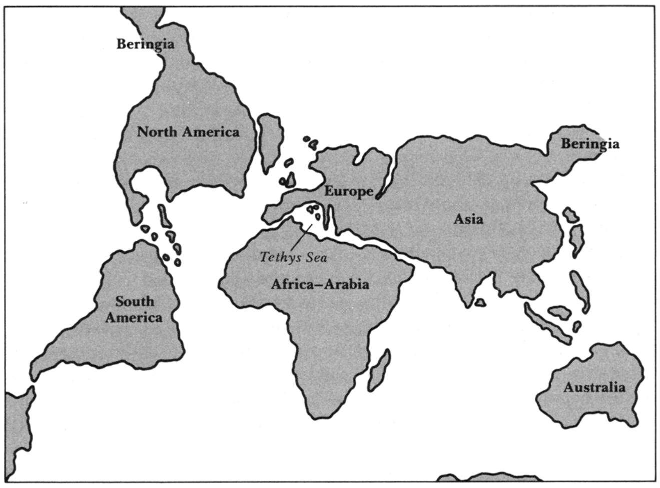
Other Eocene groups in Africa include the Propliopithecidae and the Oligopithecidae. Quite frankly no one knows what to do with the oligopithecids but the propliopithecids are more interesting. Their dentition is very similar to that of later hominoids which has led to their inclusion in the Hominoidea and their place as direct ancestors to the modern apes and humans [17]. Others, notably Fleagle [5], believe that this similarity is the result of parallel evolution and that propliopithecids are better placed before the cercopithecoid and hominoid split and delaying this split until the Miocene.

NEW WORLD PRIMATES

The South American primate fossil record is relatively sparse — especially when compared with other mammals. Two very similar late Oligocene genera have been described: Branisella and Szalatavus. These have been classified within the Ceboidea and tell us relatively little about the origin of the Platyrrhini since we only have dental remains.

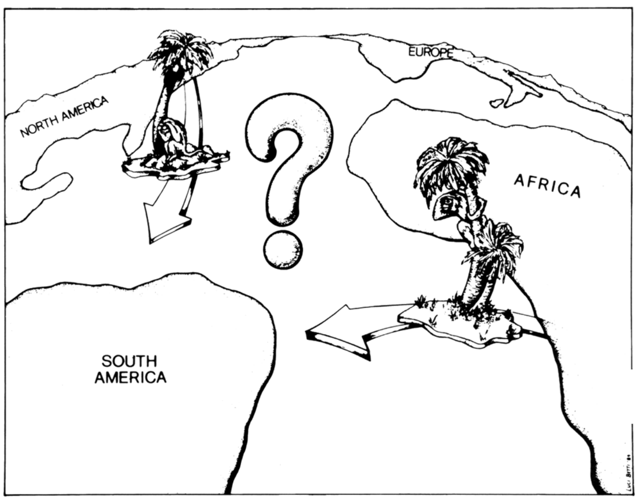
The big question for New World Primates is where did they come from. The Palaeocene fossils that we have are mainly in Europe and Asia. We have a good fossil record of Eocene primates in Africa. The Tethys Sea, from other faunal evidence, was an effective barrier to migration between Europe and Africa (see Figure 22) and there is a considerable distance between Africa and South America.

FIGURE 22. Approximate distribution of land masses in the early Oligocene (approximately 35mya) [3]



As before with Madagascar, there are two rafting hypotheses and a land-bridge hypothesis. The rafting hypotheses are illustrated in Figure 23. A rafting event from Africa produces fewer difficulties with the fossil record: we can postulate a single origin for the anthropoids in Africa and a migration and subsequent speciation in South America with the American and Eurasian early primate populations becoming extinct in the Grand Coupure. Rafting from North America seems much more likely in terms of distance and the presence of numerous Caribbean islands means that it might even have occurred in a series of easily managed stages. However this hypothesis would mean that either there was a single anthropoid origin in Europe and North America and widespread migration (with no fossil record to support this) or there was a dual origin of Anthropoid with Platyrrhines originating in North America and Catarrhines in Africa.

FIGURE 23. Diagram illustrating the two rafting hypotheses for the primate colonisation of South America [5]



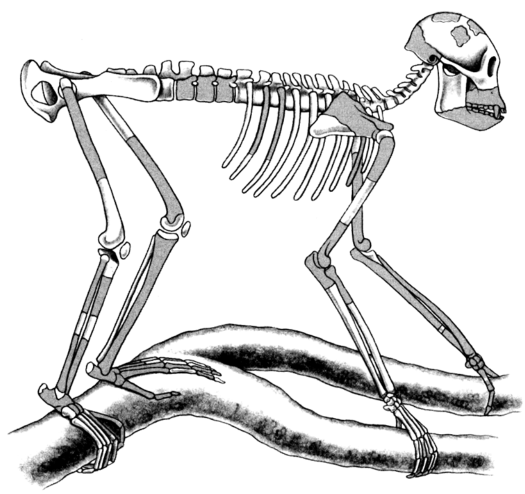
The land bridge hypothesis relies on the existence of Atlantic Ocean ridges and a fall in the sea level in the Oligocene. This would have either produced a single land bridge or a series of mid-Atlantic islands to act as stepping stones for the migration.

MIOCENE PRIMATES

By the Miocene, it seems likely that all the modern superfamilies are present and by the late Miocene the families are all present too. However the vast majority of primate fossils from early in this period have been found in Africa — it is only during the middle Miocene that we find Asian and European primates. The South American fossil record continues to be poor but again by the middle Miocene all the modern families are represented. In the early Miocene early apes are the most abundant anthropoid with early monkeys being comparatively rare. This proportion reverses by the middle Miocene with monkeys now dominating. With the very recent exception of *Homo sapiens* this trend has continued ever since with monkeys a far more successful group than the apes.

In the early Miocene the Proconsulidae family appears (see Figure 24). These are large bodied animals and we have a number of well preserved fossils that tell us that these animals were unquestionably hominoids. An equivalent phylogenetic position for the cercopithecoid monkeys is held by the Victoriapithecidae family [3][2]. Propliopithecidae are an early European hominoid family.

FIGURE 24. Reconstruction of skeleton of *Proconsul africanus* [3]



In the Middle and Late Miocene we can probably identify four distinct hominoid taxa. *Griphopithecus* from Europe and Western Asia; *Dryopithecus* from Europe and *Lufengpithecus* from Asia; *Sivapithecus* etc. from Western and Southern Asia; *Ouranopithecus* (*Graecopithecus*) from Greece and Turkey. Of these, *Sivapithecus* could well be ancestral to modern orang-utans and *Ouranopithecus* could be ancestral to the later African hominoids (gorillas, chimps and humans). This latter lineage is very uncertain since the link between *Ouranopithecus* and the later hominoids is not strong. Molecular evidence tells us that the split between gorillas, chimpazees and humans probably occurred right at the end of the Miocene or early in the Pliocene. With the possible exception of *Ardipithecus ramadus*, all the early Pliocene hominoid fossils are hominids and we know nothing about the early chimp and gorilla lineage.

FIGURE 25. Branching time of modern apes based on genetic evidence and timing of the major fossil ape groups [8]

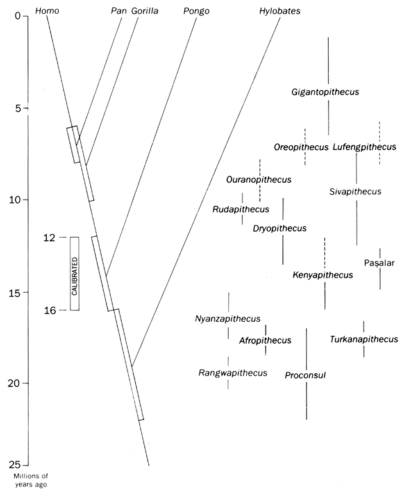
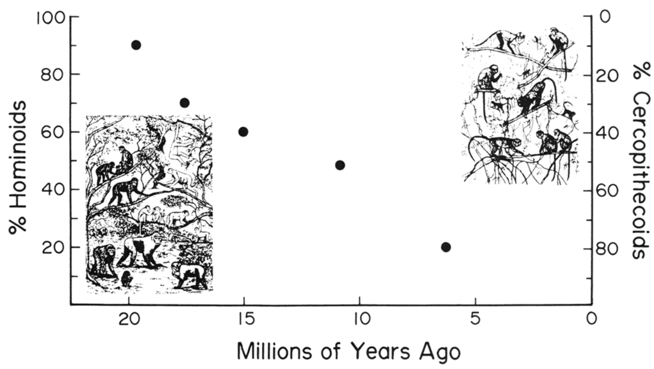


Figure 25 illustrates the major fossil ape groups and shows the timing of the splits in the hominoid phylogenetic tree. Given the uncertainty of the linkage between these groups almost any line could be drawn between groups (and has been — I checked all the main text books and they all differ).

FATE OF THE HOMINOIDS

One feature of the evolutionary history of the primates that is quite clear is that monkeys should be considered more advanced than hominoids. This may sound like anthropological heresy but it is well supported by the evidence. Hominoid species appear in great numbers early in the Miocene and their numbers decline with the rise of the cercopithecoids later in the Miocene and this trend has continued to the present day (Figure 26). There are a number of reasons why this might be the case. Various cercopithecoid species have several dietary specialisations (multi-chambered stomachs, cheek pouches, bilophodont molars) that allow the group to exist on a greater range of foodstuffs. They have evolved a large variety of different social organisations that may also extend the number of niches they are able to exploit. It has also been argued that this replacement is due to the effects of climate change.

FIGURE 26. Relative species diversity of cercopithecoids and hominoids in the last 20 million years [5]



MISSING LINKS

From this summary of the Tertiary fossil record there are a number of take-home messages. Each of the major geological epochs are characterised by major primate adaptive radiation such that a relatively few taxa dominate the primate fauna. Figure 27 shows illustrates this by showing a simplified outline of the major groups in each epoch. Within these taxa there is appreciable variation in size and anatomy and we must assume also diet and behaviour and therefore ecological niche occupied. It is relatively easy to sort out the phylogenetic relationships within these epochs but we have had very little success in mapping the relationships between them. The reason for this is that we would have to be extremely lucky to find the actual common ancestor for a current taxa. The vast majority of species become extinct and only a very few evolve into new species — otherwise the total number of species would increase with time and there is no evidence that this occurs. Thus the fossils we see are all individuals sharing a number of ancestral features with our common ancestor and having their own derived features. It is impossible to identify with any certainty which features are genuinely ancestral and which are the result of parallel or convergent evolution and for this reason it is likely to be impossible to untangle the evolutionary web. However that does not mean we should not try and as more fossils are found whilst we can never be sure we have the correct family tree we should have a much clearer idea of the possible family trees.

FIGURE 27. A very simplified outline of the primate fossil record. Names in brackets are extinct groups representative of the period.

Palaeocene	Unknown Primate Ancestors (Plesiadapiformes)					
Eocene	Strepsirhine (Adapiformes)		Haplorhine (Omomyiformes)			
Oligocene	Lemuriformes (Plesiopithecidae)		Platyrrhines (Branisellinae)		Catarrhines (Parapithecoidea)	
Miocene	Lemuroidea	Lorisoidea	Ceboidea	Pithecoidea	Hominoidea (Proconsulidae)	Cercopithecoidea (Victoriapithecidae)

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