

Primate Fossils

Introduction

Having described the taxonomy of living primates, it is important to fill in some details from fossil forms. This is because the fossil forms encompass a wider range of variation than found in extant primates and also because it provides evidence about the direction of evolutionary change. A characteristic that is found in a very old fossil is likely to be ancestral and one that is only found in recent animals is likely to be derived. Of necessity I shall concentrate mainly on bony features of these animals although occasionally behavioural characteristics can be inferred from bony structure. The classification of fossil primates is necessarily vague. It is rarely possible to produce monophyletic groupings and much of the classification is temporal rather than strictly morphological – especially for the older fossil species.

Geological Timescale

Fossils were studied a long time before there was any reliable method of dating the rocks in which they were found. Because of this, dating was done on a relative scale by looking at the types of fossils found in the rock and comparing these fossils with those found in rocks elsewhere. In the same way that there is a type specimen for a species in a museum somewhere, there is a type section: a rock sample for a particular age of rock that can be used as a reference. These type sections have names that are used to name the geological age that they come from. Thus the Devonian period is named after a piece of rock of that age found in Devon. Originally the ages of these rocks were estimated by considering places such as the Grand Canyon where you have more than a mile of rock layers. Changes in fossils can be seen as you go deeper into the canyon and estimates can be made about how quickly such rocks could form. As it happened, these estimates made in the 18th and 19th century tended to vastly underestimate the age of the rock (see the chapter in Strickberger {Strickberger, 1990} for discussion). Modern rocks are dated by a variety of methods but potassium-argon and uranium series dating are probably the commonest methods used for primate fossils (see Aitken {Aitken, 1990}). However it is important to realise that the absolute dates generated by these dating methods often have quite large margins of error attached and the dates generated by different methods on different rocks do not always closely agree. It is for this reason that we still commonly use relative dating and refer to geological time units when talking about fossils rather than assigning absolute ages. Another factor is that many rocks are still impossible to date and relative dating is still the only option.

Figure 1 shows how these various names are thought to match up with actual ages. Eras are the longest geological time units; these are subdivided into periods which are themselves subdivided into epochs. As you might now expect, epochs are themselves divided into subepochs (often Early, Middle and Late or the more confusing terms Lower, Middle and Upper referring to where in the stratigraphic column you would find them – for example Middle Pleistocene). There are also other names that you might hear that refer to the names of, for example, different ice ages or specific faunal groups. Hopefully if you do come across these it will be made clear what they are actually referring to but it is not always obvious. There are named periods and epochs in all the eras but since primate evolution takes place almost entirely in the Cenozoic, these are the only ones I have put in the table. Please note that geological time units require capital letters – even the subepoch part when you are being specific: ‘in the Early Pleistocene’ ties quite specifically to a certain group of rocks whereas ‘in the early Pleistocene’ is a more vague specification meaning sometime early on in the

Pleistocene. Also, there are some specific occasions where a single epoch is not an appropriate unit and you will see joined forms such as Plio-Pleistocene.

In actual fact, geological dating is rather more complicated than this. Named and dated rock units (groups, formations, members and beds) produce time-stratigraphic units (systems, series and standard stages) defined by the age of particular rocks in a type locality. Palaeontologists use a more abstract system that is easier to apply globally. These are the geological time units (eras, periods, epochs and land-mammal ages). They are defined by fossil contents - for example the Eocene contains 3% of extant species, the Miocene 17% and the Pliocene 67% {Conroy, 1990}.

Figure 1. Geological time units. All ages are approximate and shown in millions of years before present. Based on Lambert {Lambert, 1985}.

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)		

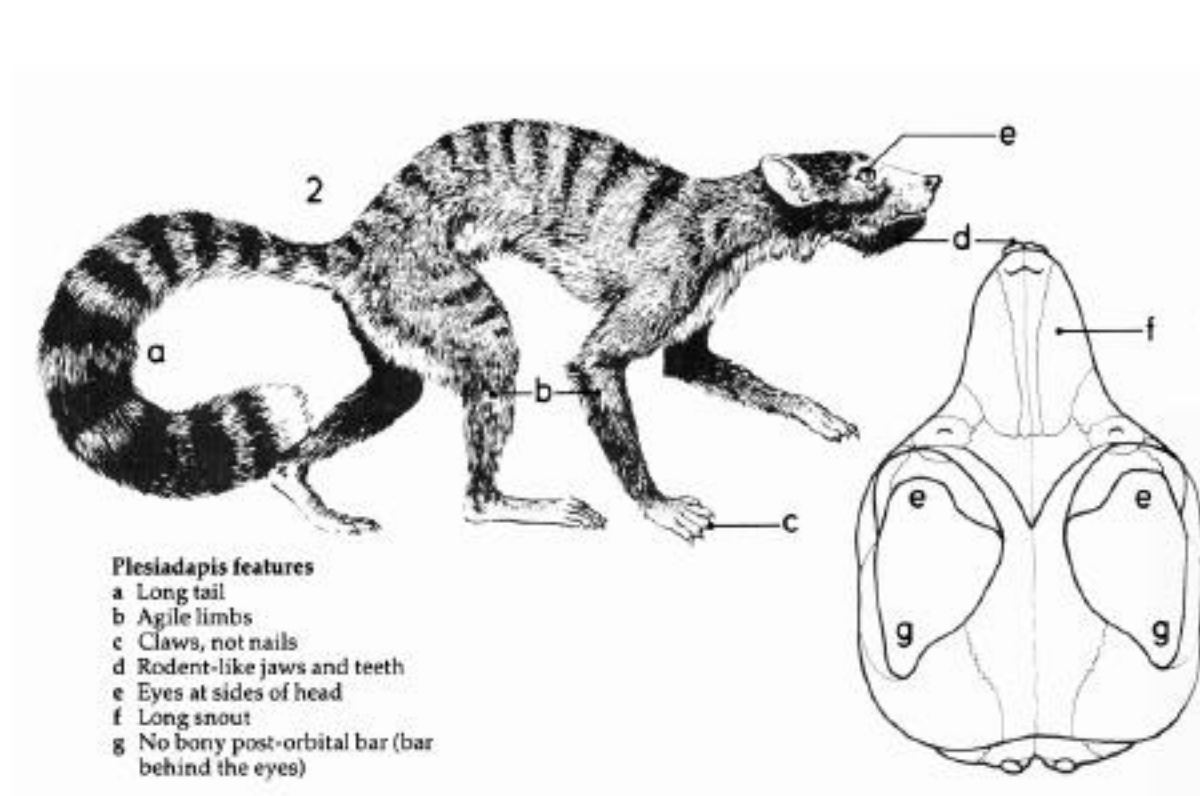
Mammals start to appear early in the Mesozoic, but it is likely that primates did not evolve until the Cenozoic. There is a single lower molar tooth that has been attributed to *Purgatorius ceratops* that was found in a late Cretaceous deposit {Van Valen and Sloan, 1965}. However since the taxonomic position of the whole suborder (Plesiadapiformes) to which this belongs (there are later, more complete fossils) is under dispute {Martin, 1986} {Gingerich, 1986}, the evidence for Mesozoic primates is not especially good!

Palaeocene Primates

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 {Fleagle, 1999}. 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 (see figure 2). Szalay {Szalay, 1977} 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 {Conroy, 1990}. The suborder Plesiadapiformes is distinct from Strepsirhini and Haplorhini in our classification scheme {Szalay and Delson, 1979} 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 {Fleagle, 1999}. 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.

Figure 2. Reconstruction of *Plesiadapis* (from Lambert {Lambert, 1987}).



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 {Fleagle, 1999} 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 our classification puts Adapiformes as a infraorder within Strepsirhini and Omomyidae as a family within Tarsiformes {Szalay and Delson, 1979}), the detailed anatomy is much more equivocal and any number of different taxonomic interpretations can be supported {Conroy, 1990}.

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 3) 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. Other adapids, for example *Adapis* itself (see figure 4) 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 3. Reconstruction of *Notharctus* (redrawn from Lambert {Lambert, 1987}).

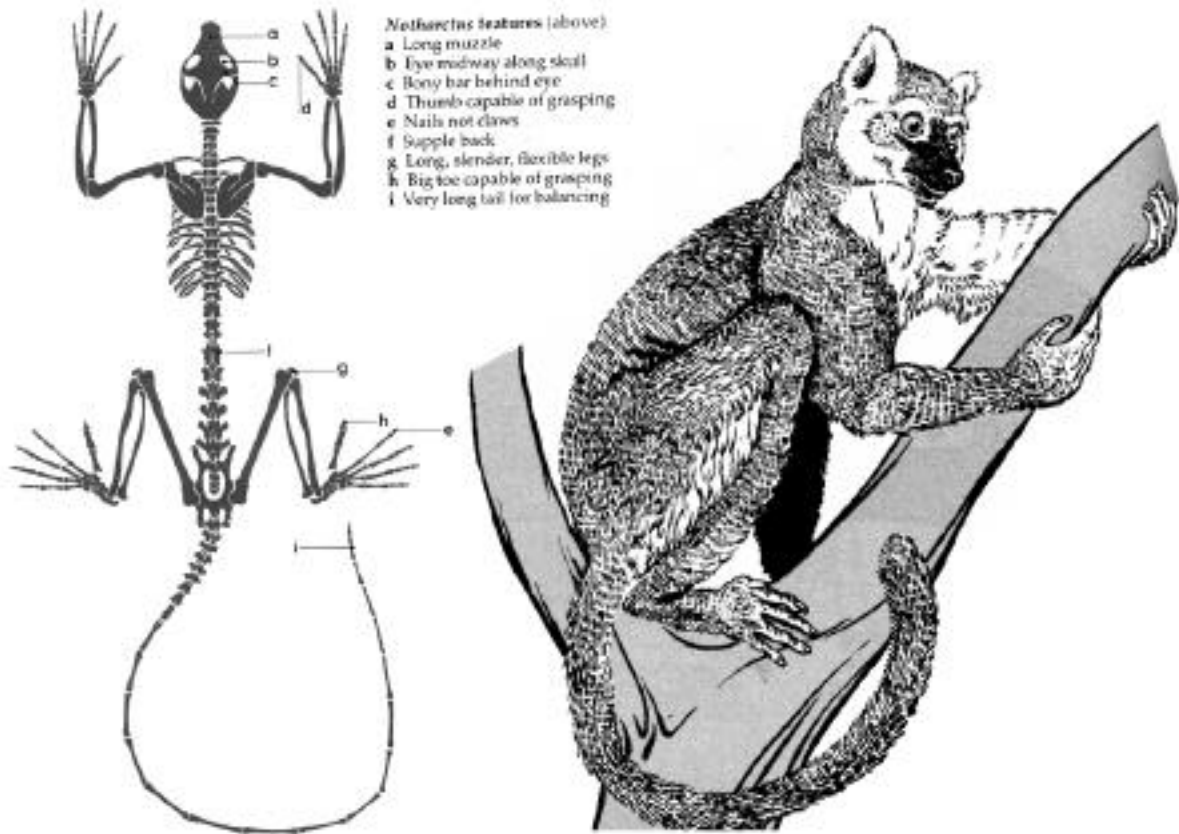
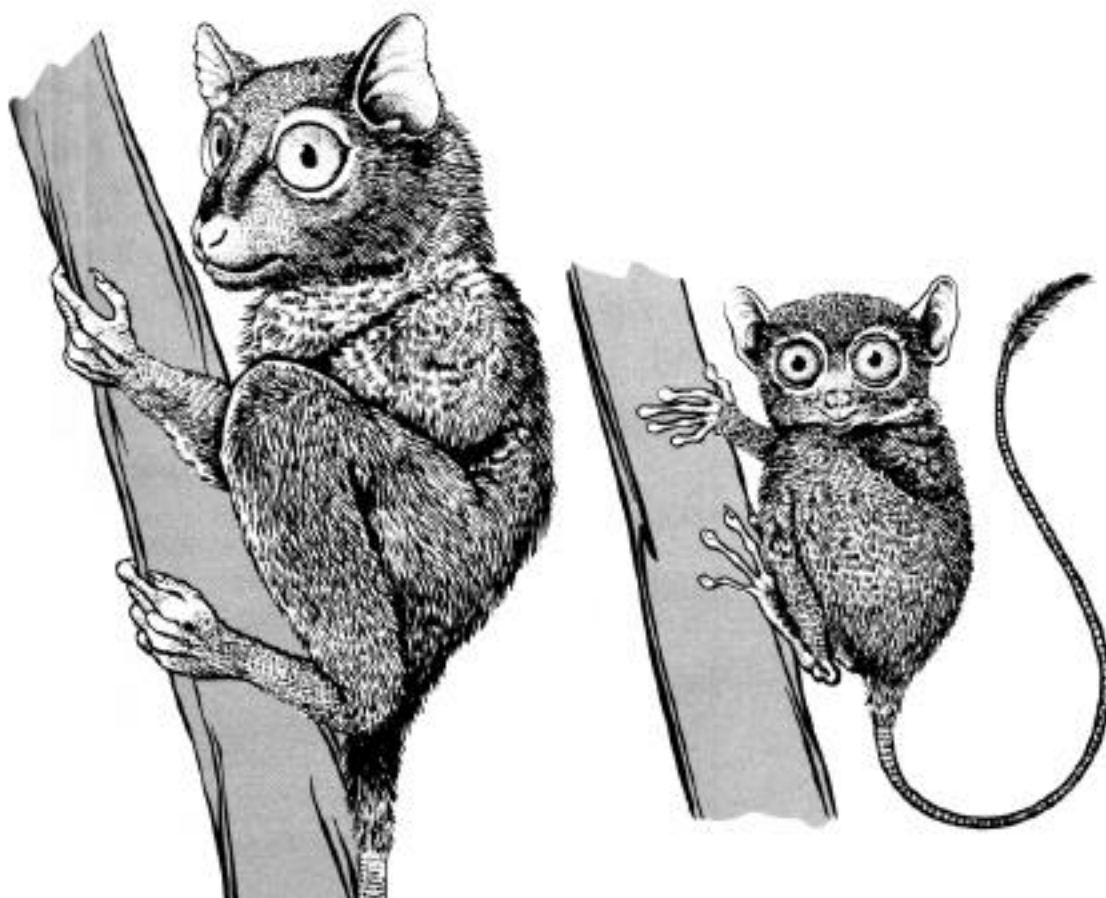


Figure 4. Reconstruction of *Adapis* (from Fleagle {Fleagle, 1999}).



Figure 5. Reconstruction of *Necrolemur* (left) and drawing of *Tarsius* (right) showing striking similarity (from Lambert {Lambert, 1987}).



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 haplorhine primates whilst all omomyids have the unfused mandibular symphysis found in strepsirhines. Omomyids have a tubular ectotympanic bone like many haplorhines and adapids have the ring-shaped ectotympanic of strepsirhines. 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.

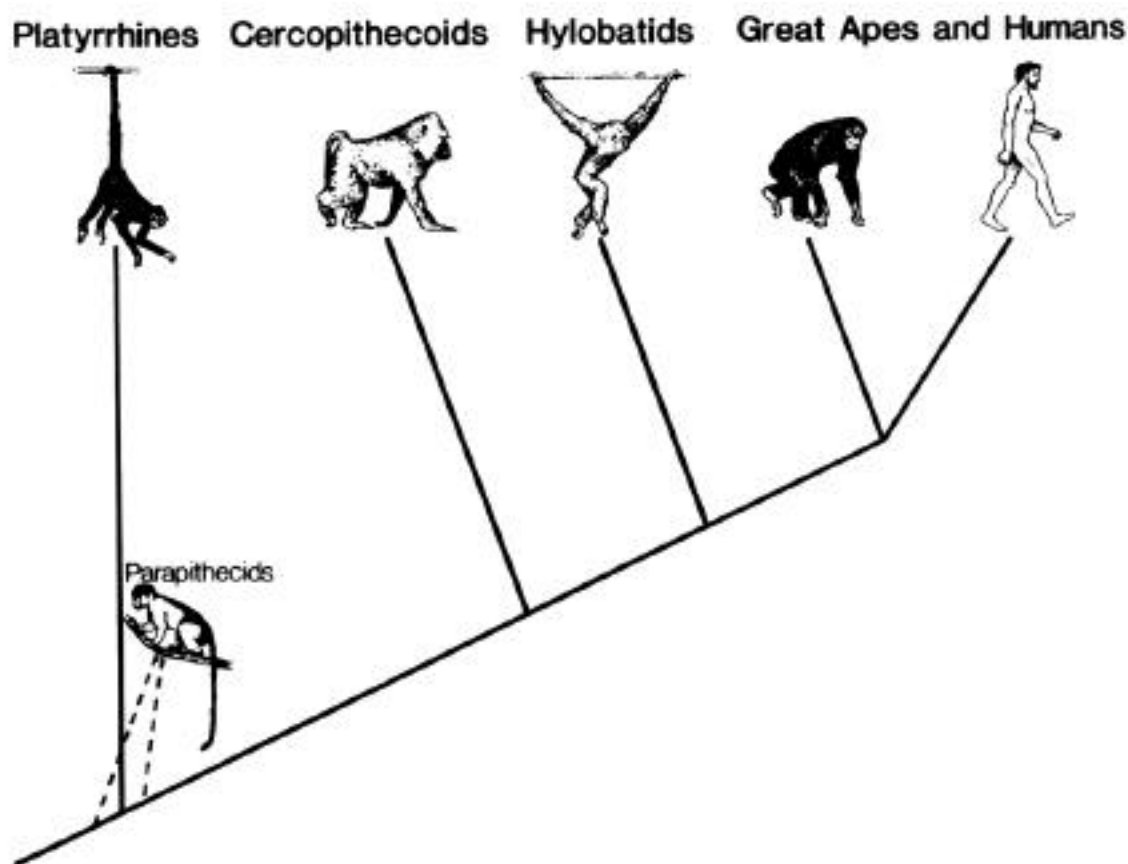
Oligocene Primates

Actually, we should really rename this section as Late Eocene because recent finds have pushed back the origin of the platyrrhines and catyrrhines (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 loroid 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 {Fleagle, 1999} classifies them within Anthroidea, superfamily *Incertae sedis* whereas Szalay and Delson {Szalay and Delson, 1979} 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 6).

Figure 6. Diagram showing the uncertain phylogenetic position of the parapithecoids (from Fleagle {Fleagle, 1999}).



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 {Szalay and Delson, 1979}. Others, notably Fleagle {Fleagle, 1999}, 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.

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 *Szalotavus*. These have been classified within the Ceboidea and tell us relatively little about the origin of the Platyrrhini since we only have dental remains.

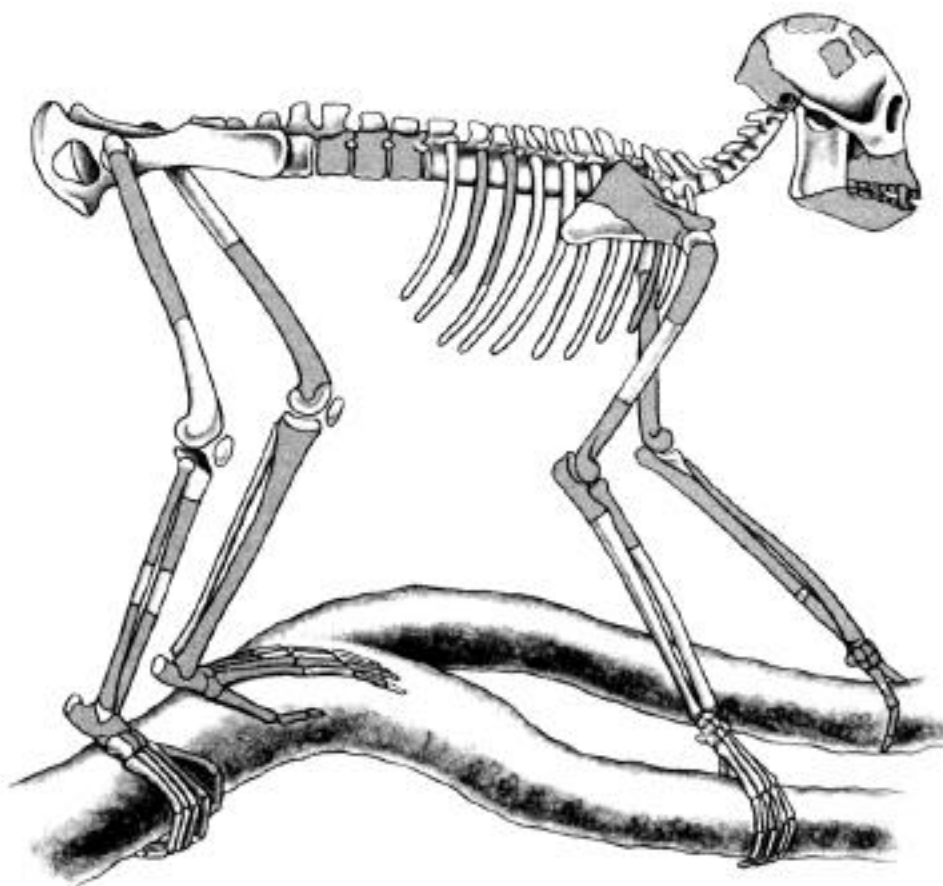
Miocene Primates

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 7). 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 {Conroy, 1990} {Benefit and McCrossin, 1997}. Propithecidae are an early European hominoid family. Later fossils can generally be fitted into a modern taxonomic framework although the phylogenetic relationships among the various species of middle to late Miocene hominoids are by no means certain and this is the area that generates the most hot air since some of these animals are likely to be directly ancestral to humans.

Figure 7. Reconstruction of skeleton of *Proconsul africanus* (from Conroy {Conroy, 1990}).



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 8 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 8. 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 (Parapithecoidae)	
Miocene	Lemuroidea	Lorisoidea	Ceboidea	Pithecoidea	Hominoidea (Proconsulidae)	Cercopithecoidea (Victoriapithecidae)

Bibliography

- Aitken, M.J. *Science-Based Dating in Archaeology*. London: Longman, 1990.
- Benefit, B.R., and M.L. McCrossin. "Earliest Known Old World Monkey Skull." *Nature* 388 (1997): 368-371.
- Conroy, G.C. *Primate Evolution*. London: Norton, 1990.
- Fleagle, J.G. *Primate Adaptation and Evolution*. London: Academic Press, 1999.
- Gingerich, P.D. "Plesiadapis and the Delineation of the Order Primates." In *Major topics in primate and human evolution*, eds. B. Wood, L. Martin, and P. Andrews. 32-46. Cambridge University Press: Cambridge, 1986.
- Lambert, D. *The Cambridge Guide to Prehistoric Life*. Cambridge: Cambridge University Press, 1985.
- Lambert, D. *The Cambridge Guide to Prehistoric Man*. Cambridge: Cambridge University Press, 1987.
- Martin, R.D. "Primates: a Definition." In *Major topics in primate and human evolution*, eds. B. Wood, L. Martin, and P. Andrews. 1-31. Cambridge University Press: Cambridge, 1986.
- Strickberger, M.W. *Evolution*. Boston: Jones and Bartlett, 1990.
- Szalay, F., and E. Delson. *Evolutionary History of the Primates*. New York: Academic Press, 1979.
- Szalay, F.S. "Phylogenetic Relationships and a Classification of the Eutherian Mammalia." In *Major Patterns of Vertebrate Evolution*, eds. M.K. Hecht, P.C. Goody, and B.M. Hecht. New York: Plenum Press, 1977.
- Valen, L.V., and R. Sloan. "The Earliest Primates." *Science* 150 (1965): 743-745.