From *Purgatorius ceratops* to *Homo sapiens*

I. Primate Evolutionary History

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Looking at ourselves today, it is a little difficult to conceive of our origins as "small, fuzzy critters" that ate insects and lived in trees. And yet, as modern biology suggests, humankind is only part (and a very small part!) of an evolutionary continuum that stretches back to the origins of the primate order, some 80 million years ago. This article attempts to trace the origin and evolution of the primate order from its beginnings as a small and obscure species in a corner of the planet to the rise and spread of humankind, the most formidable species on Earth today. The first part of this article briefly reviews the evolutionary history of primates and significant phenomena that affected the course of this evolution, while the second part of the article focuses on the important stages in human evolution.

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Extant primates comprise two main groups: the wet-nosed "primitive" strepsirrhines, including the lemurs, lorises and the bushbabies, and the dry-nosed haplorrhines that comprise the tarsiers, Old and New World monkeys, and the apes, including humans. Central to our understanding of the evolutionary history of these different groups of primates is a definition of the order itself, i.e. what are the distinctive characteristics of primates that distinguish them from other mammalian orders? This simple question, interestingly enough, has been the subject of considerable debate. Some of the earliest definitions attempted to characterize primates as mammals possessing certain anatomical adaptations like clavicle, placenta, orbits encircled by bone, three kinds of teeth, well developed caecum, two pectoral mammae, etc. Later researchers pointed out none of these traits were unique to primates; in fact no single morphological feature characterizes all living primates. Instead, it is more useful to look

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at the order as distinguished by a distinct pattern of evolutionary trends. According to this view, some of the important evolutionary trends that define the order include: (i) increased mobility and refinement of digits, particularly thumb and big toe (ii) progressive shortening of snout, and decrease in use of smell, with concomitant development of binocular, stereoscopic and colour vision (iii) increase in absolute and relative brain size, with more cerebral cortex (iv) longer life span, slower rate of reproduction and delayed sexual maturity (v) progressive development of truncal uprightness leading to bipedalism (vi) shift from individual home range based social systems to group range based social systems and complex interactions between individuals governed by elaborate sets of behaviour and long-term relationships.

Primate Evolutionary History

A simplified version of the primate phylogenetic tree begins in the Paleocene epoch 65-55 millions of years ago (mya) (*Box* 1) with the appearance of the Plesiadapiformes in Europe and North America. The Plesiadapiformes are thought to have been a group of small mammals with primate-like features. The earliest recognised species from this group, *Purgatorius ceratops*, is considered the earliest and most primitive primate. Euprimates (meaning true primates), or primates of modern aspect, appeared in the Eocene epoch (55-38 mya). Most likely descendants of the Plesiadapiformes, fossil deposits of these primates have been discovered in North America, Europe, Asia and Africa. Two important groups are identified among the euprimates: the Adapids, ancestors to the strepsirrhines, and the Omomyids, ancestors to haplorrhines. After the initial split between strepsirrhines and haplorrhines, the strepsirrhine stock diverged to form two separate lineages, the lemuriformes and the lorisiformes. The lorisiform lineage then divided into the bushbabies and the lorises. Similarly the haplorrhine stock diverged to form the tarsiers and the simians. The simian stock in turn, diverged to form two separate lineages, the New World monkeys and the Old World monkeys. The divergence of the ape

Box 1. Geological Time Periods

The concept of geologic time periods or earth-history divisions was first introduced by geologists who determined the ages of different rocks on the basis of the kinds of fossil found in the rocks, or by evidence of major climatic changes. The smallest division of geologic time is the *Epoch*, which lasts several million years. A *Period* includes two or more Epochs and lasts tens of millions of years. It is considered the basic unit of geological time, in which a single type of rock system is formed. Two or more geological Periods comprise an *Era*, which is hundreds of millions of years in duration. Two or more geological Eras form an *Eon*, which is the largest division of geologic time, lasting many hundreds of millions of years. An *Age* is a unit of geological time that is distinguished by some particular feature, for example, the Ice Age. An Age is shorter than an Epoch, usually lasting from a few million years to about a hundred million years. A simplified version of the geological time scale is presented in the table below.

EON	ERA	PERIOD	EPOCH
Phanerozoic 540 mya - today	Cenozoic 65 mya - today	Quaternary 1.8 mya - today	Holocene 12,000 ya - today
			Pleistocene 1.8 -.012 mya
		Tertiary 65 - 1.8 mya	Pliocene 5-1.8 mya
			Miocene 22 - 5 mya
			Oligocene 38 - 22 mya
			Eocene 55 - 38 mya
			Paleocene 65 - 55 mya
	Mesozoic 248 to 65 mya	Cretaceous 135 - 65 mya	Upper 98 - 65 mya
			Lower 135 - 98 mya
		Jurassic 208 - 135 mya	
		Triassic 248 - 208 mya	
	Paleozoic 540 to 248 mya	Permian 80 - 248 mya	
		Carboniferous 360 - 280 mya	
		Devonian 408 - 360 mya	
		Silurian 438 - 408 mya	
		Ordovician 505 - 438 mya	
		Cambrian 540 - 500 mya	
Proterozoic 2.5 bya - 540 mya	-	Vendian 600 - 540 mya	
		-	
Archeozoic 3.9 - 2.5 bya ago	-	-	
Hadean 4.6 - 3.9 bya	-	-	

line from the Old World monkey stock is believed to have occurred in the Miocene epoch (22 – 5 mya). Large and small ape fossils are found in Miocene deposits, and it is generally accepted that the small ape forms are ancestral to the gibbons, while the large ape forms are ancestral to the great apes (orangutans, chimpanzees, gorillas) and humans (*Figure* 1).

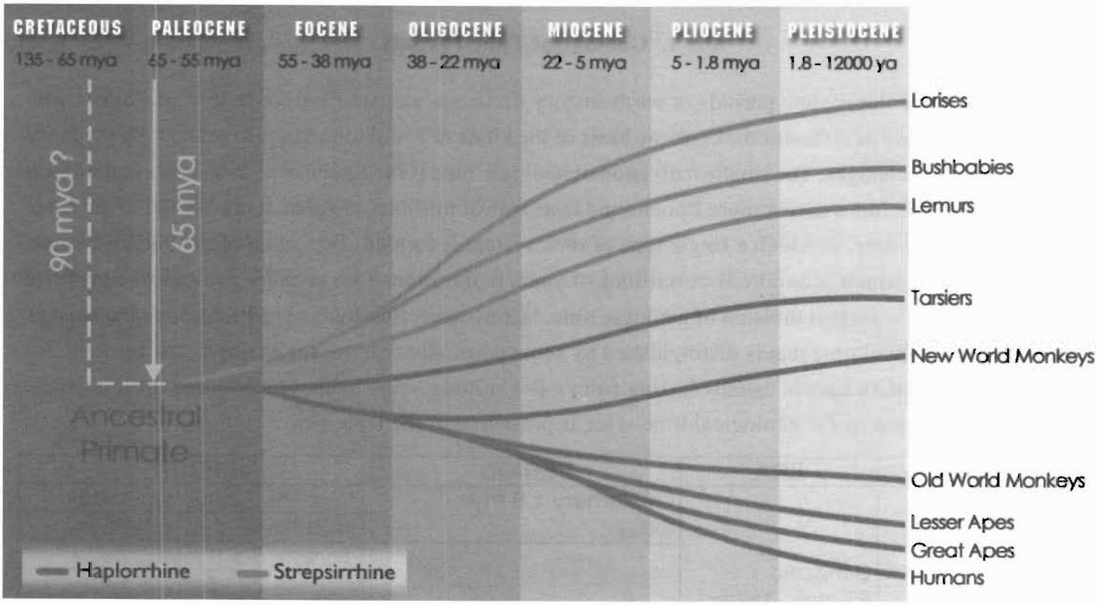

Figure 1.

In truth, primate evolutionary history is not so straightforward. Our knowledge of primate origins and evolution is primarily based on fragmentary fossils. Palaeontologists analyse the morphological characteristics discernible on such fossil fragments to come to conclusions about the relationships of the fossils to particular primate groups. In recent years, the comparative structures of chromosomes, DNA and proteins have also been used to reconstruct phylogenetic relationships and establish evolutionary timescales. Both due to the patchy fossil record and the different databases used, inferences on times of origin or divergence are usually areas of contention. A case in point is of the Plesiadapiformes. This group of mammals did not look like modern primates and retained many features lost in extant primates, such as small endocranial volume, deep post-orbital constriction and retention of claws on all digits. Hence some taxonomists do not consider them to be ancestral primates. However as a group, they commonly possess an anatomical feature, namely, the petrosal bulla (skeletal casing of the middle ear), which is a diagnostic characteristic of the primate order. It is on the basis of this morphological adaptation that they are included as ancestral members of the order.

Time of origin of the first ancestral primate is also a matter of some debate. Until recently, the time of divergence of the earliest primates from their mammalian ancestors was assumed to be around 65 million years ago. However, a team of investigators led by Simon Tavare from the University of Southern California use a mathematical model to suggest that the last common ancestor of primates existed much earlier, at 81.5 mya. Various molecular trees also indicate that primates originated much earlier than accepted, about 90 mya. New fossil findings may also add unexpected twists to established notions of primate ancestry. An interesting example of this is the discovery of fossil remains of two new lorisiform primate genera from the Eocene deposits of Egypt by E R Seiffert and his colleagues in 2001. This finding not only increases the number of known lorisiform genera, but also extends the known age of the last common ancestor of the strepsirrhines to about 50 mya.

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Prime Evolutionary Movers

The history of primate evolution offers a fascinating perspective into the myriad forces that shape our lives, involving as it does, phenomena as disparate as climatic changes, geological impacts and floral shifts. Today, the geographical distribution of non-human primates is restricted to the tropics, i.e. South and Central America, Africa and southern Asia. Yet, this was not always so; ancestral primate species once ranged over Europe and North America. Many factors have been invoked to explain the extinction of North American primates, notably, climatic changes, alterations in the forest habitats and ecological competition from rodent species. Two other factors that have crucially affected the course of primate evolution and distribution not only in North America, but over all the continents, are the geophysical process of continental drift and the rise and spread of angiosperms as the most dominant land plants.

Continental Drift

The earth's crust is made up of huge plates called oceanic and continental plates that are constantly in motion. Convection

Box 2. Pangaea

The first detailed theory of continental drift was put forward by the German meteorologist and geophysicist Alfred Wegener in 1912. Wegener proposed that about 280 mya all the continents were united in a vast supercontinent, which he called Pangaea. About 180 mya, Pangaea broke into two supercontinental masses – Laurasia to the north, and Gondwanaland to the south. Laurasia was made of the present day continents of North America, Europe, and Asia, while Gondwanaland was made of the present day continents of Antarctica, Australia and South America. The Indian subcontinent was also part of Gondwanaland and was not connected to Asia at this time. Wegener cited the fit of South America and Africa, and the presence of identical fossils and rock structures in both areas as evidence for the fact that the continents must have been linked in earlier times. As in the case of many great ideas, Wegener's theory was bitterly reviled during his lifetime, and it was only in the 60s that the geological scientific community accepted the theory of continental drift.

currents beneath the plates move them in different directions and the edges of the plates where they move against each other are sites of intense geological activity like earthquakes, volcanoes and mountain building. These processes are referred to as *plate tectonics* and the movement of the continental plates is called *continental drift* (*Box* 2). Due to continental drift, the size of the continents and their position with respect to the poles has changed over the years. The linking and separation of continental landmasses at various periods during earth history affected the dispersal of animal species over the continents. Early in the Eocene, Europe was joined to North America, and separated from Asia by the Turgai Strait. By the middle of the Eocene, North America and Europe had divided and by the end of the epoch, Europe and Asia became joined as they are today. Early primates moved from Europe to Asia through the land connection that had formed in the middle Eocene. A temporary land connection also existed between Europe and Africa in the Paleocene (65 - 55 mya), and it is hypothesised that the ancestors of Old World monkeys and apes in Africa may be the descendents of ancestral primates that crossed over from Europe through this land connection. Primates disappeared from Europe and North America during the Oligocene (38 - 22 mya), but due to the land bridges that formed between Europe and Africa in the Miocene, they reappeared in Europe and existed there until the Pleistocene (1.8 - 0.12 mya).

Changes in the size and positions of the continents also had a deep impact on the world's climate, which in turn, significantly affected primate evolution. Global cooling and increased glaciation in the Oligocene caused the mid and high latitude vegetation to change from broadleaf evergreen rainforest to deciduous forests. This appears to have triggered a mass faunal extinction event in North America and Europe, spanning about 20,000 years. The remaining primates clustered in smaller tropical forest areas near the Equator. The second disappearance of primates from Europe during the Pleistocene is also linked to the glaciations that occurred then. Over the last 800,000 years or more, the earth has been affected by alternating cold and warm phases of climate. The cold phases, called glaciations, are marked by large ice sheets in the middle latitudes of the northern continents and huge expansions of the polar ice caps, while the warm phases, called interglacials, are when the ice sheets recede and the sea level rises. The most recent glaciation began about 65,000 years ago and ended about 10,000 years ago. Tropical forests appear to have shrunk and expanded with alternating cold and warm phases in climate, resulting in the formation of small forest islands separated by vast stretches of open country savanna. Scientists have conjectured that this climatic effect has been responsible for high species endemism and diversity in Old and New World rain forests. According to the 'forest refuge theory', primate (and other animal) populations trapped in these forest islands, remained isolated from one another for many thousands of years. During this time, they diverged due to random genetic changes and local selection pressures. When the forests expanded and contact was re-established between the isolated populations, they had now diverged sufficiently from each other not to interbreed i.e., they had become separate species.

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Angiosperm Domination

Angiosperms first appeared in earth history in the Cretaceous

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period at about 135 mya. Because of their flowering mechanism, they possessed an evolutionary advantage over the gymnosperms, the dominant land plants then. Angiosperms radiated and increased and by the Eocene epoch were firmly established as the most dominant land plants. The appearance of new food resources in the form of flowers, fruit and buds led to a major radiation of many groups of small mammals, including primates. Insects that co-evolved with the flowering plants, also diversified and multiplied, opening a new ecological niche of insectivorous feeding for many mammals. The domination of angiosperms is, thus, a critical factor in primate evolution, and many primatologists consider it central to explanations of how primates originated from their mammalian ancestors.

Theories of Primate Evolution

Many theories have been developed to explain the causes that led to the divergence of primates from their mammalian ancestors. The main competing theories are:

Arboreal Theory: First proposed by G Elliot Smith in 1912 and further developed by Wood Jones in 1916, this theory holds that primate morphological traits resulted from adaptation to an arboreal way of life by a primitive, insectivorous mammal. Jones postulated that the development of forelimbs for climbing, reduction of olfaction and elaboration of vision, touch and hearing led to improved eye-hand coordination for an arboreal mode of life. Hence, primate morphological traits have developed in response to an arboreal mode of life.

Visually-oriented Predation Theory: In 1972, M Cartmill, forced a rethink on primate origins with his rejection of the arboreal theory. Cartmill argued that many arboreal mammals, e.g. tree squirrels, are successfully adapted to an arboreal mode of life, and yet do not possess characteristic primate traits. Therefore, the arboreal theory cannot explain the evolution of 'primate' traits. Instead, Cartmill proposed that (i) grasping hands and feet are advantageous to animals that forage in terminal branches and

(ii) optic convergence is largely restricted to predators that depend on vision for the detection of prey. Therefore primate adaptations actually arose from a nocturnal, visually-oriented insect predation mode of life in the terminal branches of trees and shrubs.

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Angiosperm Exploitation Theory: In a review article published in the *American Journal of Primatology* in 1991, Robert W Sussman questioned the adequacy of Cartmill's theory to explain primate origins. Sussman pointed out that (i) the majority of the primates are omnivorous, and very few eat more insects than plant material (ii) nocturnal primates depend more on hearing and olfaction than vision to catch insects. Therefore the primate visual system must have developed in response to feeding on fruits and insects in the terminal branches. Elaborating on his hypothesis, Sussman elucidates that the evolution of modern primates, and other mammals and birds, parallels the rapid diversification of angiosperms and that all these organisms are linked a in a tight co-evolutionary relationship. Primate adaptations developed from the need to exploit small food sources available on newly diversifying flowering plants and are thus a product of diffuse co-evolutionary interactions with angiosperms.

Arboreal–Predation–Angiosperm Exploitation Theory: D T Rasmussen contends that there is no single most important factor responsible for the evolutionary shift that led to the primate lineage. Angiosperm evolution led to the rich food source of fruits, flowers and insects. To exploit this, early primates needed to become arboreal and develop characteristics of visual predation. Hence all three theories are mutually interdependent and together explain the origin of primates.

Conclusion

The above pages have briefly reviewed primate evolutionary history, the past and present distribution of primates, and the major ecological factors that are likely to have affected the course of this evolution. Apart from biology, climatic factors and habitat vegetation, competition from other species has also affected the distribution and evolution of primate species. An interesting example is the failure of primates to occupy the tropical open country savannas of the New World, though primates in the Old World have colonized this habitat. It has been postulated that early invasion by New World ungulates and rodents competitively excluded primates from this ecological niche. Although competition in general is difficult to document, the tragic effects of the competition between human and non-human primates is only too clearly visible. To end in the words of Glen C Conroy: "To all creatures, still wild and free...The success of human evolution has not been kind to you."

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Suggested Reading

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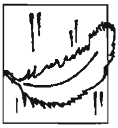

Poem by Ronald Ross, written in August 1897, following his discovery of malaria parasites in anopheline mosquitoes fed on malaria-infected patients.

This day relenting God
Hath placed within my hand
A wondrous thing; and God
Be praised. At his command,

Seeking his secret deeds
With tears and toiling breath,
I find thy cunning seeds,
O million-murdering Death.

I know this little thing
A myriad men will save,
O Death, where is thy sting?
Thy victory, O Grave?