

## Primate Evolution

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### INTRODUCTION

The mammalian order Primates includes living tarsiers, lemurs, monkeys, apes and humans. The name Primates itself, derived from Latin primus, first or foremost, betrays a characteristically immodest self-appraisal of our place in nature! When proposed by Linnaeus, in the definitive 1758 edition of his Systema Naturae, nature's center stage was indeed defined as that on which we play. Now, knowing that we are but one of 200 or so living primate species, knowing that primates are but one of 18 or so living mammalian orders, nature's stage appears much grander--claiming the center is clearly more difficult. Central or not, primates we are--human interest in human origins being what it is, primates will always hold a special fascination.

As a group, primates are distinguished from other mammals with difficulty. The history of primates is a history of gradual acquisition of minor differences without any single special morphological innovation to serve as a key diagnostic character. Bats all have wings and fly, rodents all have a single pair of gnawing incisors growing continuously, artiodactyls all have a double-pulley talus or astragalus, but primates do not have any single feature that one can point to in distinguishing them. Consequently, some authors write of "trends" or a "total morphological pattern" in attempting to define the order, but even these morphological trends and patterns fail to distinguish primates sharply from other mammals (inclusion or exclusion of tree shrews remains, for example, a perennial problem). Primates, like other orders, are grouped together because of their common evolutionary history. We must look at primate history to show that primates are a natural group. The fact that primates have no simple key defining morphological characteristics does not diminish their historical identity, nor does it diminish the reality of this group.

Primates retain many primitive morphological characteristics. They retain a primitive, generalized skeleton, with five fingers and toes on hands and feet (pentadactyly). There is some trend toward increasing the mobility of the pollex (thumb) and hallux (big toe), and a tendency to replace claws with flattened nails. The dentition usually exhibits the simple cusp pattern of generalized mammals. The facial part of the skull is reduced in more advanced primates, as is the apparatus of smell. In connection with this, the eyes face forward on the skull rather than to the sides. The brain is relatively larger and more elaborate in structure in advanced primates, particularly in the

TABLE 1-- Outline of primate classification, showing the number of living genera and species representing each of the seven major groups (superfamilies) of primates. Compiled from Honacki et al. (1982).

Classification	Living genera	Living species
Order PRIMATES		
Suborder ANTHROPOIDEA (or SIMII)		
7. Superfamily Cercopithecoidea	11	76
6. Superfamily Hominoidea	6	14
5. Superfamily Ceboidea	16	47
Suborder PROSIMII		
4. Superfamily Lorisioidea	6	13
3. Superfamily Lemuroidea	12	28
2. Superfamily Tarsiioidea	1	3
Suborder TUPAIIFORMES (or PRAESIMII)		
1. Superfamily Tupaiioidea	5	16
	Totals	197

cerebral cortex. Most primates give birth to single offspring, placentation and fetal nourishment becomes increasingly complex, and post-natal life is prolonged in more advanced forms.

As befits a group of such wide interest, there are many useful text and reference books on primates. Books reviewing the systematics, morphology, and behavior of living primates include: Hill (1953-1970), Jolly (1972), Napier (1970), Napier and Napier (1967), and Swindler (1976). The book by Napier and Napier is now somewhat out of date, much has been learned about primates in the twenty years since it went to press, but it remains among the most useful as a well organized compendium on each of the living genera. Books reviewing the fossil record and evolutionary history of primates include: Gregory (1922), Jerison (1973), Le Gros Clark (1971), Pilbeam (1972), Piveteau (1957-1961), Simons (1972), Szalay and Delson (1979), and Wolpoff (1980).

#### REVIEW OF LIVING PRIMATES

There are many classifications of primates, some differing markedly from others, but most agree in recognizing six or seven major groups of living primates (Table 1). These groups are based on the Asian tree shrew Tupaia (which some authorities would place in an order of its own), the Asian tarsier Tarsius, the Malagasy lemur Lemur, the Asian loris Loris, the South American monkey Cebus, our own genus Homo, and the African monkey Cercopithecus. Each of these genera is a good model for part at least of the larger group it represents, and one cannot progress far in understanding primates without becoming familiar with the morphological attributes and behavior of these seven living genera.

In addition, one divergently specialized lemuroid, Daubentonia, and one divergently specialized ceboid, Callithrix, are worthy of note. The chimpanzee Pan is a good representative of non-human Hominoidea. The principal morphological and behavioral characteristics of these ten living genera are summarized in Tables 2 and 3.

Living primates are almost entirely tropical and subtropical in geographic distribution. They occupy much of Central and South America, all of continental Africa (except for the Sahara), Madagascar, and all of South and Southeast Asia. Madagascar is particularly interesting because of the diversity of lemurs living there today, and because of an even greater diversity surviving there as recently as a few thousand years ago. Today, non-human primates inhabit only the southern part of Mexico and the southernmost tip of Europe at Gibraltar. They are absent from the vast expanses of temperate continental North America, Europe, Asia, and Australia. Most primates are arboreal and, as befits a visually oriented animal, diurnal, that is, they are active during the day. Primates range in weight from a minimum of about 60 grams (mouse lemur Microcebus) to 160 kilograms (large male Gorilla). Putting this in perspective, 60 grams is only about two ounces, while 160 kilograms is approaching 400 pounds. Prosimians exhibit little or no sexual dimorphism, while anthropoid males and females of the same species often differ greatly in body size, and sometimes canine tooth size as well. Among anthropoids, dimorphism is usually correlated with complex polygynous social structures (involving single-male harems or multimale groups).

Primates differ from many other mammals in having an habitual orthograde, or upright, posture, meaning that they typically cling or sit vertically when resting, and sometimes also position the body vertically when moving (as we do when walking). The locomotion of primates in the trees or on the ground ranges from scansorial quadrupedalism (active climbing, scampering) in small primates to a slower, more deliberate quadrupedalism in larger primates. Some are specialized as vertical-clingers-and-leapers, while others practice brachiation (arm-swinging), knuckle-walking, or bipedalism. The locomotor specializations of primates are often reflected in their skeletal anatomy. Scansorial tree shrews have very generalized skeletons. Vertical-clinging-and-leaping tarsiers take their name from their elongated tarsals (heel bones), which facilitate leaping. Most lemuroids have a generalized skeleton, although some practice vertical clinging and leaping. Loris itself is a slow climber with a generalized skeleton, but other lorisoids (bushbabies, genus Galago) are vertical-clingers-and-leapers with elongated tarsals. Brachiating ceboids and hominoids have greatly elongated forelimbs, and bipeds are, of course, hindlimb dominated. Cebus and its relatives in South America are the only primates to have prehensile tails, but even here all ceboids do not have such a "fifth limb." Living hominoids have no tails at all. Scansorial tree shrews retain claws on all the digits of the hands and feet, tarsiers retain claws on digits II and III of the foot, while lemurs and lorises retain claws only on digit II of the foot. The claws of tarsiers, lemurs, and lorises are used as toilet or grooming claws.

TABLE 2 -- Characteristics of representative prosimian primates.

	<u>Tupaia</u>	<u>Tarsius</u>	<u>Loris</u>	<u>Lemur</u>	<u>Daubentonia</u>
1. Location	S. E. Asia	S. E. Asia	India & Ceylon	Madagascar	Madagascar
2. Environment	Tropical rain forest	Tropical rain forest	Tropical rain forest or dry woodland	Tropical rain forest & temperate woodland	Tropical rain forest
3. Habitat	Mostly terrestrial	Arboreal	Arboreal	Mostly arboreal	Arboreal
4. Activity pattern	Diurnal	Nocturnal	Nocturnal	Diurnal	Nocturnal
5. Body size	30 - 200 g	90 - 160 g	300 g	2 kg	2 kg
6. Sexual dimorphism	No	No	Slight (color & size)	Slight (color)	No
7. Resting posture	Horizontal	Vertical	Horizontal	Vertical	Horizontal
8. Locomotion	Quadrupedal	VCL	Quadrupedal (slow climber)	Quadrupedal	Quadrupedal
9. Diet	Insects, some fruit	Insects, small animals	Insects, small animals	Fruit & leaves	Insects, some fruit
10. Dentition	$\frac{2}{3} \frac{1}{1} \frac{3}{3} \times 2 = 38$	$\frac{2}{1} \frac{1}{1} \frac{3}{3} \times 2 = 34$	$\frac{2}{2} \frac{1}{1} \frac{3}{3} \times 2 = 36$ [tooth comb] No, except II on foot	$\frac{2}{2} \frac{1}{1} \frac{3}{3} \times 2 = 36$ [tooth comb] No, except II on foot	$\frac{1}{1} \frac{0}{0} \frac{1}{3} \times 2 = 18$ [ever-growing I <sub>1</sub> ] Yes, all except big toe
11. Claws	Yes	No, except II & III on foot	No, except II on foot	No, except II on foot	Yes, all except big toe
12. Thumb	Non-opposable	Non-opposable	Partly opposable	Partly opposable	Partly opposable
13. Dominant sense	Smell	Vision	Vision	Vision	Vision & hearing
14. EQ	~1.00	1.14 - 1.35	1.56	1.77	?
15. No. of young	1-4, usually 2	1	1, sometimes 2	1	1
16. Longevity record	6 yrs.	12 yrs.	7 yrs.	27 yrs.	3+ yrs.

TABLE 3 -- Characteristics of representative anthropoid primates.

	<u>Cebus</u>	<u>Callithrix</u>	<u>Cercopithecus</u>	<u>Pan</u>	<u>Homo</u>
1. Location	C. & S. America	S. America	Africa	Africa	Pangeographic
2. Environment	Tropical forest	Tropical rain forest	Variable	Tropical rain forest to open woodland	Variable (mostly concrete forests!)
3. Habitat	Arboreal	Arboreal	Mostly arboreal	Arbor. & terrest.	Terrestrial
4. Activity pattern	Diurnal	Diurnal	Diurnal	Diurnal	Diurnal
5. Body size	1.1 - 3.3 kg	175 - 360 g	2.5 - 4.5 kg	40 - 50 kg	51 - 55 kg
6. Sexual dimorphism	Yes (size, tail length, canines)	Slight (size)	Yes (size, canines)	Yes (size, canines)	Yes (size)
7. Resting posture	Vertical	Horizontal	Vertical (ischial callosities)	Vertical	Vertical
8. Locomotion	Quadrupedal -- prehensile tail	Quadrupedal	Quadrupedal	Quadrupedal (knuckle-walk)/brachiation	Bipedal
9. Diet	Fruit, insects	Insects, some fruit	Fruit & leaves	Fruit, leaves, insects, animals	Variable
10. Dentition	$\frac{2}{2} \frac{1}{1} \frac{3}{3} \frac{3}{3} \times 2 = 36$	$\frac{2}{2} \frac{1}{1} \frac{3}{3} \frac{2}{2} \times 2 = 32$	$\frac{2}{2} \frac{1}{1} \frac{2}{2} \frac{3}{3} \times 2 = 32$	$\frac{2}{2} \frac{1}{1} \frac{2}{2} \frac{3}{3} \times 2 = 32$	$\frac{2}{2} \frac{1}{1} \frac{2}{2} \frac{3}{3} \times 2 = 32$
11. Claws	No	Yes, all except big toe	No	No	No
12. Thumb	Partly opposable	Non-opposable	Opposable	Opposable	Opposable
13. Dominant sense	Vision	Vision	Vision	Vision	Vision
14. EQ	2.5 - 4.8	1.5	1.6 - 2.7	2.2 - 2.5	7.4 - 7.8
15. No. of young	1	2	1	1	1 (twins 1/88 births)
16. Longevity record	40 yrs.	10 yrs.	31 yrs.	38 yrs.	100+ yrs.

Anthropoids have flat nails on all digits, except for small scansorial Callithrix and its relatives, which have evidently secondarily reacquired claws as an adaptation for climbing on tree trunks of large diameter. Callithrix has presumably lost the opposability of its thumb, another anthropoid characteristic, as part of the shift from nails back to claws.

Small primates are insectivorous and frugivorous (fruit-eating), while larger ones tend to be frugivorous and folivorous (leaf-eating). The distribution of body weights in primates is bimodal, insectivore-frugivores falling below 500 gm body weight and frugivore-folivores falling above 500 gm body weight (Kay, 1975). Kay's 500 gm threshold applies as well to fossil primates, giving some insight into the diet of extinct species (Fleagle, 1978). Within each of these broad dietary categories, insectivores usually have sharply pointed cheek teeth to puncture the exoskeletons of their prey, frugivores usually have blunt rounded cusps and flat molar crowns for pulping fruit, and folivores have sharply crested cheek teeth for shearing leaves. The dental formula of generalized eutherian mammals is I3/3, C1/1, P4/4, M3/3, and all except the very earliest primates exhibit some reduction from this primitive condition. As noted above, the dentition of primates is generally conservative. Primates can often be distinguished in having broadly basined upper and lower molars, with wide talonids relative to trigonid width. Some primates have very distinctively specialized anterior teeth: tarsiers have enlarged pointed central incisors, lemurs and lorises have specialized incisor-canine tooth combs used in grooming and in feeding, and Daubentonia has ever-growing gnawing incisors resembling those of rodents. Among anthropoids, cercopithecoids are the most distinctively specialized in having strongly crested bilophodont upper and lower molars. Primates feed with their hands, and their short faces may reflect this. Short faces probably also reflect a shift from olfaction to vision as the dominant sense in primates. Primates have more forwardly directed orbits than most other mammals do, permitting a larger field of stereovision. This has traditionally been explained as an adaptation for locomotion in a complex arboreal environment, but more recently Cartmill (1974) has reasoned that orbital frontation is related to visually oriented predation rather than arboreal locomotion.

Humans, and to varying degrees other anthropoids, are distinguished by large brain size. Yet if one asks "Which has the larger brain, a man or an elephant?" -- the answer is clearly an elephant. Humans have a brain averaging about 1200 grams in weight (or cubic centimeters in volume -- the density of brain tissue is very nearly 1.0), while elephants have a brain averaging about 5700 grams. This example serves to dramatize the fact that we are not interested in brain size per se, but in brain size as a proportion of body size. Jerison (1973) worked out a very simple encephalization quotient (EQ) to measure relative brain size as a function of total body size. This measure is scaled to make the EQ of an average mammal equal to 1.0 (Martin, 1981 and others have improved Jerison's approach significantly, but their results do not alter the principle involved here). Tree shrews have EQs of about 1.0, and they thus represent a typical mammalian baseline for comparison with

other primates. Coming back to man and elephant, elephants have larger brains in an absolute sense, but their EQ value, their relative brain size, is only about 1.3. Humans generally have EQs in the range of 7.4-7.8. Our brains are about seven and a half times the size one would expect for an average mammal of our body weight. The brain of primates, at least that of anthropoids, is specialized in having an expanded and richly convoluted cerebral neocortex (the outer layer covering much of the forebrain, including visual, auditory, tactile, and motor centers, as well as association areas; Radinsky, 1975).

#### PRIMATE FOSSIL RECORD

Molecular biologists, zoologists, anthropologists, and even some paleontologists claim from time to time that molecules tell us more about the phyletic branching patterns of primates and other mammals than fossils do, the implication being that fossils are somehow too few, too fragmentary, and too imprecisely dated to contribute much to understanding phylogeny. However few, however fragmentary, and however imprecisely dated they might be, fossils are still the only direct evidence we have that primates have a history. More than a hundred skulls of fossil primates, partial or complete, are known from the Cenozoic, and these are supplemented by tens of thousands of informative dental remains from Africa, Asia, Europe, North America, and South America. Gaps remain, as they always will, but the fossil record of primates discovered to date is sufficient to constrain at least an outline of primate history, providing the only real historical basis for testing current ideas about rates and patterns in the evolution of molecular and comparative anatomical traits.

One of the traits most commonly studied in fossils is the evolution of body size. As noted above, Kay's 500 gm body size threshold separating insectivorous from folivorous primates can be recognized in primates of the past as well as those living today (Fleagle, 1978). Body size is highly correlated with tooth size in living mammals (Figure 1), and this correlation can be used to infer the body size of fossils from their tooth size. Tooth size is easily measured in fossils, and size is very useful for characterizing species in the fossil record. Tooth size varies within well defined limits in living primate species (the  $\ln$  of crown length multiplied by crown width is consistently about 0.40 in living species), and this variability can be used as a standard in studying samples of extinct species from restricted stratigraphic zones. The same species can often be recognized in successive stratigraphic intervals, and these can be compared quantitatively by stacking successive intervals one above the other as they occur in time. The result is an outline history or phylogeny of the given species or lineage, showing, first, whether or not the lineage or lineage segment changed over time, and, if it changed, how this took place. Many lineages do not change significantly in the intervals over which they are sampled in the fossil record, but others clearly do. The latter are most interesting from an evolutionary point of view in telling us how change takes place when it does occur.

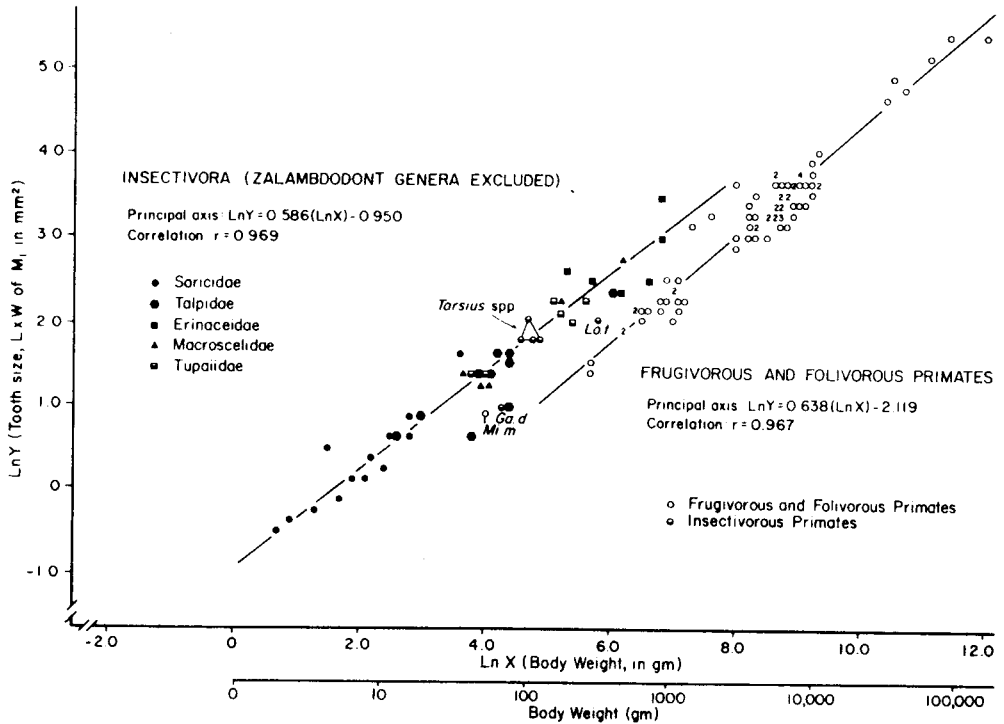


Figure 1-- Relationship of tooth size to body size in Primates and Insectivora. Note that the crown area of the first lower molar scales as the 0.59-0.64 power of body weight, a scaling coefficient below that expected for geometric scaling (0.67), and much below that expected for metabolic scaling (0.75). Note also that insectivores, including insectivorous primates generally have larger molars than do frugivorous and folivorous species of the same body weight. Figure reproduced from Gingerich and Smith (1984).

The primate fossil record provides some exceptionally detailed examples of evolution at the species level. One of the best is the history of North American lemuroid Adapidae in the early and middle Eocene of the Bighorn, Wind River, and Bridger basins, Wyoming (Figure 2). Here the earliest species, *Cantius ralstoni*, becomes larger as it is traced upward through time. Four successive species are known before the principal lineage of *Cantius* branched, giving rise to both *C. frugivorus* and *C. venticolis*. The genus *Notharctus* is probably a direct descendent of *C. venticolis*, and indeed this species has often been classified in *Notharctus* in the past. Each species of *Cantius*, diagnosed on the basis of tooth size and relative development of accessory cusps on upper and lower molars, is seen to grade into a later descendent (the one exception being *C. abditus* to *C. venticolis*, which probably took place outside the Bighorn Basin area). Similar examples of gradual change between successive species of early Eocene tarsioid Omomyidae of the Bighorn Basin are outlined by Rose and Bown (1984).



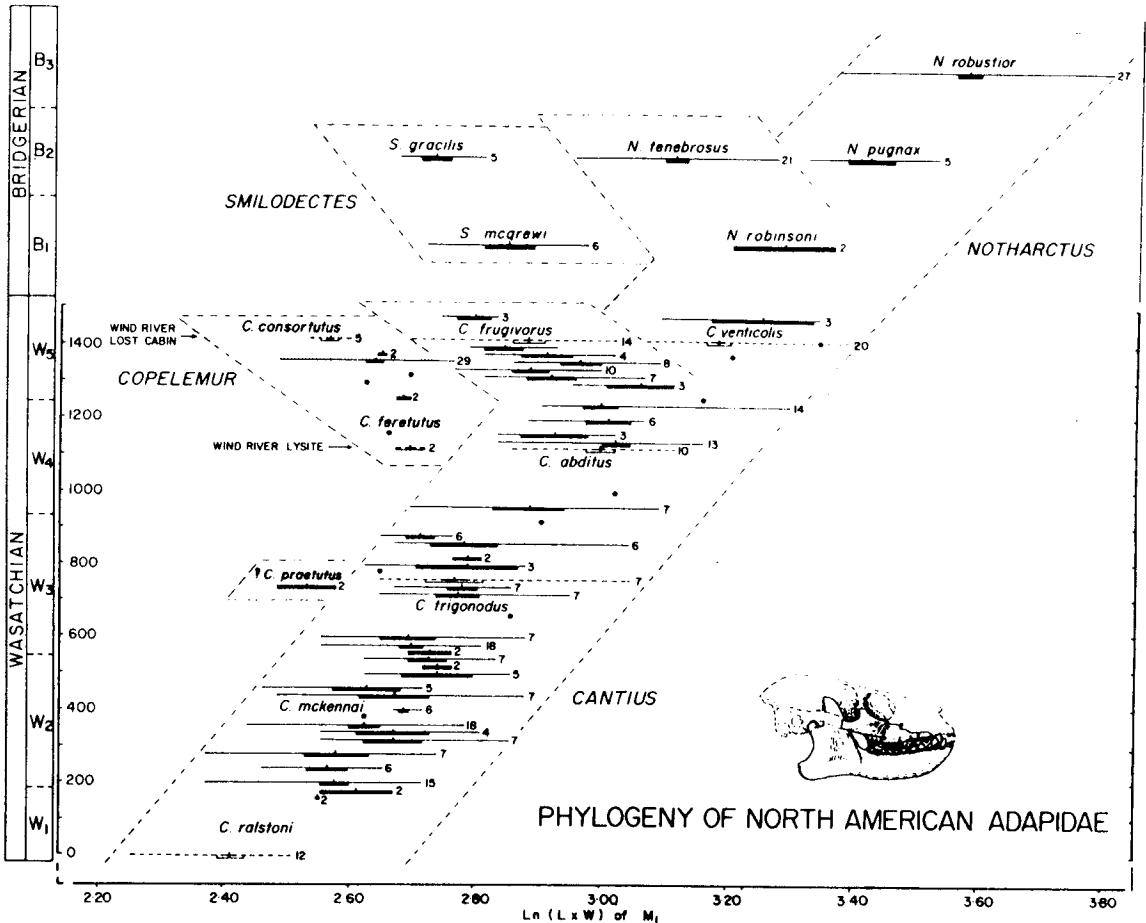


Figure 2-- Outline phylogeny of North American species of Adapidae based on early Eocene specimens from the Bighorn and Wind River basins, Wyoming, and middle Eocene specimens from the Bridger Basin, Wyoming. Comparison with Figure 1 indicates that the lineage from Cantius ralstoni to Notharctus robustior increased in body size from about 1200 gm to 7800 gm (equivalent to the difference between the living bushbaby Galago crassicaudatus and a large howler monkey Alouatta seniculus) in 5-6 million years. Figure modified from Gingerich (1979).

The same principles used to construct the species-level phylogeny of North American Adapidae shown in Figure 2 can be used to construct a family or superfamily-level phylogeny of the entire order Primates. In both cases, all available fossils are first organized by stratigraphic interval, and then grouped within each interval based on overall similarity. Living groups, here superfamilies Tupaiioidea, Tarsiioidea, Cercopithecoidea, Hominoidea, Ceboidea, Lorisioidea and Lemuroidea, can then be traced backwards in time as collections from progressively older intervals are linked together. The result is summarized in the outline phylogeny shown in Figure 3. This approach to phylogeny is the one traditional in paleontology. I have labeled it "stratophenetic" (Gingerich, 1976b) to emphasize its stratigraphic and phenetic basis, contrasting this with inductive cladistic approaches based solely on

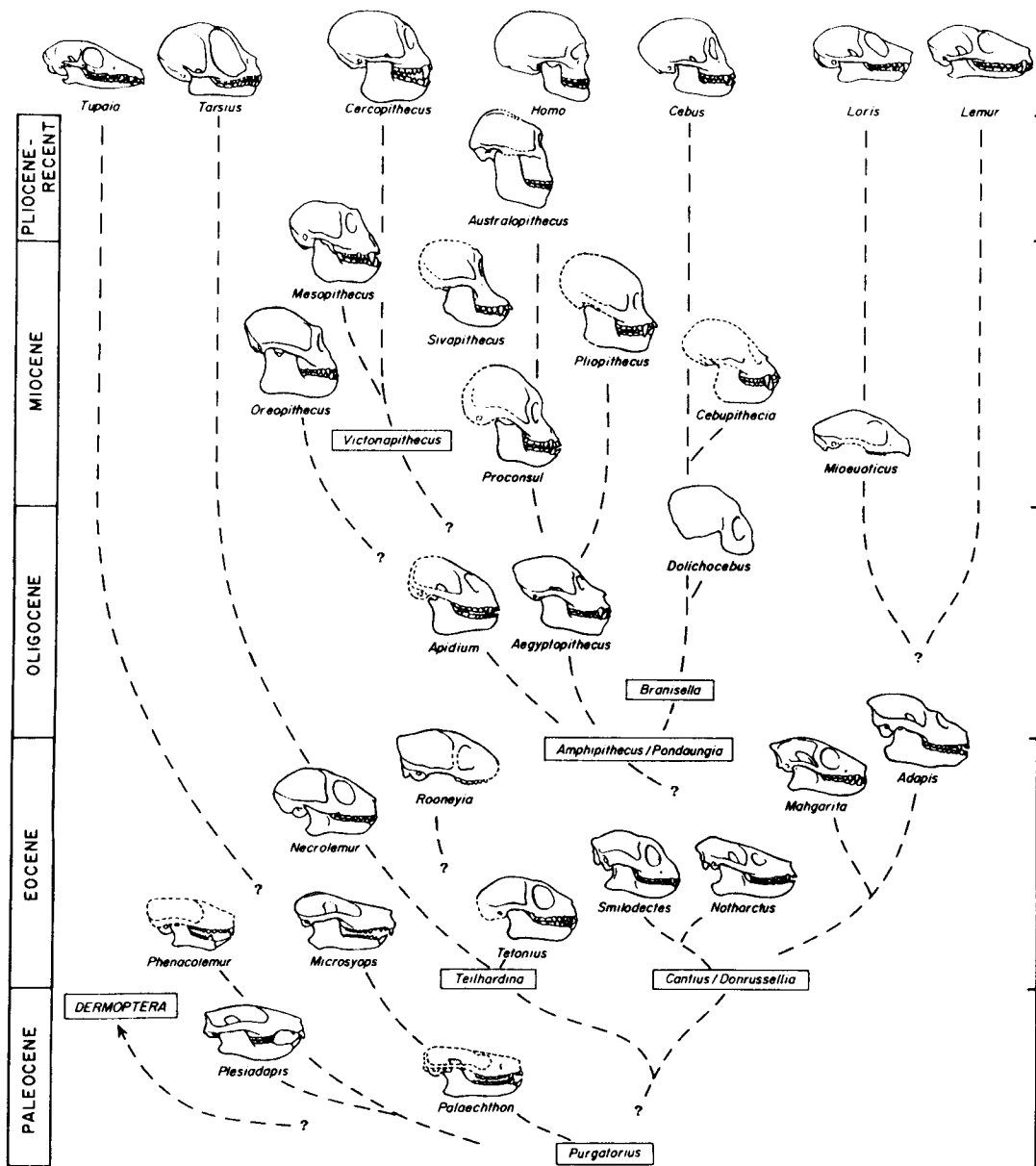


Figure 3-- Outline of primate phylogeny at the family or superfamily-level, based on stratophenetic linking of known fossil primates. The most important skulls are shown whenever possible. Boxed names represent important genera not yet known from skulls. Note that praesimian Tupaioida may be linked to primitive microsyopoids like *Purgatorius* if they are primates at all. Prosimian Tarsioida and Lemuroidea have a good Eocene fossil record (assuming adapids to be correctly classified in Lemuroidea). Lorisoida are first known from the early Miocene. Anthropoids first appear in the fossil record in the late Eocene or early Oligocene, and Ceboidea, Hominoidea, and Cercopithecoidea have a good Miocene-Recent fossil record. Figure from Gingerich (1984).

living forms and ignoring the age of fossils. Cladistic methods are valuable for detailed analysis of relationships between smaller groups within this broad outline, and the outline as a whole is valuable in testing current ideas about the tempo and mode of morphological and molecular evolution in primates (Gingerich, 1984).

Primates first appear in the early Paleocene of western North America. The oldest genus, Purgatorius, is known from a number of jaws with teeth (Clemens, 1974). Judging from its tooth size, Purgatorius probably weighed about 20 gm and it was undoubtedly insectivorous. All Paleocene primates are grouped together in the suborder or infraorder Plesiadapiformes (a coordinate group equivalent to Tupaiiformes of Table 1). Plesiadapiformes include two superfamilies, Microsyopoidea and Plesiadapoidea, derived from Purgatorius or a Purgatorius-like ancestor. Palaechthon is the oldest microsyopoid for which the skull is known. Palaechthon was studied by Kay and Cartmill (1977), who concluded that it was a 100 gm, predominantly terrestrial, insect-eater. Plesiadapis itself includes many species, all larger than Palaechthon. Judging from their dentitions, skulls, and partial skeletons, species of Plesiadapis were larger (460-5200 gm), predominantly terrestrial, and herbivorous (Gingerich, 1976b). Some plesiadapiform primates survived into the Eocene, but most became extinct at or near the Paleocene-Eocene boundary.

Primates of modern aspect first appeared in the early Eocene of Asia, Europe, and North America. Two major groups are represented, Omomyidae and Adapidae, which are conventionally classified in the modern superfamilies Tarsiioidea and Lemuroidea, respectively. Resemblances of Adapidae to modern Lemuroidea are all based on primitive features, and it is possible that adapids represent a third superfamily Adapoidea with no particularly close relationship to Lemuroidea. Omomyids differ from adapids in having more pointed and often enlarged central incisors, in having a tubular external auditory meatus, and in having elongated tarsal bones reminiscent of those in Tarsius and lorisoid bushbabies. Omomyids also differ from adapids in body size. Most omomyids are smaller than Kay's 500 gm body size threshold, while most adapids exceed this threshold. Both groups are known from partial or complete skeletons indicating that they were probably arboreal like tarsioids and lemuroids living today. We can visualize Eocene omomyids as small leaping insectivores and frugivores, while Eocene adapids were larger quadrupedal frugivores and folivores.

Two genera of omomyids are represented in the early Eocene of Asia, Altanius and Kohatius, but little is known of either of these. Adapids are not yet known with certainty from the early Eocene of Asia. Early Eocene omomyids and adapids are much better known in Europe and in North America. Interestingly, the earliest omomyid genus Teilhardina, and the earliest adapid genus Cantius are known from both continents. Teilhardina and Cantius appear to be part of a large cosmopolitan Holarctic mammalian fauna shared between Europe and North America at the beginning of the Eocene. Shortly after the beginning of the Eocene, and just after this cosmopolitan fauna became established in Europe and

North America (and possibly Asia), continued rifting completed opening of the North Atlantic Ocean, severing any continental connection between Europe and North America. Teilhardina gave rise to separate Eocene radiations: Microchoerinae (Necrolemur et al.) in Europe, and Anaptomorphinae (Tetonius) and Omomyinae in North America (Szalay, 1976; Gingerich, 1981a). Cantius too gave rise to separate Eocene radiations: Adapinae (Adapis) in Europe and Notharctinae (Notharctus, Smilodectes) in North America (Gingerich, 1981b, 1981c). Notharctines declined precipitously after the middle Eocene, and adapines declined near the end of the Eocene. A typical Eurasian adapine, Mahgarita (Wilson and Szalay, 1976), appears near the end of the Eocene as part of a Eurasian immigration possibly foreshadowing the appearance of Old World anthropoids in the Oligocene of South America. There are two later records of Omomyidae: Rooneyia is known from the early Oligocene of Texas (Wilson, 1966) and Ekgmowechashala occurs in the latest Oligocene or early Miocene of South Dakota and Oregon (Rose and Rensberger, 1983). Geologically, Ekgmowechashala is the youngest nonhuman primate known from North America. One group of adapids, represented by Sivaladapis, survived in an arboreal folivore niche in South Asia until 7-8 m.y. ago when they were replaced by leaf-eating cercopithecoids (Gingerich and Sahni, 1984).

At the end of the Eocene or early in the Oligocene (depending on how one recognizes this boundary), there was a marked change in worldwide climates, with a sharp decrease in mean annual temperature and a pronounced increase in climatic seasonality (Bucharadt, 1978; Wolfe, 1978). Interestingly, this event was first described by a German-speaking Swiss paleontologist, H. G. Stehlin, in one of the few papers he ever published in French (Stehlin, 1909). Stehlin noted a sharp break, what he called a "Grande Coupure", in the mid-Cenozoic sequence of European mammalian faunas. Climatic cooling and increasing seasonality explain why primates declined during the late Eocene and disappeared from Europe and North America during most or all of the Oligocene.

The earliest anthropoid primates appear in the fossil record in the late Eocene or early Oligocene. Two genera from the late Eocene of Burma, Amphipithecus and Pondaungia, are known from fragmentary dentitions that could represent either advanced adapids or early anthropoids (Ba Maw et al., 1979). Undoubted anthropoids occur in more equatorial areas in deposits of Oligocene age. One genus, Branisella from Bolivia, is known from fragmentary dental remains (Hoffstetter, 1969) that resemble comparable parts of the skeleton of modern squirrel monkeys (Saimiri) closely in size and form. Branisella is most important in establishing the presence of anthropoid-grade primates in South America by the early Oligocene. It is widely accepted that anthropoids originated in the Old World, in Africa or South Asia, and two theories have been proposed to explain how anthropoids reached South America: by rafting directly from Africa, or by dispersal through Asia and North America. Mahgarita, mentioned above, provides some evidence favoring the latter hypothesis (Gingerich, 1981a), but the question is clearly not yet settled.

A far richer Oligocene primate fauna is known from the Fayum province of Egypt. Here some six genera are known from three distinct stratigraphic intervals. The lower fossil wood zone has yielded remains of a probable adapid, Oligopithecus (this genus, like Amphipithecus and Pondaungia, is sometimes regarded as a primitive anthropoid), and a different, much smaller anthropoid Qatrania (Simons and Kay, 1983). An intermediate interval in the Fayum has yielded fragmentary remains of a generalized parapitheid, Apidium, and a more advanced small ape, Propliopithecus. The upper fossil wood zone has yielded a small tarsioid as well as abundant remains of four genera of anthropoids: two parapitheids, Apidium and "Parapithecus", and two small apes, Propliopithecus and Aegyptopithecus. The latter genus is represented by numerous jaws and teeth, by one nearly complete cranium and several partial skulls, and by numerous postcranial elements (Fleagle et al., 1980; Kay et al., 1981; Fleagle and Simons, 1982; Simons, 1983, 1984). Sedimentological and paleoecological analyses indicate that the Fayum area was a forested subtropical to tropical coastal plain during the Oligocene (Bown et al., 1982), and Aegyptopithecus is reconstructed as a robust 6-7 kg frugivore, a sexually dimorphic, slowly moving, arboreal quadruped most like the howler monkey Alouatta among living primates (Kay and Simons, 1980; Fleagle and Simons, 1982).

Aegyptopithecus is important as the first well known representative of a distinctly anthropoid grade of primate evolution-- it is most comparable to living Ceboidea in many anatomical and functional features. Aegyptopithecus is also important in extending the documented record of African Hominoidea back to the Oligocene, some ten million years before there is any clear evidence of Cercopithecoidea in the fossil record. Aegyptopithecus may well be the common ancestor of later Hominoidea and Cercopithecoidea, but it is distinctly hominoid in features, like the dentition, that distinguish these superfamilies today. The morphology of Aegyptopithecus, in context of the rest of the fossil record, indicates that our traditional (and simplistically linear) scala naturae, based on the comparative anatomy of living forms, is misleading. The evolution of anthropoids was not from (1) New World monkey (ceboid) grade to (2) Old World monkey (cercopithecoid) grade to (3) ape (hominoid) grade to (4) human, but rather from (1) ceboid grade to (2) hominoid grade to (3) cercopithecoid grade, with humans representing a lateral offshoot from hominoids. If the term "monkey" applies to ceboids and cercopithecoids today, then Aegyptopithecus was certainly a "monkey" in grade, although it was at the same time clearly an ape by clade. As befits a fossil of intermediate age, Aegyptopithecus exhibits a mosaic of primitive and advanced features linking Eocene prosimians and primitive ceboid-grade anthropoids to later hominoids and cercopithecoids.

The Miocene primate record is important in providing the first evidence of a number of modern superfamilies. Some of these first records (Tupaioidea, Lorisoidea) belong to primates that were small, easily overlooked, living forms inferred to have separated from praesimian or prosimian ancestors much earlier in time, while others (Cercopithecoidea) are larger and more distinctive, and thus probably

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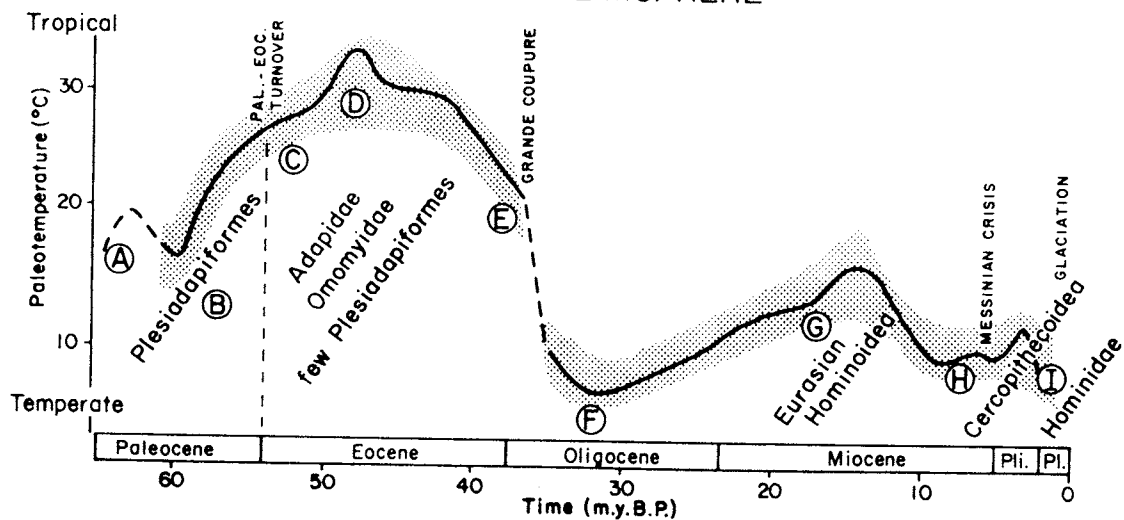


Figure 4-- Overview of primate evolution in the northern hemisphere viewed in context of changing climates affecting their biogeographic distribution (climatic curve from Buchardt, 1978). A, appearance of Purgatorius following terminal Cretaceous cooling. B, radiation of plesiadapiform primates during cool phase of middle and late Paleocene. C, appearance of primates of modern aspect in Europe and North America during phase of climatic warming (primates of modern aspect probably evolved in more equatorial areas, possibly in Africa); followed by final opening of North Atlantic. D, acme of primate diversity in Europe and North America, coinciding with warmest climates. E, decline and extinction of Eocene primate lineages in Europe and North America, coinciding with climatic cooling; Mahgarita apparently migrated to North America from Eurasia just before the Grande Coupure in the latest Eocene or early Oligocene. F, nadir of primate diversity in northern continents; known primate faunas are all in more equatorial areas (Bolivia, Egypt). G, appearance of Hominoidea in Europe and Asia during climatic warming of middle Miocene. H, disappearance of Hominoidea in northern continental faunas coinciding with cooler, dryer climates during Messinian crisis; major diversification of savanna- and woodland-adapted Cercopithecoidea; emergence of Hominidae. I, rapid evolution and dispersal of humans during Pleistocene climatic fluctuations.

making their first evolutionary appearance in the Miocene. Tree shrews are known from the middle Miocene of South Asia (Jacobs, 1980). Lorisoids make their first appearance in the fossil record in the early Miocene of East Africa (Walker, 1978), and they are known too from the middle Miocene of South Asia (Jacobs, 1981). The first evidence of cercopithecoid monkeys comes from the early Miocene of North Africa (Prohylobates) and East Africa (Victoriapithecus). Both of these genera have high-crowned cheek teeth and the bilophodonty characteristic of

later cercopithecoids, although bilophodonty is not as well developed as seen in later genera. The major radiation of Cercopithecoidea began about 7-8 m.y. ago, at or near the beginning of the "Messinian crisis," a worldwide climatic cooling and drying event leading, most spectacularly, to dessication of the Mediterranean basin.

The Miocene is perhaps best known for its major radiation of Hominoidea. Few groups have enjoyed less interpretive and taxonomic stability in the past two decades. Simons and Pilbeam (1965) adopted a "single-species" (or, in this case, single-genus) view of larger Miocene hominoids, grouping almost all of them in Dryopithecus, and Pilbeam (1969) went so far as to propose that different size groups of Dryopithecus from the early Miocene of East Africa represented the ancestors of living chimpanzees (Pan) and gorillas (Gorilla). Ramapithecus is a late Miocene hominoid from East Africa and South Asia with some advanced features possibly foreshadowing later human characteristics, and it has long been viewed as a likely human ancestor. With this simplified "single-genus -- Miocene apes are Dryopithecus" view as a kind of null hypothesis, new discoveries and new interpretations have, in recent years, led to a great proliferation of names for Miocene apes, indicating that there is significant morphological diversity within Miocene Hominoidea, and that the fossil record is probably as yet inadequate for the task of determining the Miocene history of hominoid evolution. This is an area in which some progress is made each year, and it is an area in which we still have much to learn.

The Messinian crisis may have been good for Old World monkeys in providing conditions under which they could radiate widely, but it was not good for most Hominoidea. Hominoids enjoyed their greatest morphological diversity and broadest geographic range during the Miocene. It is possible that Sivapithecus from the late Miocene of South Asia (Pilbeam, 1982, 1984) represents the ancestral stock of orangutans, but little is known of the ancestry of other living apes. The Messinian interval, from about 8 m.y. to 4 m.y. before present, represents a major and unfortunate gap in our knowledge of most primate lineages. The Messinian interval probably represents a time of restricted geographic ranges and unusual environmental stress--conditions often leading to new morphological innovation and taxonomic diversity. Ironically, the two groups favored over apes by climatic and environmental deterioration in the Messinian were humans and cercopithecoid monkeys. We probably owe our emergence, in part at least, to this environmental crisis.

Acknowledgments-- I thank Karen Klitz for preparing the figures. Research supported by National Science Foundation grant BNS 80-16742.

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