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Anthropoidea
Higher primates, including platyrrhine (also called New World monkeys) and the c
carnivore monkeys, apes and humans of the Old World. Pre-
viously ranked taxonomically as a suborder of primates, they
are here placed at the next lower rank, hystricomorpha (including Anthropoidea and Tarsiformes) and Strepsirrhini. Anthropoids are the most successful survivors of the three major extant lineages of primates originating long ago in the Early Tertiary. The once-florescent tarsiform group is now represented by a single new genus, Pongi, in the remote evolutionary outpost of the Philippines and Indonesia, and the remaining lemurs
include the lemurs of Madagascar, mainland Africa, and the
Indian subcontinent in yet less distant than the anthropoids, taxonomically and adaptively. How the larger-bodied members of the anthropoids and anthropoids would have compared during the Pliocene, however, is another mat-
ter. We are only beginning to learn how many and which
kinds suffered extinction in human populations extended into their habitats in all areas of the world.

Geographical Background

The success of the anthropoids has been influenced by geogra-
phy in a number of ways. Their history unfolded in two
distinct theaters: in South America and in Africa-South-
one large in area and the other relatively restricted. The oc-
cupation of four continents across two hemispheres makes
their total areal distribution large. As a consequence, there
have been many and varied opportunities for differentiation
within and between regions, even to the extent of abandon-
ing the tropical and subtropical habitats fundamental to the
evolution of the eocene. Epidemic mass extinctions, with changing in sea level, continental collisions, and climatic gra-

tuations have all contributed to the complex development
and composition of the Old World fauna, which span an
eonous part of the globe. For the placentals, in contrast,
continental fragmentation has been a long-term macromolecular factor, with but a few notable

The geographical separation of placentals and cat-
archines is a fundamental feature of the primates' radiation,
aque which we know little due to lack of fossils. It has
been in effect ever since their common eocene ancestor, where-
ever it lived, split into two or more lineages. The timing of
this separation is important, for after the original arachines be-
came established in South America the original block and
strongly filtered all primate migrations into or out of the continen
tuliacus the Pliocene/Pleistocene ancestor ca. 3 Ma.
Thus, placental primate groups were permanently isolated from conge-
tatives with nonplacentals in the Americas, at least for 27 Mya and
perhaps for as long as 40 Mya. The composition and balance
of the current placentals fauna may, therefore, reflect a ho-
mmorphy achieved over many epochs. One of the pressing
questions is whether the living forms are samples of the first
and only placental radiation or of a successor to an earlier
division thus was replaced. Some fossil evidence suggests that
a significant degree of taxonomic and morphological ex-
change occurred among the arachines, and this may reflect a genoral
macroevolutionary pattern related to a minimum diversity.

The Old World radiation presents a contrasting geogra-
phy. There continents were less termed than in one another.
continents were less similarly than one another.
continents were less similarly than one another.
continents were less similarly than one another.
continents were less similarly than one another.

Facts of placentals and catarchines monkeys, suggesting
the similarities and differences of their eocene and fossil
monkeys. after A. H. Schultz. The Life of Primates. University Press. 1969. This figure shows the number of recognized genera and species of each and sex classes in the three estrous categories and different countries are not in parenthesis before each species.

Genus

New World monkey
Old World monkey
Genus 15-18 5-8
Species 50-55 7-90
ENTAD 10-13 15-25 EXTINCT

Figures showing the number of recognized genera and species of each and sex classes in the three estrous categories and different countries are not in parenthesis before each species.
boundaries for certain times during the Cenozoic, and the interruption of species ranges would have fostered speciation, differentiation, secondary adaptations, and replacement. Such conditions may have set an evolutionary premium on change rather than stasis and upon adaptive improvements, or novelties. The fossil evidence suggests that there have been a number of successive catarrhine radiations, each with its own character. Apes, for example, are new in their mode, having been displaced by quite a different type of primates, the cercopithecoid monkeys, which we fairly new on the scene.

The summation of these centrifugal effects produced an anthropoid radiation of tremendous variety and success. One might even speculate that some of the evolutionary paralogies between platyrhines and hominoids have resulted indirectly from their geographical separation—had they occurred together, competition would surely have driven them further apart anamorphically and perhaps have pushed some forms into extinction. Geography, however, hardly explains the success of Anthropoidea or its real nature. Special adaptations set anthropoids apart from the other members of their order, and that foundation created the potential to exploit a broad spectrum of ecological niches, unsurpassed by any other group of primates during their 65 Myr history.

Morphology and Adaptation

The skull, more than any other part of the skeleton, embodies novel anthropoid characteristics. In the simplest terms, the outward appearance of the anthropoid head is human-like in aspect, having a relatively flat "face" with a vertical arrangement of eyes, nose, and mouth. Superficial structures, such as the external ears, lips, and nose, also tend to resemble us in shape and proportion. If there is a singular feature that sets humans apart typologically from the universal design of the anthropoid head, it is our recently evolved, bimanual forebrain, although the little squirrel monkeys might even rival us there.

The major adaptive elements of this anatomical ensemble are the special senses of sight and smell, the cognitive function, of the brain, and the design of the maxilloincus apparatus. The anthropoid braincase is large and rounded, accommodating as much volume as possible within a small space. As a consequence, the foramen magnum is situated rather posteriorly within the skull base, which also makes head carriage more erect. The relatively small, dome-shaped sockets face directly forward, maximizing stereoscopic vision. With the lower face tucked, as highest the eyes, nasal bones tend to be short and deep, although muscle length has increased secondarily in such forms as baboons and howler monkeys. The olfactory apparatus, such as the size of the nasal cavity, the paper-thin mucous inside it, and the endocranial space for the olfactory bulbs, are all reduced, reflecting a diminished sense of smell. The mandible is fixed solidly at the symphysis, and, like the premaxillary bone above, it supports and stabilizes a battery of broad, vertical incisors. The lower jaw is also hinged well above the tooth rows, giving the chewing muscles good leverage. The midline metopic suture between the frontal bones also fuse early in life. The premaxilla and the maxilla vary in shape, but they tend to be blunt rather than streamlining sharp. The perorbital bone covering the middle of the orbit has a tendency to develop very small cells and/or partitions within it, contrasting with the balloon-like capsule found commonly among nonanthropoids.

By comparison with infraorders, olfactory cues are less important to an anthropoid than are visual signals. Apart from having a small main olfactory bulb, the secondary olfactory
bulb and its acceptance element, the Organ of Jacobson, are also reduced. Whereas the former structure is an all-purpose mediator of 
sense, the latter is important in sexual contexts. Its reduction indicates that anthropoids have diverged to a more diverse, "person" system of intraspecific and social 
communication, involving more elaborate bodily collocation and 
surroundings, facial gestures, postural signals, vocalizations, and 
close-up, interactive displays. Thus, more scene-producing 
 gambits will play a role in communication, especially among 
the platyrrhines, sensory input from the environment comes 
chiefly via the ears and eyes. As J. Eisenberg points out, like 
other mammals (such as field carnivores) which have come 
to capitalize upon size, both the eye and the brain have 
enslaved specializations that make this possible. The feature 
most obvious to us is the enlargement in brain size.

This reliance upon vision is predicated on a critical 
adaptive shift achieved by the nearest relatives of the anthropoids, an earlier-evolving group that passed on its traits to 
the latter's ancestral species. That shift was the adoption of a 
distinct lifestyle by the ancestral hominines, members of an 
umbrella taxonomic group whose existence we are able to 
recognize through two surviving descendants living among 
anthropoids and their relatives. From the early hominines, anthropoids inherited structural predations to enhance stereoscop
copic vision via a refined visual system, a rod-and-cone system 
of photoreceptor cells in the eye aimed to good color vi
sion. A dexterity that aids at pinpoint focusing, a complex network of 
crosswise optical fibers within the brain that send nerve im
pulses to both sides for simultaneous processing, and 
enslaved visual nerves of the brain.

This pattern may have given great selective value to 
anthropoid ancestors not because of any particular advan
tages but because of its generality. A visually precise image of 
the environment is one filled with the discriminations of size, 
shape, pattern, texture, color, and distance. Nothing could 
better serve an animal in the highly complex habitat of all 
arthropod environments. Sight is far richer in information than 
smell or taste. It also requires a complex system of memory 
storage, which in turn imbues more storage space and higher 
memory functions to record and decode the data. Thus, the 
world of the anthropoid is a more complex world of seeing and 
understanding, where the hue of a flower reveals its ripeness, the 
texture of a branch suggests flexibility, and the glint of an eye 
may spell trouble from a neighbor. 

Anthropoids are the only mammals to have evolved a 
separate sensory compartment housing the eyestalk. This 
paralleled the development of the posterior septum, a 
thin sheet of bone that forms the eye socket from behind, 
thereby also bridging the bony bones of the face and the 
braincase. The origin of this adaptation, however, may have 
nothing to do with good eyesight. While it may safeguard the 
delicate eyestalk from injury or shock, it is from the muscularly 
acting masses being behind it, these may be only secondary 
benefits. The structure of this area of the skull sug
gests that the septum served also as a mechanical brace to 
force the connection between the face and the skull. This role 
is an elaboration of the original function of the posterior 
septum, the ancestral structure from which the septum evolved.

The posterior bar is a vertical bar of the elliptic 
arch, a horizontal ridge that supports chewing muscles 
under the cheek, spanning from the skull to the base of the 
mandible. It appeared first among the ancestral euprimates, 
ancestors of all the modern primates. Then the bar served to 
secure the tail to the body and to minimize the 
heaving and twisting effects of chewing at the 
tongue and jaw. Then, it evolved into 
the mammalian joint and in mammals 
to the masticatory function. These 
loads may be acute in an anthropoid primate because the 
mammalian synovial joint is fixed rather than mobile, as it is in most nonanthropoids. Hence, the synovial does 
not convert into the more muscular forces of the jaw. 
And so, from the right side of the head as the animal chewed on its left. Such
internal stress is also difficult to balance or distribute within the head because of the shape of the anthropoid face. With their close-set eyes and reduced nostrils, there is less centralized bony mass to take up the forces of mastication. This is where the septum probably adds additional support. It compensates for acting as a lateral pillar, in this position, the potential plate can also directly resist the tension of the powerful masticatory muscle. Thus, one of the important innovations of the anthropoid head is associated with feeding. Whether as origin related to a new dietary preference or a second mechanical approach to an existing feeding pattern is unclear. But since anthropoids also have a considerably enlarged set of incisal teeth, an obvious source for much of the mechanical stress the head is designed to endure, it is likely, if the major dietary staple was originally fruit, perhaps species of plantain or huckle that had to be torn apart to access the nutritionally valuable core. Among the other adaptations that make anthropoids unique, those pertaining to life-history strategies are probably the most important. As relatively large primates, anthropoids tend to have long gestation periods, long-lived juveniles and adult female dependency, and a long postpartum life. Thus, intelligence, learning, socialization, and many other facets are major features of the anthropoid life cycle. The production of an offspring with a large birth size is also probably related to a novel parental development. The outer fetal membranes are attached to the wall of the uterus in an arrangement designed to accommodate one large fetus, whereas in other primates it tends to be Y-shaped, having a central cavity and two horns where multiple fetuses can attach.

Origins and Evolutionary Hypotheses of Ancestry

Although primate cladists now are confident that the characteristics shared by the anthropoids indicate that they are monophyletically related, this issue at times has been a matter of serious debate and discussion. Even until the 1970s, some maintained that placentalia and cainogorilla were independent, meaning that the anthropoid "grade," or stage of evolution, was attained separately as each evolved from different lower primate ancestors. Biology figured importantly in this theory, the separation of the placentarians and the cainogorilla does imply a complex history. In fact, the anthropoids were frequently cited as a model case illustrating the principle of parallelism. Such a theory was comfortably restated in a number of different ways, especially in the texts written by the naturalist and Victorian idealist of social progress, sought to promote adaptive improvements as the major driving force of the evolutionary machine. Then and thereafter, prominent researchers claimed that the similarities to a higher, primate grade was a common phenomenon. Some reckoned it happened as many as four times, once among the placentarians, twice among the cainogorilla, and once among the Malagasy primates. The puzzle of anthropoid origins has been a major focus of research for more than a century. During the 1990s, a wealth of new fossils from Africa and Asia, combined with new investigations of previously known forms has sharpened interest in this question. Comparative morphological study of modern primates has reported that anthropoids are most closely related to the tarsiers, with which they share derived features of vision (loss of specialised eyelids, presence of animal fur, and at least partial preorbital closure), olfaction (reduction of various receptors and presence of dry circumventricular area with middle upper lip, and placentaion. Unfortunately, most of these haploidine characteristics are not discernible in fossils. Moreover, the great majority of primate fossil teeth are dental, and the tarsier dentition is quite distinctive, not at all like that of anthropoids. Thus, the quest for understanding the origin and early evolution of anthropoids has been divided between searches of modern morphology and the search for extinct (or extant) groups that might be closely related to anthropoid ancestors. Three such groups have been widely advanced: the adapids and omomyids (herb-eaters) and the ankar, including the living tarsier and a few fossil allies. In the 1990s, the discovery of a monkey-like fossil has led to a fourth hypothesis, that some of these extinct forms represented a non-adapt/nonomomyid ancestral stock for anthropoids. We will evaluate each of these views and then look more closely at some of the fossils that have been proposed as the earliest anthropoids, finishing with a survey of biogeographical models for anthropoid dispersal. The adapid/anthropod hypothesis is based largely on a pair of shared features of the ancestral dentition and hand. The notion was first proposed in the nineteenth century, but P.D. Gingerich has given it new force. For example, he argues that both adapids and anthropoids have fused metacarpal symphysis, vertical spatial interossei, and interlocking and acutely dimorphic canines with cranium/proboscis bearing. However, by refining the anatomy and introducing functional reasoning to assess possible linking homologies, it has been shown that this entire suite of adapid-anthropoid similarities resulted from convergent evolution. A second prominent objection is that the adapids were probably already symplesiomorphic phylogenetically. The framing and expansion of different adaptive strategies, instead of being constrained by an initial set of conditions. In the deinonychus, dinosaur and avian skeletons, adapids frequently display derived characters that alter them with modern anthropoids. Beyond and above these difficulties, one specific subgroup of adapids that is becoming better represented as fossils, the cercopithecoids (also termed Purgadulidae or Primadulidae by some researchers), has often been portrayed as evolutionarily more similar to early anthropoids. Newly discovered genera (and new fossils of known taxa) may include Badenocercus and Mabebeinisa from China (45–60 Ma). Atlantomia from the Egyptian Fayum (Quarry 1–411 ca. 50 Ma), and possibly Zygoloph from Morocco (ca. 45 Ma). Although these fossils have been suggested by some authors as similar to the early anthropoids alogohyrax from their lower molars (usually with an occlusal entoconid and hypoconid) and canin-anterior prefer.
<table>
<thead>
<tr>
<th>Epoch</th>
<th>Asian-African LOCALITIES and African-Robusta LOCALITIES</th>
<th>Asian &amp; other LOCALITIES of Asian breeds from the above (Asia + Europe + South Asia)</th>
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<tr>
<td>Early Eocene</td>
<td>- Paleocene - Pseudophallodes - Kolobophallides - Antidorsalgus - Antigonus - Africa - Madagascar - Greenland</td>
<td>- Sauria (Sauria) - Cretaceous - Oligocene - Miocene - Pliocene - Pleistocene - Holocene</td>
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<td>Late Eocene</td>
<td>- Oligocene - Paleocene - Miocene - Pliocene - Pleistocene - Holocene</td>
<td>- Sauria (Sauria) - Cretaceous - Oligocene - Miocene - Pliocene - Pleistocene - Holocene</td>
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<td>Middle Eocene</td>
<td>- Oligocene - Paleocene - Miocene - Pliocene - Pleistocene - Holocene</td>
<td>- Sauria (Sauria) - Cretaceous - Oligocene - Miocene - Pliocene - Pleistocene - Holocene</td>
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<tr>
<td>Early Oligocene</td>
<td>- Oligocene - Paleocene - Miocene - Pliocene - Pleistocene - Holocene</td>
<td>- Sauria (Sauria) - Cretaceous - Oligocene - Miocene - Pliocene - Pleistocene - Holocene</td>
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*Stratigraphic and geographic occurrence of the earlier anthropoids and afro-primates which have figured in discussions of anthropoids (and primates) origons. All E-Asian and African Paleogene primates are included, as their taxon has been defined by different studies, as can be in the range and early evolution of anthropoids. In addition, the first New World anthropoids and selected European primates discussed in the text are indicated. The locations of many sites are shown in the map following. Note that there is no attempt to list all of the sites as is given or, in the list is intended as the list below, within square brackets [ ]. Note also that although the Anthropoida and Orangidae formed part of stem primates in the Early Miocene, the Olorian and/or Oligocene is included in the data column for reasons of space.*
molar complex (when known), they are still adapis in detail and thus probably not relevant to anthropoid origins.

Arguing that fossils are not highly informative here, M. Cartmill and coworkers have reasoned that the tarier is the most likely sister group of anthropoids. While a still broader version of this hypothesis—that extant relatives of the tariers are likely candidates—is supported by many, it seems unlikely that tariers themselves would be closer cladistically to anthropoids than their less-radial-tarsiform relatives. The tarier lineage per se has always been too advanced anatomically to be the model of an anthropoid stock. The anatomy of the middle ear, postorbital-epiural, coroidal arthritis, and reproductive systems of tariers and anthropoids share important derived or-actual details, but these point to a more abstract synapomorphy connection, via a group less bizarre a-pertently than the tariers. The unique particulars that could potentially link tariers more closely with anthropoids are probably parallelistms. For example, the postorbital wall of tariers most likely arose in relation to their frontally large eyeballs, which is not the case in anthropoids, who have relatively small eyes. Hence, they are not uniquely de- rived features of phylogenetic value.

A third hypothesis (considered the most plausible by a majority of current researchers) is that anthropods arose during the Eocene from a subgroup of omnomyid primates that was widely distributed across North America and Eurasia. Omnomyids are generally accepted as being closely related to tariers (together they are called tarsiiforms), and omnomyids are well represented in the fossil record by many species, but the collections consist mostly of teeth and jaws. Omomyia stearnsi, a form from the Late Eocene of Utah, is classified as an omnomyid tarsiiform, but its dental anatomy may be a good model for the praeanthropoid pattern, as E.J. Simons and others have pointed out. Unfortunately, it is still known only from dental elements. Given that the modern anthropoid head is so full of higher-primate novelty, the skulls of such praeanthropoids would be more telling. The known skulls of omnomyids do, at least, indicate a significant morphological heterogeneity, including patterns that are much more primitive than the expected tari- seriform departures. New evidence also demonstrates that some omnomyids, known informally as neocomomys, were close relatives of living tariers, as early workers had thought, and were also distributed broadly in Laurasia. This makes it all the more likely that another omnomyid stock, ancestral to both the playtherines and the cebelines, was widespread and sufficiently primitive to have evolved into the first anthropoids.

Recently, as a result of the discovery of new primitive fosi- lls (such as Eomomys, Apatolestes, and others) from China and Northwest Africa, a fourth model has been suggested. Although the details vary among advocates, the underlying concept is that some of these new forms represent a previ- ously unknown group of Eocene praeanthropoids, neither adapis nor omnomyid. This "third major radiation" concept implies a more ancient origin for the anthropoids and re- quires further evaluation of the new fossils. However, it pre- sented some significant difficulties. For example, it has yet to be clearly established that any number of the fossils mosuar- tatively of that hypothesis. Tariers are probably tarsiiform. One of the fossils in question, Eomomys, shows an extraordinary series of derived researches to tariers, and it is more likely to turn out to be a basal tarsiiform instead of an ancestral anthropoid. If these fossils are indeed tarsiiforms, this concept would restore the omnomyid-anthropoid hyp- othesis in slightly different terms.

Origins and Evolution: Fossil Evidence

Four groups or classes of fossils are important in the attempt to understand the origin and early evolution of the anthropoids: (1) the earliest generally accepted anthropoids—the Parapithecidae and Propliopithecidae, mainly from the Early Eocene Fayum deposits of Egypt (the first playtherines are too fragmentary to be of much help and, moreover, are later in time); (2) the Oligopithecidae, especially Campithecus and Oligopithecus, two earlier Fayum fossils that researchers have argued are true anthropoids; (3) a variety of (mostly) newly discovered Eocene fossils from North Africa and eastern Asia; and (4) known Eocene, late tarsiiforms (omomyids) that may re- present a "basal stock" for anthropoids. Propliopithecus presents a suite of generalized anthropoid features, such as fusion of the manus metacarpal and the frontal bones in the midline, full postorbital closure, sparsely, nearly vertical incisors, strongly expressed canine dimorphism, and lower molaris with relatively flat crowns (trigonid and talonid of even height). Within Anthropoids, the propliopithec- oids are closely cebelines, with such unique dental fea- tures as loss of pu, well-developed dural midline hypsodonts on lower molars, and general molar structure. These derived states are conserved in nonhuman anthropoids (playtherine-
like conditions, such as a ringlike eutopicystic (external ear opening) and several postcranial features.

The better-known parasaurolophids (Parasaurolophus and Dinosauria) are the type of typical anthropoid conditions as the protopithicoids. These are combined, however, with several more conservative than in the cetaceans, such as a somewhat smaller hyoid bone and the retention of P4, along with uniquely derived traits (central cusp on the upper premolars, tendency to extra cusps on molars, loss of lower incisors in some forms) and several postcranial features more 'primitive' than those found in either plesiosaurs or cetaceans. On this basis, parasaurolophids are now placed by most authors as the sister-taxon of all other antropoids, thus among the most ancient and conservative members of the hipparids. It is with the parasaurolophids that other fossil genera purportedly considered anthropoids must be compared.

From late Eocene horizons in the Fayum some two genera that have also been placed within the Antropoidea by many, but not all, researchers. Ctenomylodon is known from several partial skulls and lower jaws that present a remarkable mosaic of ancestral and derived character states. The frontal bone is solidly fused, and the orbit appears to have been reduced, as in an antropoid. Moreover, the upper incisors seem to be at least somewhat similar. But the mandibular symphysis appears to be unknown, and the molars are not anthropoid-like: The lower teeth are relatively high and long and a generally elongate shape more commonly found in lower primates; the upper molars also are less elliptical. Ctenomylodon has one or two small and low premolars, the molars do not look like those of anthro-

The parasaurolophids share some aspects of the molar shape (proximally of the hyoid bone and the development of the lower teeth). Their dentition shows similarities to those of the parasaurolophids. Either molar shape or (more likely) premolar patterns must thus have evolved at least twice, in ceratopsians and in some early anthropoids. Here the ogelpithicons are considered less derived than the parasaurolophids, but still early anthropods.

Among them, a contemporaneous of Ctenomylodon, was thought to be closely related but has since been distant, as it preserves three premolars; it might provide a link of sorts between ogelpithicons and the derived parasaurolophids (see below). However, its molus morphology is exceedingly primitive, resembling tarsiers and other early anthropoids, and it is likely not an anthropoid. Carnotaurus and Ogelpithicon may be more derived members of a true protopithicon stock, but they are not late in time as now known to be actual ancestors of later anthropoids. They suggest that the complex of features that is thought to characterize anthropoids did not all appear at one time, but instead, as is often the case in evolution. About a dozen genera of less well-known fossil primates have been touted in the 1990s as protopithicons, Algers-
primate is *Enomios*, known from two Middle Eocene locali-
ties in China, one the same age as *Hapalodromeus*, the "slightly more" slightly earlier (ca. 46-45 Ma). Most of the other Asian primates are moderately large, but *Enomios* is tiny, comparable to *Ali-
serius*, and slightly later than *Cainotherium*. The in-
cidence of the enaptids in *Enomios* are relatively-commonly and broadly similar to those of some early anthropoids. This condition and a selection of cheek-tooth features has led to some taxonomists suggesting that *Enomios* is a basal anthropoid, representing an ancient primate diverging more or less from both the plesiadapiforms and omomyids (see above).

In some ways, this is an analogous to the suggestion that *Aiolitherium* and especially the early *Parapithecus* represented an equivalent stock in North Africa. But the morphology of these two primitive primate groups differs strongly, so only one (at most) could be representative of a real anthropoid ancestry. In fact, the cheek teeth of *Enomios* (especially the very tall in the early developing postcanines) and the maxillary pterygoid ramus from the same site are assigned to this genus, suggesting that it is better understood as an omomyid relative. At least placement is uncertain within that complex, but, stripping away the tarsier-like features, *Enomios* confirms a broad omomyid-based ancestry for anthropoids by proving the existence of ancestral anthropoid features within this group (at least in the Asian Eocene). While waiting for additional fossil evidence of these Eocene primate-like species, the next question to examine is paleogeography: How did early anthropoids disperse across the Palaeogene world?

**Origins and Evolution: Geography**

Today, of course, the two main anthropoid groups, Platyrrhini and Catarrhini, occur in the geographically dis-
joint regions of the neotropics and the Old World, respec-
tively. Platyrrhines have apparently always been restricted to the New World, while the eutherian definitive anthropoids are now seen to be (northern) Africa—only one possible once known as the Oligocene site in Angola. There are, thus, two separate but related questions to ponder. How and when did the primate lineages reach Africa, and how did the primate-
ly ancestors reach South America? Both were island conti-
nents in the Palaeogene, with mainly distinctive faunas. 

When the principle of plate tectonics and continental drift was first applied to primates during the mid-1960s, it was widely argued that the ancestral stock of platyrhines and cercopithecines occupied a single great southern land-mass that later rifted apart (as the southern Atlantic Ocean grew) in the mid-Miocene, to the north, and finally divided into South America, Africa, and Asia during the early Oligocene (ca. 130-110 Ma). This model placed fra�e primates were separated from the two continents in the 38 Myr previous to the very first primates were documented in the fossil record.

In the face of counter-evidence, modifications to this hypothesis have been proposed. One postulates that eutherian ancestors of modern primate groups may have dispersed across the various continents of the Atlantic. Nearly all of these are now submerged, but they could have been landbridges for primates dispersing across the ocean. This stepping-stone hypothesis was also popular a century before continental drift was even estab-
lished. Combined with floating rafts of natural vegetation between islands, this idea is prominent in most late-Tertiary cenozoic views of primate evolution. One re-
tros of problems relating to any eutherian raft-crossing refers to the dangers of exposure, lack of fresh water and food.—Mi-
crotherium-like flehmen is unlikely in an early anthropoid. Moreover, neither the Fayum anthropoids nor as some have suggested, the *Nycticebus* are morphologically recognizable as ancestors for platyrhines. However, if the anthropoids indeed represent an archaic anthropoid group that now extends back to the Middle Eocene, it is conceivable that an as-yet unknown (North)/West African relative might have been a plausible Eocene prosopithecine. A global recession of sea level, such as the one that occurred in the Late Eocene, might have narrowed the Atlantic gap suffi-
ciently to permit a crossing.

A different idea suggests that an ancestral stock of omomyid-derived primate groups occupied an assembly of northern continents, Laurasia, where Early Eocene primates were flourishing contact between the Eastern and Western hemispheres was possible at intervals across the Bering region. Spurred on by a cooling of the Northern Hemisphere and the ex-
pansion of grasslands, most northern primates became extinct, but some shifted their range to the south, possibly in both the Eastern and the Western hemispheres. Among these may have been the two primate groups, who found their way across the water barrier to reach the island continents of Africa and (later) South America during different organism episodes of low water. Passage into South America seems to have been the more remarkable one, for it may have involved fewer other mammals. The *Hyracotherium* noda, relatives of the mod-
ern porcupines, may have been the primates' only travelling companions. In fact, it is their geographic association that led such researchers as R.I. Hoffstetter to propose an African ori-
gin for platyrhines in the first place: Bush hyracotheres and pliarctotheres may have their closest living relatives in Africa.

Some would argue that possible East Asian (*Enomios*) and North African (*Dyellemia*, *Alikertrio*) primate-like groups are of comparable Middle Eocene age, whether *Alika-

— is, indeed, related to this group. In the primate evolution, models of Asian ancestry for Fayum anthropoids depend upon in-
terpretations of *Parladocetus* and *Amphimemi*, but the pro-
posed Early Eocene pathway around the southern Bering of an Area that had never extended with India is still plausible. If that collision occurred in the early to mid-Eocene, migra-
tion could even have proceeded across the contact zone at some point. What is most important to realize is that with-
out acceptable morphological relatives (mammal-taeni) in place, no paleoanthropological hypothesis is worth formulating. It would be nothing but speculation, no matter how good the evidence.
Macrovolutionary Patterns in Catarrhines and Platyrrhines

To comprehend and compare the evolutionary histories of the major divisions of the anthropoids, we need many more fossils documenting changes in the taxonomic diversity, adaptations, and geographical distributions of the platyrhines and the catarrhines. For the crucial Paleogene phase in the Old World, we have only the evidence from the Egyptian Fayum (36–33 Ma) and from La Salle, Bolivia (27 Ma). We have data at the Paleogene-Neogene boundary only, which means we know a bit about Africa and next to nothing about South America. Information on later epochs is even more biased in favor of the Old World. Therefore, reconstructions and comparisons must draw heavily upon the living forms for at least one side of the story. Nonetheless, as a start, E. Delson and A.L. Rosenberger began to examine the macrovolutionary histories of platyrhines and catarrhines, concluding that each group experienced distinctly different patterns.

Among the catarrhines, both the fossil record and the extant forms indicate a dichotomization of adaptive zones into relatively nonoverlapping arboreal and terrestrial spheres. This is paralleled by an expansion out of the classical humid tropics into more xeric and even colder climates of the Old World. Terrestriality is also associated with the attainment of large body size in many catarrhines. Second, the terrestrial zone seems to be of recent vintage. The earliest catarrhines, ancestors of both the monkeys and the apes, appear to be arboreally adapted. The ancestral Old World monkey stock shifted to a terrestrial habit, as indicated by their many ground-related postcranial adaptations, and this probably explains a large part of their geographic success. Among the apes, terrestriality seems to be superimposed upon an indelible arboreal heritage.

Third, the morphology of the ceropithecoid radiation is surprisingly simple; there is little variety other than in size and size-related features. The apes, on the other hand, are far more diverse anatomically; given that they include a small number of taxa.

The New World monkeys present a contrasting picture. Abundant grallinoids appeared in South America during the Cenozoic, but platyrhines probably never evolved an open-country, terrestrial lineage. If they did, we seem to have no descendants of that group among the modern species. There is still no good explanation for the apparent absence of a terrestrial lineage, for these ancient sarcocebus supported large populations of herbivores, as in Africa and Asia where ceropithecoids eventually flourished. Perhaps the larger catarrhines were more formidable competitors vis-à-vis other mammals than the platyrhines; or maybe the grassland florae were quite different in the Old and the New worlds.

Rather than invade such an ecological terrain, platyrhines flourished among the trees by finely dividing their niche. This is what makes for their great intergeneric diversity, each genus evolving distinctive adaptations to permit coexistence with its close, sympatric relatives. A second factor contributing to their relative diversity is that platyrhines radiated at the small end of the anthropoid body-size spectrum. This enabled some of the smaller bodied species to utilize three feeding niches rarely (if at all) exploited by the larger catarrhines. One is the hard-fruit/seed-eating niche, occupied by a whole subfamily, pitheciines. The second is the invertebrate-frugivore (or animalivore-frugivore) niche, from which catarrhines are excluded due to their larger body size. A third, related paradigm is the gum-eating niche, central to the adaptations of the smaller marmosets.

Altogether unclear is what happened at the opposite end of the size spectrum, but hints are mounting that our notions of platyrhine diversity and uniqueness will continue to change. New fossil discoveries in the Brazilian Late Pleistocene led C. Cartelle and W.C. Hawking to determine that monkeys existed there twice as large as the biggest ones alive today. Does this foretell of other adaptive responses to arboreality? Or does it pave the way for realizing a terrestrial option, with baboon-sized platyrhines milling about as giant ground sloths browsed? Another contrast between the radiations of platyrhines and catarrhines is their temporal patterning. Lineage stasis has been a more common occurrence among platyrhines than among catarrhines.

To properly evaluate this hypothesis, we need good biostratigraphic information over geological time, which is severely lacking, especially for the platyrhines. In looking at the moderns and the fossils, however, it appears that genetic lineages have a much longer duration in the New World. Among all of the Old World catarrhines, the macaques and orangs show the greatest geologic longevity. Specimens attributed to Macaca are known from deposits of 8–6 Ma, but there are few, if any, derived characters to clinch the identification. Conures of Pingo go back only as far as the Pleistocene, but the craniodental morphology that marks it as a generic entity is well developed in late Stegodonerauza at 9 Ma, and these are preceded by deino-eruciform remains of probable congers older than 12 Ma. In the Old World, these examples are the only two cases of anagenetic/taeniodont stasis from a fossil record that is strikingly rich by comparison with the South American data.

Among the modern New World monkeys, Saimiri is phylogenetically linked through a Colobeuroid species named by J. Bateman in 1987. It ranges from 12 to 13 Ma to Delichobrus, as at 19 Ma. In the Old World, these examples are the only two cases of anagenetic/taeniodont stasis from a fossil record that is strikingly rich by comparison with the South American data.

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Further Readings


