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REPRINTED FROM:

Encyclopedia of Human Evolution and Prehistory, 2nd ed; E. Delson, I. Tattersall, J. A. Van Couvering and A. S. Brooks, eds. Garland: New York. 2000

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Anthropoidea

Higher primates, including platyrrhine (also called ateloid or previously ceboid) monkeys of the New World, and the c

tarrhine monkeys, apes, and humans of the Old World. Previously ranked taxonomically as a suborder of primates, they are here placed at the next lowest rank, hyporder, to retain subordinal rank for Haplorhini (including Anthropoidea and Tarsiiformes) and Strepsirhini. Anthropoids are the most successful survivors of the three major extant lineages of primates originating long ago in the Early Tertiary. The once-flourishing tarsiiform group is now represented by a single tiny genus, *Tarsius*, in the remote evolutionary outpost of the Philippines and Indonesia, and the remaining lemur-like strepsirhines of Madagascar, mainland Africa, and the Indian subcontinent are far less diverse than the anthropoids, taxonomically and adaptively. How the larger-bodied members of the strepsirhines and anthropoids would have compared during the Pleistocene, however, is another matter: We are only beginning to learn how many and what kinds suffered extinction as human populations expanded into their habitats in all areas of the world.

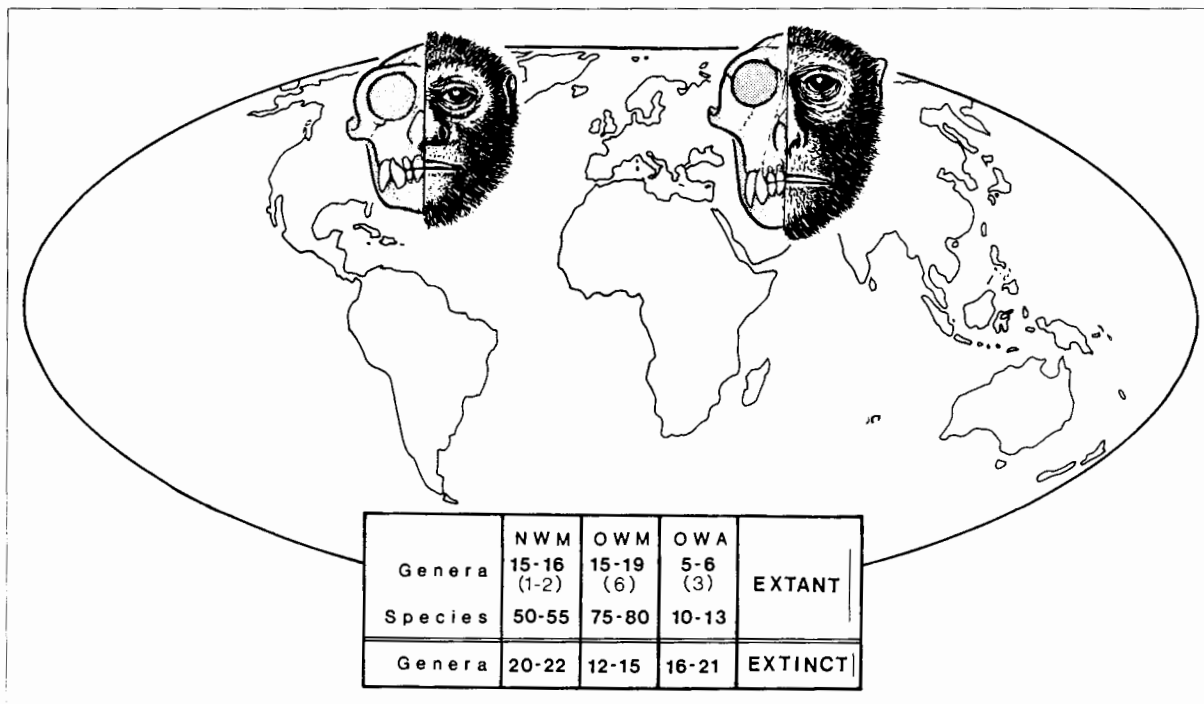
Geographical Background

The success of the anthropoids has been influenced by geography in a number of ways. Their history unfolded in two distinct theaters, in South America and in Afro-Eurasia—one large in area and the other relatively restricted. The occupation 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 abandoning the tropical and subtropical habitats fundamental to the evolution of the order. Episodic mountain building, eustatic changes in sea level, continental collisions, and climatic gra-

dations have all contributed to the complex development and composition of the Old World faunas, which span an enormous part of the globe. For the platyrrhines, in contrast, continental quarantine has been a predominant long-term macroevolutionary factor, with but a few notable caveats.

The geographical separation of platyrrhines and catarrhines is a fundamental feature of the primate radiation, one about which we know little due to lack of fossils. It has been in effect ever since their common ancestral stock, wherever it lived, split into two or more lineages. The timing of this separation is important, for after the original ateloids became established in South America the oceans blocked or strongly filtered all primate migrations into or out of the continent until the Panamanian isthmus arose ca. 3 Ma. Thus, platyrrhines were permanently insulated from competition with nonplatyrrhine primates, at least for 27 Myr and perhaps for as long as 40 Myr. The complexion and balance of the current platyrrhine fauna may, therefore, reflect a homogeneity achieved over many epochs. One of the pressing questions is whether the living forms are samples of the first and only platyrrhine radiation or of a successor to an earlier division that was replaced. Some fossil evidence suggests that a significant degree of taxonomic and morphological stasis occurred among the ateloids, and this may reflect a general macroevolutionary pattern related to continental insularity.

The Old World situation presents a contrasting geography. There continents were less isolated from one another. Faunal turnovers were probably more common, as Africa, Europe, and Asia shifted their respective positions and points of contact, mixing their occupants. Their paleodistribution maps of extinct genera cross today's continental



Faces of platyrrhine and catarrhine monkeys, suggesting the similarities and differences of their cranial and facial structures, after A. H. Schultz, *The Life of Primates*. Universe Books, 1969. The table shows the number of recognized genera and species of extinct and extant primates: the ranges reflect differences of opinion among researchers as to how many taxa should be accepted as distinct genera; the numbers in parentheses below extant genera indicate how many such genera have significant fossil records. (Abbreviations: NWM, New World monkey; OWM, Old World monkey; OWA, Old World ape, including humans.)

boundaries for certain times during the Cenozoic, and the interruption of species ranges would have fostered speciation, differentiation, secondary contacts, competitive interactions, and replacement. Such conditions may have set an evolutionary premium on change rather than stasis and upon adaptive improvement, 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 now at their nadir, having been displaced by quite a different type of primate, the cercopithecoid monkeys, which are fairly new on the scene.

The summation of these continental effects produced an anthropoid radiation of tremendous variety and success. One might even speculate that some of the evolutionary parallelisms between platyrrhines and hominoids have resulted indirectly from their geographical separation—had they occurred together, competition would surely have driven them further apart anatomically and perhaps have pressured 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.

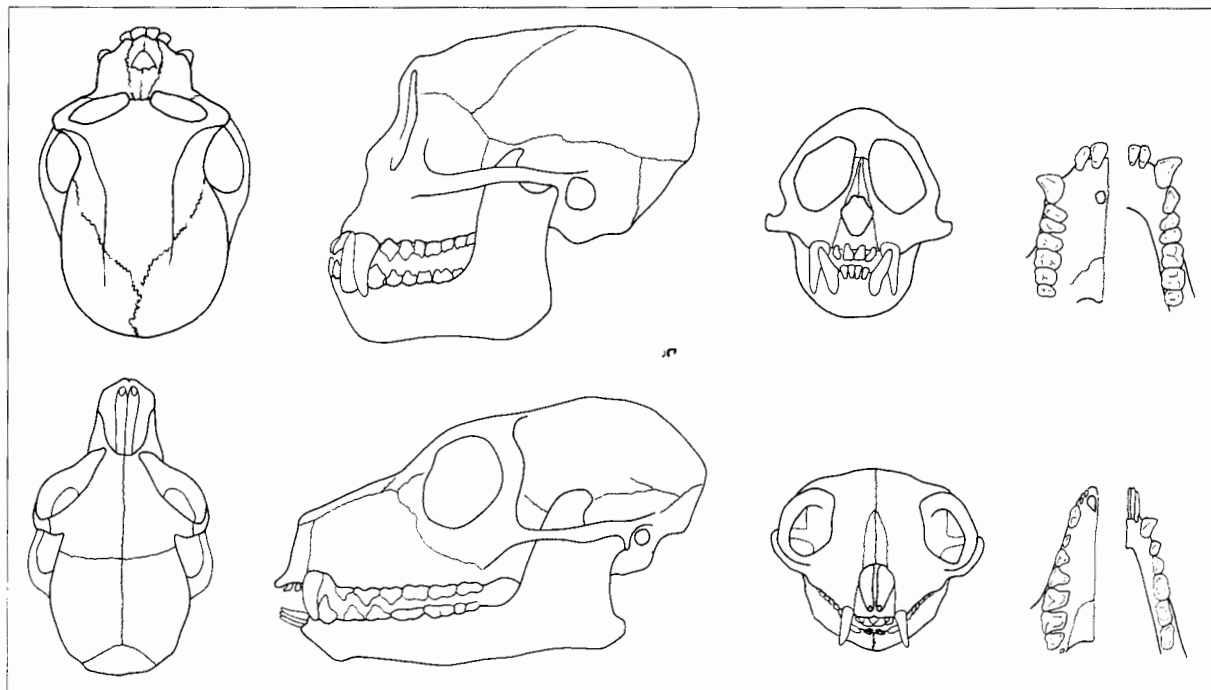
Morphology and Adaptation

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 re-

semble 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, bloated forehead, 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 functions of the brain, and the design of the masticatory 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 anteriorly within the skull base, which also makes head carriage more erect. The relatively small, close-set eye sockets face directly forward, maximizing stereoscopic vision. With the lower face tucked in beneath the eyes, facial bones tend to be short and deep, although snout length has increased secondarily in such forms as baboons and howler monkeys. The olfactory components, such as the size of the nasal cavity, the paper-thin scrolls inside it, and the endocranial space for the olfactory bulb, are all reduced, reflecting a diminished sense of smell. The mandible is fused 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 fuses early in life. The premolars and the molars vary in shape, but they tend to be blunt rather than penetratingly sharp. The petrosal bone covering the middle-ear region has a tendency to develop many small cells and/or partitions within it, contrasting with the balloon-like capsule found commonly among nonanthropoids.

By comparison with strepsirhines, olfactory cues are less important to an anthropoid than are visual ones. Apart from having a small main olfactory bulb, the secondary olfactory



Main differences between the cranial and dental morphologies of an anthropoid, represented by *Cebus* (top), and a generalized euprimate, represented by *Lemur* (bottom). After Rosenberger, 1986; courtesy of Alfred L. Rosenberger.

bulb and its receptor element, the Organ of Jacobson, are also reduced. Whereas the former structure is an all-purpose mediator of scent, the latter is important in sexual contexts. Its reduction indicates that anthropoids have shifted to a more direct, "personal" system of intersexual and social communication, involving more elaborate bodily coloration and adornment, facial gestures, postural signals, vocalizations, and close-up, interactive displays. Although scent-producing glands still play a role in communication, especially among the platyrrhines, sensory input from the environment comes chiefly via the eyes and ears. As J. Eisenberg points out, like other mammals (such as felid carnivores) which have come to capitalize upon sight, both the eye and the brain have evolved specializations that make this possible. The feature most obvious to us is the enlargement in brain size.

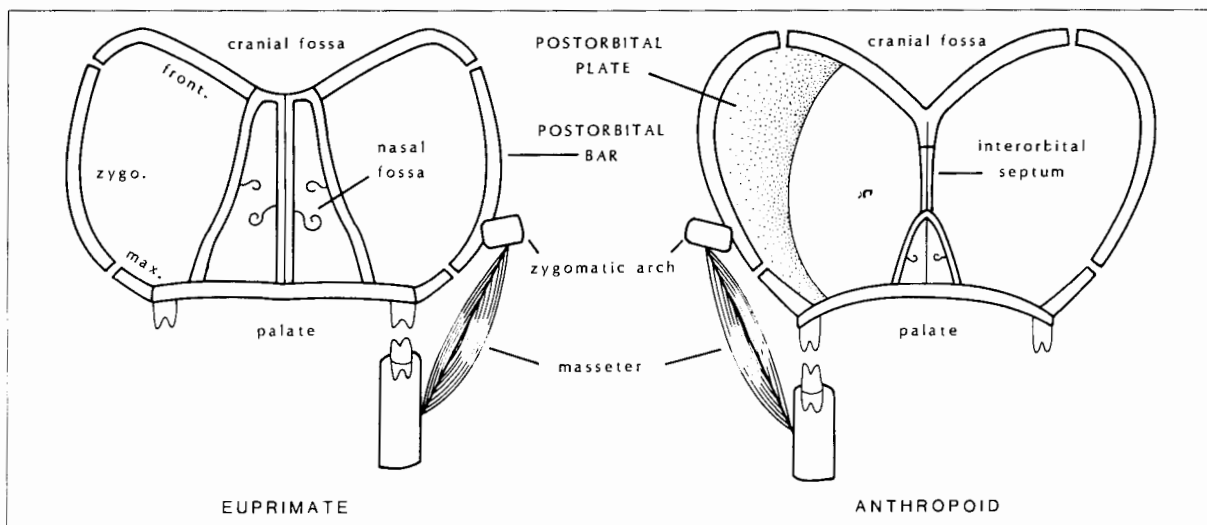
This reliance upon vision is predicated on a critical adaptive shift achieved by the nearest relatives of the anthropoids, an earlier-evolving group that passed on its traits to the latter's ancestral species. That shift was the adoption of a diurnal lifestyle by the ancestral haplorhines, members of an umbrella taxonomic group whose existence we are able to recognize through two surviving descendant lineages: anthropoids and tarsiers. From the early haplorhines, anthropoids inherited structural preadaptations to enhance stereoscopic vision via a reorganized skull, a rod-and-cone system of photoreceptor cells in the eye attuned to good color vision, a dense packing of cells near the retinal fovea making the eye adept at pinpoint focusing, a complex network of crossover optical fibers within the brain that send nerve impulses to both sides for simultaneous processing, and enlarged visual centers of the brain.

This pattern may have been of great selective value to ancestral anthropoids not because of any particular advantages but because of its generality. A visually precise image of the environment is one filled with the discriminants of size, shape, pattern, texture, color, and distance. Nothing could better serve an animal in the highly complex fabric of an arboreal environment. Sight is far richer in information than

sound or taste. It also requires a complex system of memory storage, which in turn implies more storage space and higher cognitive functions to encode and decode the data. Thus, the world of the anthropoid is a complex world of learning and subtleties, where the hue of a fruit 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 bony compartment housing the eyeball. This appeared with the development of the postorbital septum, a thin sheet of bone that forms the eye socket from behind, thereby also bridging the lateral 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 eyeball from injury or shield it from the masticatory actions of muscles lying behind it, these may be only secondary benefits. The structure of this area of the skull suggests that the septum serves also as a mechanical brace to reinforce the connection between the face and the skull. This role is an elaboration of the original function of the postorbital bar, the ancestral structure from which the septum evolved.

The postorbital bar is a vertical branch of the zygomatic arch, a horizontal girder 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. There the bar served to stabilize the zygomatic arch and the tooth row against the pull of the masseter muscle and to minimize the shearing and twisting effects of chewing at the junction between braincase and face. As anthropoids tear and grab at food with their large incisors or chew tough foods with the cheek teeth, they are prone to generate relatively high levels of stress in the zygomatic arch and at the craniofacial junction. These loads may be acute in an anthropoid primate because the mandibular symphyseal joint is fused rather than mobile, as it is in most nonanthropoids. Hence, the symphysis does not convert into motion the muscular forces delivered, say, from the right side of the head as the animal chews on its left. Such



Mechanical model of the anthropoid postorbital plate (right), contrasted with the euprimate postorbital bar (left). The postorbital plate reinforces the connection between the facial and neurocranial parts of the skull in the absence of an enlarged nasal fossa and interorbital region, well developed in lower primates. Courtesy of Alfred L. Rosenberger.

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 snouts, there is less centralized bony mass to take up the forces of mastication. This is where the septum provides additional support. It compensates by acting as a lateral pillar. In this position, the postorbital plate can also directly resist the tension of the powerful masseter muscle. Thus, one of the important innovations of the anthropoid head is associated with feeding. Whether its origin related to a new dietary preference or a revised mechanical approach to an existing feeding pattern is unclear. But since anthropoids also have a conspicuously enlarged set of incisor teeth, an obvious source for much of the mechanical stress the head is designed to endure, it is likely that the main dietary staple was originally fruit, perhaps species with resistant husks that had to be torn apart to access the nutritionally valuable content.

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, lengthened phases of juvenile and adolescent dependency, and a long postreproductive life. Thus, intelligence, learning, socialization, and many other factors are major features of the anthropoid life cycle. The production of an offspring with a relatively large brain at birth is also possibly related to a novel prenatal development. The outer fetal membranes are attached to the wall of the uterus in an intimate way, so that fetal capillaries and maternal blood vessels exchange nutrients, immunogens, and waste materials very effectively. This hemochorial placenta is similar to the condition found in tarsiers. The anthropoid uterus is also an unusual bell-shaped chamber 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 Evolution: Hypotheses of Ancestry

Although primatologists 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 doubt and discussion. Even until the 1970s, some maintained that platyrrhines and catarrhines arose independently, meaning that the anthropoid "grade," or stage of evolution, was attained separately as each branch evolved from different lower primate ancestors. Geography figured importantly in this theory; the separation of the platyrrhines and the catarrhines 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 comfortable to nineteenth-century zoologists especially, who, influenced by the *scala naturae* doctrine and Victorian ideals of social progress, sought to epitomize adaptive improvement as the major driving force of the evolutionary machine. Then and thereafter, prominent researchers claimed that the transition to a higher-primate grade was a common phenomenon. Some reckoned it happened as many as four times, once among the platyrrhines, twice among the catarrhines, and once more 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 revealed that anthropoids are most closely related to the tarsiers, with which they share derived features of vision (loss of tapetum lucidum, presence of retinal fovea, and at least partial postorbital closure), olfaction (reduction of various receptors and presence of dry circumnasal area with mobile upper lip), and placentation.

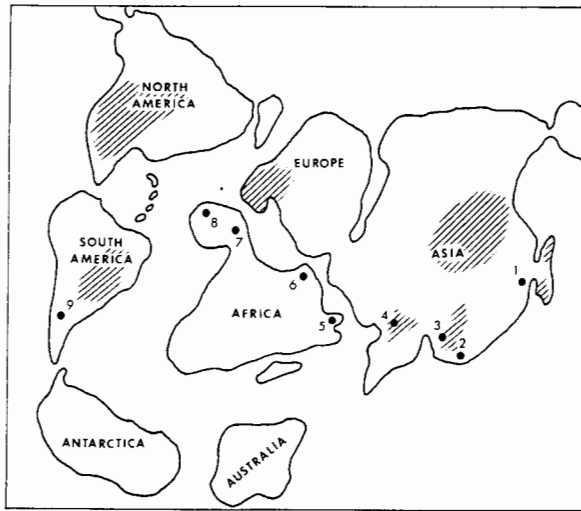
Unfortunately, most of these haplorhine characteristics are not discernable in fossils. Moreover, the great majority of primate fossil remains are dental, and the tarsier dentition is quite distinctive, not at all like that of anthropoids. Thus, the quest for understanding the origin and early evolution of anthropoids has been divided between studies 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 advocated: the adapids and omomyids (both extinct) and the tarsiiids, including the living tarsier and a few fossil allies. In the 1990s, the discovery of new, apparently unique fossils has led to a fourth hypothesis, that some of these extinct forms represented a non-adapid/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 biogeographic models for anthropoid dispersal.

The adapid-anthropoid hypothesis is based largely on jointly shared features of the anterior dentition and mandible. This notion was first proposed in the nineteenth century, but P.D. Gingerich has given it new force. For example, he argued that both adapids and anthropoids have fused mandibular symphyses, vertical spatulate incisors, and interlocking and sexually dimorphic canines with canine/premolar honing. However, by restudying 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 these adapids were possibly already strepsirhines phylogenetically rather than a formative euprimate stock ancestral to all of the modern groups. In their dentition, skull, and postcranial skeleton, adapids frequently display derived characteristics that align them with modern strepsirhines.

Above and beyond these difficulties, one specific subgroup of adapids that is becoming better represented as fossils, the Cercamoniinae (also termed Protoadapinae or Protoadapini by some researchers), has often been singled out as dentally most similar to early anthropoids. Newly discovered genera (and new fossils of known taxa) may include *Rencunius* and *Hoanghoni* from China (45–40 Ma), *Afiamonius* from the Egyptian Fayum (Quarry L-41, ca. 36 Ma), and possibly *Djebelemur* from Morocco (ca. 45 Ma). Although these forms have been suggested by some authors as similar to the early anthropoid oligopithecids in their lower molars (usually with adjacent entoconid and hypoconulid) and canine-anterior pre-

Age (Ma)	Epoch	Afro-Arabian LOCALITIES and <i>Primate Fossils</i> [taxa in brackets are continued from the line above]	Asian & other LOCALITIES and <i>Primate Fossils</i> (A=Asia; E=Europe; S=South America)	
26	O L I G O C E N E	LOTHIDOK <i>Kamoyapithecus</i> (earliest Hominoidea)	SALLA (S) <i>Branisella Szalatavus</i>	
27				
28				
29				
30				
31				
32			MALEMBE ? <i>Propliopithecidae</i>	
33				BOULDNOR & NEUSTADT (E) last <i>Adapis</i> ====GRANDE COUPURE====
34		Late Eocene	F JQ-4 <i>Propliopithecus Apidium Parapithecus Afrotarsius</i> A JQ-3 <i>Propliopithecus Apidium ?Parapithecus [Qatrania]</i> Y JQ-2 <i>Oligopithecus Qatrania ?omomyine</i> U JQ-1 <i>Catopithecus Qatrania Proteopithecus Serapia</i> M [<i>Arsinoea Plesiopithecus Wadilemur Aframoniuss Anchomomys</i>]	TAQAH (A) " <i>Moeripithecus</i> " <i>Oligopithecus</i> [<i>Shizarodon Omanodon</i>]
35				
36			NEMENTCHA (BIR EL ATER) <i>Biretia</i>	
37				
38	Middle E O C E N E			WAI LEK (A) <i>Wailekia Siamopithecus</i>
39			PONDAUNG (A) <i>Amphipithecus Pondaungia</i>	
40				
41				
42			GLIB ZEGDOU <i>Algeripithecus Tabelaia</i>	
43				GONGLANGTOU (A) <i>Asiomomys</i>
44				
45			CHAMBI <i>Djebelemur</i>	HETI (A) <i>Eosimias Hoanghoniuss Rencuniuss</i>
46				SHANGHUANG (A) <i>Eosimias Tarsius</i> [<i>Adapoides Macrotarsius</i>]
47				LUSHI (A) <i>Lushius</i>
48				
49	Early Eocene		KULDANA Fm. (A) <i>Kohatius Panobius</i>	
50				
51				
52				
53				SPARNACIAN (E) first <i>Adapidae</i> & <i>Omomyidae</i>
54			WUTU (A) <i>Carpocristes Chronolestes</i> BUMBIN NURU (A) <i>Altanius</i>	
55	P A L E O C E N E			
56		ADRAR MGORN 1 <i>Altiatlasius</i>		
57				
58				NANXIONG (A) <i>Petrolemur</i>
59				
60				
61				WANGHUTUN Fm. (A) <i>Decoredon</i>
62				

Stratigraphic and geographic occurrence of the earliest anthropoids and other primates which have figured in discussions of anthropoid (and primate) origins. All Afro-Arabian and Asian Paleogene primates are included, as these continents have been claimed by different authors as central to the origin 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 on the map following. Note that when there is not enough space to list all of the taxa present at a given site, the list is continued on the line below, within square brackets []. Note also that although the Arabian Peninsula formed part of Afro-Arabia into the Early Miocene, the Omani locality of Taqah is included in the Asia column for reasons of space.



Reconstruction of the world's continents during the later Eocene. (After D.E. Savage and D.E. Russell, 1983, *Mammalian Paleofaunas of the World*, Addison-Wesley.) Parallel lines indicate areas with significant fossil mammal assemblages. Numbers indicate major later Eocene and Oligocene sites on the southern continents yielding fossil primates discussed in the text: (1) Shanghuang (China); (2) Wai Lek (Thailand); (3) Pondaung (Burma); (4) Kohat (Pakistan); (5) Thayinini and Taqab (Oman); (6) Fayum (Egypt); (7) Chambi (Tunisia) and Nementcha (Algeria); (8) Adrar Mgorn and Glib Zegdou (Algeria); (9) Salla (Bolivia). By L. Meeker.

molar complex (when known), they are still adapids 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 tarsier is the most likely sister group of anthropoids. While a still broader version of this hypothesis—that extinct relatives of the tarsiers are likely candidates—is supported by many, it seems unlikely that tarsiers themselves would be closer cladistically to anthropoids than their less-radical tarsiiiform relatives. The tarsier lineage per se has always been too advanced anatomically to be the model of an anthropoid stock. The anatomies of the middle ear, postorbital septum, carotid arteries, and reproductive systems of tarsiers and anthropoids share important derived structural details, but these point to a more abstract taxonomic connection, via a group less bizarre adaptively than the tarsier. The unique particulars that could potentially link tarsiers more closely with anthropoids are probably parallelisms. For example, the postorbital wall of tarsiers most likely arose in relation to their fantastically large eyeballs, which is not the case in anthropoids, who have relatively small eyes. Hence, they are not uniquely derived features of phylogenetic value.

A third hypothesis (considered the most plausible by a majority of current researchers) is that anthropoids arose during the Eocene from a subgroup of omomyid primates that was widely distributed across North America and Eurasia. Omomyids are generally accepted as being closely related to tarsiers (together they are called tarsiiiforms), and omomyids are well represented in the fossil record by many species, but the collections consist mostly of teeth and jaws. *Ourayia uintensis*, a form from the Late Eocene of Utah, is classified as an omomyid tarsiiiform, but its dental anatomy

may be a good model for the protoanthropoid pattern, as E.L. 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 novelties, the skulls of such protoanthropoids would be more telling. The known skulls of omomyids do, at least, indicate a significant morphological heterogeneity, including patterns that are much more primitive than the expected, tarsierlike departures. New evidence also demonstrates that some omomyids, known informally as necrolemurids, were close relatives of living tarsiers, as early workers had thought, and were also distributed broadly in Laurasia. This makes it all the more likely that another omomyid stock, ancestral to both the platyrrhines and the catarrhines, was widespread and sufficiently primitive to have evolved into the first anthropoids.

Recently, as a result of the discovery of new primate fossils (such as *Eosimias*, *Algeripithecus*, 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 previously unknown group of Eocene protoanthropoids, neither adapid nor omomyid. This “third major radiation” concept implies a more ancient origin for the anthropoids and requires further evaluation of the new fossils. However, it presents some significant difficulties. For example, it has yet to be clearly established that any number of the fossils motivating this hypothesis are definitely anthropoid rather than tarsiiiform. One of the fossils in question, *Eosimias*, shows an extraordinary series of derived resemblances to tarsiers, and it is more likely to turn out to be a basal tarsiioid instead of an ancestral anthropoid. If these fossils are indeed tarsiiiforms, this concept simply restates the omomyid-anthropoid hypothesis 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 Oligocene Fayum deposits of Egypt (the first platyrrhines are too fragmentary to be of much help and, moreover, are later in time); (2) the Oligopithecidae, especially *Catopithecus* 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 tarsiiiforms (omomyids) that may represent a “basal stock” for anthropoids.

Propliopithecus presents a suite of generalized anthropoid features, such as fusion of the mandibular symphysis and the frontal bones in the midline, full postorbital closure, spatulate, nearly vertical incisors, strongly expressed canine dimorphism, and lower molars with relatively flat crowns (trigonid and talonid of even height). Within Anthropoidea, the propliopithecids are clearly catarrhines, with such diagnostic dental features as loss of P₂, well-developed distal midline hypoconulids on lower molars, and general molar structure. But these derived states are combined with conservative anthropoid (platyrrhine-

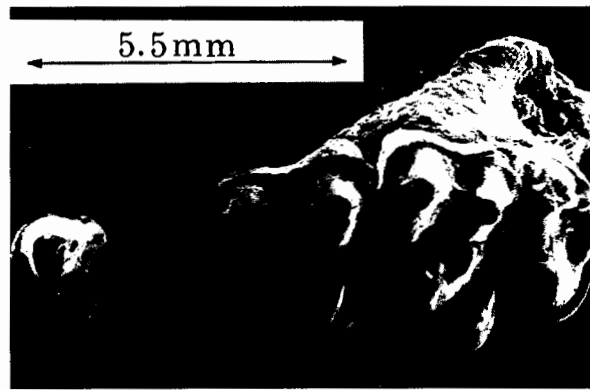
like) conditions, such as a ringlike ectotympanic (external ear opening) and several postcranial features.

The better-known parapithecids (*Parapithecus* and *Apidium*, especially) share the same typical anthropoid conditions as the propliopithecids. These are combined, however, with states more conservative than in catarrhines, such as a somewhat smaller hypoconulid and the retention of P_2 , along with uniquely derived dental conditions (central cusp on upper premolars, tendency to extra cusps on molars, loss of lower incisors in some forms) and several postcranial states more “primitive” than those found in either platyrrhines or catarrhines. On that basis, parapithecids are now placed by most authors as the sister-taxon of all later anthropoids, thus among the most ancient *and* conservative members of the hyporder. It is with the parapithecids that other fossil groups putatively considered anthropoids must be compared.

From latest Eocene horizons in the Fayum come two genera that have also been placed within the Anthropoidea by many, but not all, researchers. *Catopithecus* 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 show full closure, as expected in an anthropoid. Moreover, the upper incisors seem to be at least somewhat spatulate. But the mandibular symphysis appears to be unfused, and the molars are not anthropoidlike: The lowers have relatively high and long trigonids and a generally elongate shape more commonly found in lower primates; the upper molars also are less squared-up than in most anthropoids, with a small and low hypocone; premolars also do not look like those of anthropoids. *Catopithecus* shares some aspects of P_4 and molar shape (proximity of hypoconulid and entoconid, hypocone development) and lack of P_2 with *Oligopithecus*, which also has a P_3 with a large surface for honing, or sharpening, the upper canine, as do many catarrhines. Some authors place these forms close to propliopithecids (two premolars, with honing on the front one), while others think the conservative molars place them evolutionarily “below” the three-premolar parapithecids. Either molar shape or (more likely) premolar pattern must thus have evolved at least twice, in catarrhines and in some early anthropoids. Here the oligopithecids are considered less derived than the parapithecids, but still early anthropoids.

Proteopithecus, a contemporary of *Catopithecus*, was thought to be closely related but has since been distanced, as it preserves three premolars; it might provide a link of sorts between oligopithecids and less-derived parapithecids (see below). However, its molar morphology is exceedingly primitive, resembling tarsiiforms and other early euprimates, and it is likely not an anthropoid. *Catopithecus* and *Oligopithecus* may be late-surviving members of a true protoanthropoid stock, but they are too 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 in stages, as is often the case in evolution.

About a dozen genera of less well known fossil primates have been touted in the 1990s as protoanthropoids. *Algeri-*



Occlusal view of P_4 - M_2 of *Proteopithecus sylviae* from Fayum Quarry L-41. Courtesy of Elwyn L. Simons.

pithecus and *Tabelia* are small forms whose isolated teeth have low rounded cusps like those of the parapithecoid anthropoid *Apidium* and the omomyid *Microchoerus*; both of the former were discovered at the Middle Eocene site of Glib Zegdou (Algeria). Although originally suggested as close to propliopithecids, they now both appear to be provisionally referable to the Parapithecidae, as is *Biretia* from Bir el Ater (Algeria). The 42–36 Ma age of these forms significantly increases the time range of parapithecids, known in the Fayum from ca. 35–33 Ma. Slightly older (46–45 Ma?) are a lower jaw named *Djebelemur* and several isolated teeth perhaps representing other species from Chambi (Morocco). Some of these may be cercamoniine or similar adapiforms while the one upper molar is similar to *Algeripithecus* but even smaller. Two genera from the Early Oligocene of Oman (*Shizarodon* and *Omanodon*) were originally and probably correctly described as adapiforms, but they have also been mentioned as possible anthropoids, for which there is little evidence. The most ancient North African primate is *Altiarlasius*, from the Late Paleocene (ca. 58–55 Ma) of Adrar Mgorn 1 (Algeria). About a dozen isolated teeth of this genus reveal a conservative morphology: The hypocone is lacking on the upper molars although a cingulum extends entirely around the lingual edge, and the lower molar trigonid is large and, especially, tall compared to the talonid; however, the cusps are bunodont, as in the previous taxa. *Altiarlasius* is surely not an anthropoid, or probably even a protoanthropoid, and is best considered a euprimate of uncertain affinity. Nonetheless, it has some similarities to oligopithecids, which (if derived homologies) may indicate a source for that group.

In eastern Asia, the Late Eocene (ca. 40–39 Ma) Pondaung fauna of Burma yielded two primates early in the twentieth century, *Pondaungia* and *Amphipithecus*. Both were poorly known until the 1980s, when a few additional jaws were recovered. Each has been called an adapiform or an early anthropoid, but most authors accept the former designation for both. Of similar age in China are *Hoanghoni* and *Rencunius*, both noted above as probable cercamoniine adapiforms. The contemporaneous *Wailekia* from Thailand, although described as a possible oligopithecoid, probably belongs with the same group. The most intriguing new Asian

primate is *Eosimias*, known from two Middle Eocene localities in China, one the same age as *Hoanghoni*, the other slightly older (ca. 46–45 Ma). Most of the other Asian forms are moderately large, but *Eosimias* is tiny, comparable to *Algeripithecus*, and slightly larger than *Catopithecus*. The incisors and the canine of *Eosimias* are relatively vertical and broadly similar to those of some early anthropoids.

This condition and a selection of cheek-tooth features has led to some researchers suggesting that *Eosimias* is a basal anthropoid, representing an ancient protoanthropoid ancestry separate from both adapiforms and omomyids (see above). In some ways, this is analogous to the suggestion that perhaps *Altiatlasius* and especially the early ?parapithecids represented an equivalent stock in North Africa. But the morphology of these two putative protoanthropoid groups differs strongly, so only one (at most) could be reflective of actual anthropoid ancestry. In fact, the cheek teeth of *Eosimias* (especially the very tall trigonids and the strongly developed trigonid crests), and the tarsiiformlike postcrania known from the same site and assigned to this genus, suggest that it is better understood as an omomyid relative. Its exact placement is unclear within that complex, but, stripping away the tarsierlike features, *Eosimias* confirms a broadly 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 protoanthropoids, the next question to examine is paleogeographic: How did early anthropoids disperse across the Paleogene world?

Origins and Evolution: Geography

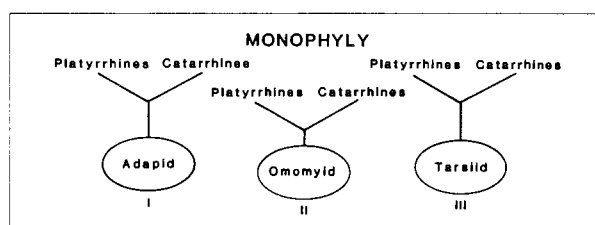
Today, of course, the two main anthropoid groups, Platyrrhini and Catarrhini, occur in the geographically disjunct regions of the neotropics and the Old World, respectively. Platyrrhines have apparently always been restricted to the New World, while the earliest definite anthropoids are now seen to be (northern) African—only one possible tooth is known from an Oligocene site in Angola. There are, thus, two separate but related questions to ponder: How and when did the protoanthropoids reach Africa, and how did the proplatyrrhines reach South America? Both were island continents in the Paleogene, with mainly distinctive faunas.

When the principles of plate tectonics and continental drift were first applied to primates during the mid-1960s, it was briefly argued that the ancestral stock of platyrrhines and catarrhines occupied a single great southern landmass that later rifted apart (as the South Atlantic Ocean grew), expanded to the north, and finally divided into South America and Africa during the early Cretaceous (ca. 130–110 Ma). Formative platyrrhines were thus passively separated from catarrhine forerunners, without crossing an oceanic water gap. This model led to the idea that the parapithecid primates of the Fayum Oligocene were direct platyrrhine ancestors, a notion that has been generally rejected on anatomic grounds. The dating of this event and the paleopositions of continents would also require, if this hypothesis were true, that anthropoid primates were in existence more than 30 Myr before the very first primates are documented in the fossil record.

In the face of counterevidence, modifications to this theory have been proposed. One postulates that tectonic mechanisms produced a system of east-west oceanic ridges or islands within the Atlantic. Nearly all of these are now submerged, but they could have been footholds for primates dispersing across the ocean. This stepping-stone hypothesis was also popular a century before continental drift was an established fact. Combined with floating on rafts of natural vegetation between islands, this idea is prominent in most late-twentieth-century views of platyrrhine origins. One series of problems relating to any oceanic raft-crossing refers to the dangers of exposure, lack of fresh water and food—*Microcebus*-like hibernation is unlikely in an early anthropoid. Moreover, neither the Fayum parapithecids nor, as some have suggested, the propliopithecids are morphologically reasonable as ancestors for platyrrhines. However, if the parapithecids 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 proplatyrrhine. A global recession of sea level, such as the one that occurred in the Late Eocene, might have narrowed the Atlantic gap sufficiently to permit a crossing.

A different idea proposes that an ancestral stock of omomyid-derived protoanthropoids occupied an assembly of northern continents, Laurasia, where Early Cenozoic primates were flourishing; contact between the Eastern and the Western hemispheres was possible at intervals across the Bering region. Spurred by a cooling of the Northern Hemisphere and the expansion 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 rare protoanthropoids, who found their way across the water barriers to reach the island continents of Africa and (later) South America during different regression episodes of low water. Passage into South America seems to have been the more remarkable one, for it may have involved few other mammals. The hystricomorph rodents, relatives of the modern porcupines, may have been the primates' only traveling companions. In fact, it is their geographic association that led such researchers as R.I. Hoffstetter to propose an African origin for platyrrhines in the first place: Both hystricomorphs and platyrrhines may have their closest living relatives in Africa.

Some would argue that possible East Asian (*Eosimias*) and North African (*Djebelemur*, *Algeripithecus*) protoanthropoids are of comparable Middle Eocene age, unless *Altiatlasius* is, indeed, related to this group. In the past, models of Asian ancestry for Fayum anthropoids depended upon interpretations of *Pondaungia* and *Amphipithecus*, but the proposed Early Eocene pathway around the southern margin of an Asia that had not yet collided with India is still plausible. If that collision occurred in the early to mid-Eocene, migration could even have proceeded across the contact zone at some point. What is most important to realize is that without acceptable morphological relatives (sister-taxa) in place, no paleozoogeographical hypothesis is worth formulating: It would be nothing but speculation, no matter how good the pathway.



Three hypotheses of the ancestral stock from which anthropoids arose monophyletically. Courtesy of Alfred L. Rosenberger.

Macroevolutionary Patterns in Catarrhines and Platyrrhines

To comprehend and compare the evolutionary histories of the major divisions of the anthropoids, we will need many more fossils documenting changes in the taxonomic diversity, adaptations, and geographical distributions of the platyrrhines 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 Salla, 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 macroevolutionary histories of platyrrhines 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, all 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 cercopithecoïd radiation is fascinatingly simple; there is little variety other than in size and size-related features. The apes, on the other hand, are fairly diverse anatomically, given that they include a small number of taxa.

The New World monkeys present a contrasting picture. Abundant grasslands appeared in South America during the Cenozoic, but platyrrhines 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 savannahs supported large populations of herbivores, as in Africa and Asia where cercopithecoïds eventually flourished. Perhaps the larger catarrhines were more formidable competitors vis-à-vis other

mammals than the platyrrhines; or maybe the grassland flora were quite different in the Old and the New worlds.

Rather than invade such an ecological terrain, platyrrhines flourished among the trees by finely dividing their microhabitats. 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 platyrrhines radiated at the small end of the anthropoid body-size spectrum. This enabled some of them 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, the pitheciines. The second is the insectivore-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 smallest marmosets.

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

To properly evaluate this hypothesis, we need good biostratigraphic information over geological time, which is severely lacking, especially for the platyrrhines. In looking at the moderns and the fossils, however, it appears that generic lineages have a much longer duration in the New World. Among all of the Old World catarrhines, the macaques and oranges 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. Congeners of *Pongo* go back only as far as the Pleistocene, but the craniofacial morphology that marks it as a generic entity is well developed in late *Sivapithecus* at 9 Ma, and these are preceded by dento-gnathic remains of probable congeners older than 12 Ma. In the Old World, these examples are the only two cases of anagenetic/taxonomic 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 Colombian species classified either in the same genus or as *Neosaimiri*, at 14–12 Ma, to *Dolichocebus*, at ca. 21–19 Ma. The recently discovered *Chilecebus*, which may, in fact, be the same as *Dolichocebus*, is dated at 20 Ma and adds new evidence of a *Saimiri*-related stock. Equivalent in age to *Neosaimiri* is *Aotus dindensis*, the first recognized example of a living primate genus to occur deep in the fossil record. *Aotus* is also closely related to, if not a descendant of, the fossil genus *Tremacebus*, 21–19 Ma. *Alouatta* is probably a descendant, and at least a sister genus, of *Stirtonia*, at 14–12 Ma. In fact, it is difficult to distinguish

the latter two at the generic level. Other fossils, such as *Soriacebus ameghinorum*, 18–16 Ma, and *Laurentiana annectens*, *Cebupithecia sarmientoi*, and *Mohanamico herskovitzi*, 14–12 Ma, indicate that major higher taxa such as subfamilies and tribes of platyrrhines also had remote origins.

See also Adapidae; Altiatlasius; Americas; Asia, Eastern and Southern; Aelidae; Branisellinae; Catarrhini; Cebidae; Cercopithecoidea; Diet; Eosimiidae; Haplorhini; Hominoidea; Oligopithecoidea; Omomyidae; Paleobiogeography; Parapithecoidea; Pitheciinae; Plate Tectonics; Platyrrhini; Propithecidae; Skull; Tarsiiformes; Tarsiioidea; Teeth. [A.L.R., E.D.]

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