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Warren G. Kinzey

Editor



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About the Editor

The late **Warren G. Kinzey** (1935–1994) was head of the anthropology department at City College of the City University of New York; he also taught at the CUNY Graduate Center and the CUNY Medical School. His research and field studies on the primates of the Peruvian Amazon focused on the relationship between diet and distinctive tooth wear patterns. Among his earlier writings were an edited volume, *Evolution of Human Behavior: Primate Models*, and numerous contributions to professional journals in anthropology and primatology.

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Platyrrhines, Catarrhines, and the Fossil Record

JOHN G. FLEAGLE and RICHARD F. KAY

Introduction

With 16 genera, over 70 species, and up to 16 sympatric species, living platyrrhines comprise a taxonomically and adaptively diverse radiation. Considering the extensive living radiation in the Neotropics today and the relatively good fossil record for other South American mammals, the fossil record of New World monkeys is relatively poor. Until recently, a large shoe box could contain the primate fossils from all of South America and the Caribbean from the last 30 million years. However, in the past two decades the platyrrhine fossil record has been expanding rapidly and provides a broad overview and many tantalizing hints about the evolutionary history of the group. In this review, we will examine the platyrrhine fossil record, discuss the clues it provides about the geographic, phylogenetic, and adaptive history of the group, and outline some of the major unresolved issues in platyrrhine evolution. For convenience, fossil platyrrhines are divided into four groups on the basis of age and geography: (1) the earliest platyrrhine fossils from a single late Oligocene locality in Bolivia; (2) several difficult to interpret genera from the early and middle Miocene of southern Argentina and Chile; (3) an array of relatively modern genera from the late Miocene of Colombia; and (4) a number of unusual species from Pleistocene or Recent deposits in the Caribbean and Brazil (Figures 1.1 and 1.2).

The Earliest Platyrrhines

The earliest platyrrhine fossils are *Branisella* and *Szalatavus*, all specimens of which come from a single stratigraphic level of late Oligocene (Deseadan Land Mammal Age) rocks near the village of Salla, Bolivia:



Figure 1.1. Map showing the location and age of sites yielding fossil platyrrhines.

Today this locality is more than 13,000 feet above sea level, but at the time of deposition was probably at around 3,000 feet. *Branisella* is a small monkey, the size of an owl monkey. The low, rounded cusps of the molars suggest a frugivorous diet and the small P2 and the shape of the mandible suggest a short-faced monkey. No clear indications of a relationship of *Branisella* to any particular group of later platyrrhines have been demonstrated.

The possible presence of a second monkey of similar size named *Szalatavus* has been proposed recently by Rosenberger and colleagues (Rosenberger et al., 1991). Recovery of many new specimens of monkeys from Salla in the past 3 years by Japanese, American, and Bolivian scientists suggest *Branisella* and *Szalatavus* may be the same species (Kay and

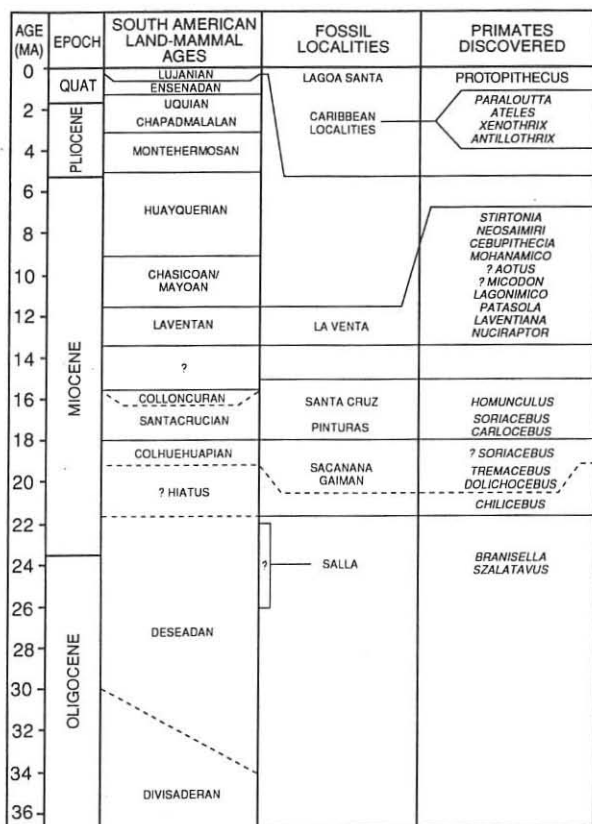


Figure 1.2. The geochronology of fossil platyrrhines.

Williams, 1995). Moreover, the recovery of a 32-million-year-old Chilean rodent (another immigrant element of the South American biota frequently linked with primates as having entered South America from Africa in the middle Cenozoic) suggests platyrrhines may have a longer undocumented history in South America than presently documented (Wyss et al., 1993).

The Patagonian Platyrrhines

In the early and middle Miocene of southern Argentina, informally known as Patagonia, there were over a half dozen genera and species of platyrrhines—part of a rich fauna dominated by rodents, endemic ungulates, sloths, and marsupials. These monkeys are now known from hundreds of fossils, mostly isolated dental and postcranial remains.

However, the phyletic relationships of these fossil monkeys to particular living subfamilies are the subject of considerable debate.

Dolichocebus gaimanensis is from deposits of the Colhuehuapian Land mammal Age (earliest Miocene) near Gaiman, in Chubut Province, southern Argentina. *Dolichocebus* is a medium-sized platyrrhine (2–3 kg) known from a nearly complete but damaged skull, numerous isolated teeth, and a talus. It has dimorphic canines, three premolars, and upper molars that resemble the same teeth in *Saimiri*, *Callicebus*, or *Aotus*. The molar morphology of *Dolichocebus* suggests a frugivorous diet (Fleagle et al., 1996). The skull of *Dolichocebus* has a narrow, posteriorly widening snout, complete postorbital closure, moderate-size orbits, a very narrow interorbital dimension, and relatively large tooth roots. Rosenberger (1979, 1982) has argued that *Dolichocebus* had an interorbital foramen linking the right and left orbits—an unusual cranial feature found only in *Saimiri* among living primates. The talus of *Dolichocebus* is most similar to that of *Cebus* or *Saimiri*, suggesting either a rapid arboreal quadruped or a leaper.

On the basis of the interorbital foramen and several other aspects of the cranial morphology of *Dolichocebus*, Rosenberger (1979) argued that this genus is the sister group of the living squirrel monkey. However, Hershkovitz argued that the Oligocene monkey is too distinctive in other cranial features, such as the palate shape, and molar root morphology to bear any close relationship to living platyrrhines. Analysis of the isolated teeth found in association with *Dolichocebus* yield a similarly dichotomous picture of the relationships of this genus; it is either closely related to the squirrel monkey, or the sister group of all living platyrrhines (Fleagle and Kay, 1989).

Tremacebus harringtoni is from the Colhuehuapian (early Miocene) locality of Sacanana, also in Chubut, Argentina. It was a smaller (1–2 kg) monkey than *Dolichocebus*. The type specimen and only fossil clearly attributable to this species is a nearly complete but broken skull with a relatively short, broad snout and larger orbits than any diurnal platyrrhines. *Tremacebus* shows greatest cranial similarities to the extant platyrrhines *Callicebus* and *Aotus*. On the basis of the moderately enlarged orbits, Rosenberger (1984) suggested that it is an ancestor of the living owl monkey, and other authorities have noted similarities to *Callicebus*. A difficulty is the lack of any dental evidence—the skull of *Tremacebus* has only tooth roots and a few broken crowns—or postcranial bones.

Chilicebus carrascoensis is a newly described fossil monkey from early Miocene (~20 mya) deposits in the Andes of Chile (Flynn et al., 1995). It was a medium-sized monkey (1200 g) with square upper molars suggesting a frugivorous–folivorous diet.

From slightly younger deposits of the Santacrucian Land Mammal

Age (early–middle Miocene) in Santa Cruz Province, Argentina there are several additional genera and species of fossil platyrrhines. These fossil monkeys come from two main geographic and geologic areas—the slightly older Pinturas Formation (17.5–16.5 mya) in the West and the younger Santa Cruz Formation (16.5–16.0 mya) in the East.

The Pinturas Formation preserved in the western part of southern Argentina in the foothills of the Andes has yielded an abundant fauna of fossil birds, reptiles, and mammals, including two genera and four primate species (Fleagle, 1990; Fleagle et al., 1996). Evidence from the sediments, fossil pollen, fossil birds, and abundant nests of fossil insects indicate that the Pinturas primates lived in a forested habitat in what must have been a time of climatic fluctuations, with periods of relative wetness separated by periods of desiccation (Bown and Lariestra, 1990).

The best known, and most unusual of the Pinturas primates is *Soriacebus*, with two species—the saki-sized *S. ameghinorum* and the tamarin-sized *S. adrianae*. *Soriacebus* has large procumbent styliiform lower incisors that form a continuous arcade with the large canine, a tall P2, tiny posterior premolars, narrow lower molars, and a deep jaw. The upper teeth have large dagger-like canines, broad premolars, and small triangular molars. The facial skeleton is very deep. It was probably frugivorous and may have used its large front teeth for seed predation, as is the case for the Pitheciinae, sakis and uakaries of the Amazon and Orinoco Basins. The few postcranial elements of *Soriacebus* suggest quadrupedal running and leaping habits, with some clinging. The affinities of *Soriacebus* have been debated: some regard it as a basal pitheciine on the basis of the large incisors and the deep mandible (Kinzey, 1992; Rosenberger, 1992). Others suggest these similarities to be the result of adaptive convergence for seed predation (Kay, 1990).

The other fossil platyrrhine from Pinturas is *Carlocebus*, also with two species—the saki-sized *C. intermedius* and the larger *C. carmenensis*. The dentition of *Carlocebus* is more generalized than that of *Soriacebus*, with small vertical incisors, a small canine, and relative larger premolars and molars. As in *Soriacebus*, the mandible is relatively deep. The upper dentition is characterized by very broad premolars and molars (Fleagle, 1990). Dentally, *Carlocebus* appears to have been frugivorous with some folivory. Its dentition is most comparable to that of *Callicebus*, the titi monkey. Postcranial remains of *Carlocebus* suggest arboreal quadrupedal habits (Meldrum, 1993).

Homunculus patagonicus, from the early–middle Miocene (16.5 million years ago) Santa Cruz Formation on the Atlantic coast of southern Argentina, was one of the earliest fossil platyrrhines discovered (Ameghino, 1891), and for many years all fossil platyrrhines were placed in

this genus. It was a medium-size monkey, with the largest individuals probably weighing nearly 3 kg. The dental formula is 2.1.3.3. The lower incisors are narrow and spatulate; the canines are probably sexually dimorphic, and the molars are characterized by relatively small cusps connected by long shearing crests; they have a small, square trigonid and a broader talonid with a prominent cristid obliqua. The mandible is relatively shallow compared with that of the Pinturas primates. *Homunculus* was probably frugivorous and folivorous. The cranium of *Homunculus* has procumbent upper incisors, a relatively short face and a long, gracile brain case with no sagittal crest (Tauber, 1991).

The limb elements resemble those of a callitrichid (Ciochon and Corruccini, 1975), and suggest that *Homunculus* was partly saltatory in its locomotion; however the hindlimb was not particularly long and it seems more likely that *Homunculus* was largely quadrupedal (Meldrum, 1993). In some details of its limbs, such as the great size of the lesser trochanter on the femur, *Homunculus* resembles the early anthropoids from Egypt in what are probably primitive features.

As the name indicates, Ameghino (1891) originally thought *Homunculus* was in the ancestry of humans; it is not. Most later studies have noted either the unique features of the genus or dental similarities to *Aotus*, *Callicebus*, or *Alouatta* (Bluntschli, 1931). In describing a new cranium of *Homunculus*, Tauber (1991) noted many similarities to pitheciines. The similarities in the dentitions of *Homunculus* and *Carlocebus* are striking, and seem to indicate that the two are closely related, whatever their relationship to later primate radiations.

All the Patagonian platyrrhines show unusual combinations of features linking them with what are, today, distinct clades of platyrrhines. In phylogenetic analyses each has been placed with a distinct extant clade (e.g., *Dolichocebus* with *Saimiri*; *Tremacebus* with *Aotus*, *Soriacebus* with pitheciines) or viewed as outgroups to all modern subfamilies. There are several possible explanations for this phenomenon, which are not mutually exclusive. In an "ecological vicar model" the Patagonian primates are viewed as a geographically isolated radiation of early platyrrhines that is collateral to the evolution of all extant platyrrhines. This hypothesis is compatible with both their morphological distinctiveness and geographic origin near the tip of South America. Patagonia has a long history as a separate biogeographic area within South America containing a distinct flora and invertebrate fauna. An alternative hypothesis asserts that the living subfamilies of platyrrhines diverged early in platyrrhine evolution to fill many of the ecological niches that they occupy today, and that Patagonian Miocene forms are primitive representatives of those clades. In this latter view, the unusual combination of features reflects the fact that many of these fossil taxa are very near the

initial split of modern clades, before most acquired the larger suite of features that characterizes their living members. This hypothesis is consistent with their age. There is no doubt that part of our inability to clearly resolve the phylogenetic position of these monkeys is that we lack a clear understanding of the polarity of the features characterizing extant platyrrhines—which features are primitive retentions and which are derived specializations in different groups. However, neither of these hypotheses can be adequately tested without similar-aged primates from elsewhere in the continent.

A More Modern Community

The oldest fossil platyrrhines from more tropical parts of South America come from La Venta in Colombia in deposits approximately 11.5 to 13.5 million years old. Compared with the Patagonian fossil platyrrhines, many of the fossil monkeys from La Venta are strikingly similar to modern platyrrhines and clearly belong in living subfamilies. Comparison of the La Venta fauna with modern South American faunas indicates a wet tropical environment for this region in the late Miocene (Kay and Madden, 1996).

Several taxa from La Venta belong to the Pitheciinae, the sakis and uakaries that today inhabit wet tropical forests. Living pitheciines eat fruits and are capable of opening very tough exocarps to extract nutritious seeds that are unavailable as food for other monkeys. *Cebupithecia sarmiento* was similar in size (2–3 kg) and many aspects of anatomy to living pitheciines, with its stout canines, procumbent incisors, and flat cheek teeth with little cusp relief. Like living pitheciines, *Cebupithecia* probably ate mainly fruit and used its large anterior dentition for opening seeds. The *Cebupithecia* skeleton shows more similarities to the leaping *Pithecia* than to the more quadrupedal sakis such as *Chiropotes*, but retains many skeletal features found in other platyrrhine subfamilies while lacking some shared derived features of living pitheciines (Meldrum and Lemelin, 1991). It is probably very near the origin of the modern pitheciine radiation (Kay, 1990).

A recently described pitheciine, *Nuciraptor*, was similar in body size to *Cebupithecia*. It has procumbent and styliiform lower incisors as in the living taxa, but its canines were less specialized for prying open tough fruits and its cheek teeth suggest more soft fruit in its diet (Meldrum and Kay, 1996).

Mohanamico hershkovitzi is a small (1 kg) fossil monkey that is known from a single mandible (Luchterhand et al., 1986). It has been placed near the base of the evolutionary radiation of the pitheciines, certainly

before *Cebupithecia* or *Nuciraptor*, on the basis of its large lateral incisor and the structure of the canine and anterior premolar. It was probably frugivorous.

Setoguchi and Rosenberger (1987) described a new species of owl monkey, *Aotus dindensis*, from La Venta. A small facial fragment suggests that the Miocene species could have had large orbits similar to those of the nocturnal owl monkey (but see Kay, 1990). There has been some debate about the similarities between *Aotus dindensis* and *Mohanamico*, illustrating the conservative nature of mandibular dentition in small-sized frugivorous platyrrhines.

Stirtonia, the largest (6 kg) of the La Venta primates, is known from two species, a larger, older species, *Stirtonia victoriae*, and a younger smaller one, *S. tatacoensis*. The latter has many dental similarities in its upper and lower dentition to the living howling monkey (*Alouatta*), including long lower molars with relatively small trigonids and very large upper molars with well-developed shearing crests and styles. It was a folivore. Isolated molars that resemble *Stirtonia* (and *Alouatta*) also have been recovered from late Miocene deposits at Rio Acre in western Brazil (Kay and Frailey, 1993).

Neosaimiri fieldsi is very similar in size and morphology to the living squirrel monkey. It differs most clearly in incisor proportions and in having less developed molar shearing, suggesting it was possibly more frugivorous and less insectivorous than *Saimiri*. An isolated humerus from the same deposits is indistinguishable from the same bone in *Saimiri*. Recently named *Laventiana annectens* (Rosenberger et al., 1991) is very similar to *Neosaimiri*, differing only in the variable development of a postentoconid notch, an unusual character not seen in any living platyrrhines. Many others now place *L. annectens* in the same genus or even species with *Neosaimiri fieldsi* (Kay and Meldrum, 1996; Takai, 1994).

One of the most obvious gaps in the platyrrhine fossil record for many years has been the absence of any evidence for the ancestry of callitrichines—marmosets, tamarins, and *Callimico*. In recent decades and years several putative fossil callitrichines have been described, each with different morphologies and different implications for the origin of the group. One thing most paleontologists agree about is a link between callitrichines and squirrel monkeys (e.g., Kay, 1994; Kay and Meldrum, 1996; Rosenberger, 1980; Rosenberger et al., 1991; Takai, 1994). In this regard, two newly described La Venta species are particularly important.

Patasola magdalena is a new species from La Venta that is slightly smaller than the living squirrel monkey. It shares most dental features with *Callimico*, *Saimiri*, and *Neosaimiri*, but the deciduous premolars bear a closer resemblance to some callitrichines such as *Saguinus* or *Leon-*

topithecus. On the basis of the latter synapomorphies, *Patasola* is identified by its describers as a callitrichine, more closely related to marmosets and tamarins than is *Callimico* (Kay and Meldrum, 1996).

Lagonimico conclucatus is another new species from La Venta. It was roughly the size of an owl monkey and has been described by Kay (1994) as a giant tamarin. Based on a different set of features, mainly upper molar shape, he placed it with marmosets and tamarins. While the phyletic position of *Lagonimico* and *Patasola* is similar with respect to living callitrichines, both are placed between marmosets and tamarins on the one hand and *Callimico* on the other, their morphology is very different. *Patasola* much more closely resembles squirrel monkeys and *Callimico*, whereas *Lagonimico* far more closely resembles tamarins. The absence of upper molar hypocones in a monkey the size of *Lagonimico* suggests that acquisition of the distinctive marmoset and tamarin molar morphology did not necessarily evolve in conjunction with small size.

Micodon kiotensis is a poorly known species from La Venta that is based on three small, isolated teeth (Setoguchi and Rosenberger, 1985). It has been described as a fossil marmoset, primarily on the basis of size. The validity of the species has been challenged, in particular, whether the collection of three teeth even belong to the same taxon, let alone whether it has affinities with callitrichines.

The presence of several putative fossil callitrichines at La Venta is exciting, but clearly demands further analysis, since each offers a somewhat different picture of the origin and early evolution of the group. It is almost certain that the origin of this group involved a rather bushy phylogeny as evidenced by the parallel and convergent features found in marmosets, tamarins, and *Callimico*. The fossils reinforce this view. Analyses of these fossils also appear to support the view that callitrichines are the sister taxon of the squirrel monkey, *Saimiri*, as suggested by Rosenberger (1981, 1992). However, we are still far from understanding many details of the origin and radiation of these very successful platyrrhines.

Despite the debated taxa (*Mohanamico*, *Micodon*) and various contradictions in the proposed phylogenetic relationships among some of the platyrrhines, the fauna from La Venta indicates that the major groups of extant platyrrhines were clearly differentiated and present in central Colombia by 13.5 million years ago. Among all this diversity, the absence of any putative relatives of either *Cebus* or *Callicebus*, two of the most widespread modern genera, and the absence of any spider or woolly monkeys are notable. The modernness of the La Venta fauna may reflect its relatively late age, the geographic location of La Venta closer than other fossil localities to the Amazon Basin, where living New

World monkeys are most abundant, or, most probably, both of these relationships. In the absence of other faunas of comparable age from elsewhere, these issues cannot be answered.

Aside from a few isolated teeth from the latest Miocene in the upper reaches of the Amazon (Kay and Frailey, 1993), and some remains from latest Pleistocene or Recent cave faunas in Brazil described below, the Laventa fauna is the youngest fossil deposit yielding platyrrhines from all of Central and South America. Thus, while the pre-Pleistocene fossil record of South America provides documentation of the major diversification of some subfamilies and major clades, we have very little knowledge of platyrrhine species diversity or biogeography in the past, since fossil platyrrhines of different ages tend to be from different geographic areas.

Pleistocene Platyrrhines

The lack of any clear understanding about geographic and temporal patterns of platyrrhine diversity is underscored by the fact that the youngest fossil platyrrhines, those from Pleistocene and Recent caves of the Caribbean and Brazil, are among the most unusual. One of the earliest fossil primates ever recovered and recognized to be unlike living forms was found in a Brazilian cave in the 1830s by the Danish naturalist Peter Wilhelm Lund. In 1836, alongside remains of *Homo*, *Callithrix*, *Cebus*, and *Alouatta*, Lund found a proximal femur and distal humerus of an ateline-like primate of Latest Pleistocene or Recent age (8,000–12,000 years old) that was nearly 50% larger than the same bones in the largest living platyrrhines and probably had a body weight nearly two and a half times as large (Figure 1.3). The distinctiveness of this fossil, *Protopithecus brasiliensis*, which more than doubles the known body size of New World monkeys, has only recently been appreciated (Hartwig, 1995). Recent discoveries of additional fossil monkeys from Pleistocene caves in Brazil (Cartelle, 1992) promise to reveal an even greater unsuspected diversity of New World monkeys in the very recent past.

Xenothrix mcgori is a latest Pleistocene or Recent primate from the island of Jamaica, where there are no extant nonhuman primates. It is a medium-sized platyrrhine (2 kg) known from postcranial material and a mandible with a dental formula of 2.1.3.2 resembling that of marmosets and tamarins. However, the molars are very different in having large bulbous cusps, and a second molar larger than the first. *Xenothrix* was probably a frugivorous species, or may have fed on insect larvae, like the aye-aye of Madagascar. Postcranial remains attributed to *Xenothrix* evidence an unusual type of slow quadrupedal locomotion that has no counterpart among living platyrrhines (MacPhee and Fleagle, 1991).

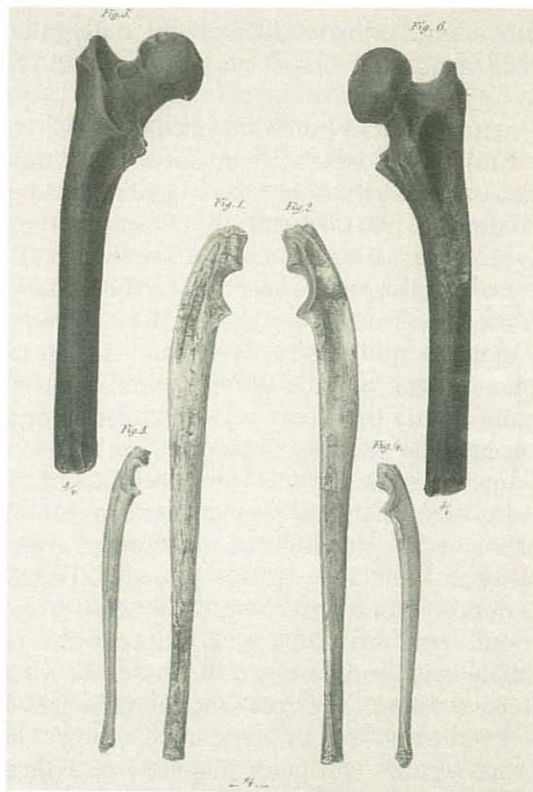


Figure 1.3. Primate remains collected in 1836 by Lund from the Pleistocene/Recent cave of Lagoa Santa in Brazil, with a modern titi monkey for comparison. From top to bottom, *Protopithecus brasiliensis* (fossil), *Alouatta* sp. (fossil), *Callicebus personatus*. Courtesy of Walter Hartwig.

In recent years, it has become clear that *Xenothrix* is just one of several platyrrhines that lived in the Caribbean prior to the first appearance of humans several thousand years ago. Other fragmentary platyrrhine fossils have been found in two other Jamaican caves. Both specimens are proximal femora and are quite different from *Xenothrix*, suggesting at least three primates on that island (Ford, 1990).

Numerous, largely undescribed, dental specimens and a tibia from Pleistocene and Recent cave deposits in Haiti and the Dominican Republic have been recently assigned to the species *Antillothrix bernensis* (MacPhee et al., 1995). The dental remains, which may be as much as 100,000

years old, indicate a large primate (2–3 kg) with a dentition reminiscent of living *Callicebus* or possible *Cebus*, suggesting a diet of hard fruit or seeds.

New Pleistocene platyrrhines from Cuba include a well-preserved skull, a mandible, and numerous isolated teeth of a very large platyrrhine, *Paralouatta varonai*, originally thought to be related to the howling monkey (Rivero and Arredondo, 1991). More recent studies have shown many differences between *Paralouatta* and *Alouatta*. Another fossil primate from Cuba "*Montanea anthropomorphus*" appears to be the remains of a modern spider monkey, possibly brought to the island by native peoples.

The recovery of many, quite distinctive primate fossils from the Caribbean, often from sites that predate human colonization of the islands, demonstrates quite clearly that there was an endemic primate fauna in the Caribbean until quite recently. Interestingly, island biogeographic studies of the larger islands "predict" the presence of more small- to medium-sized frugivores than had previously been described. This unveiling of an extensive Caribbean fauna raises even larger issues about the origin and ultimate extinction of these primates. The simplest explanation of the Caribbean fauna is over-water dispersal from nearby parts of Central and South America; Cuba is very close to the Yucatan Peninsula, where primates are found today and Venezuela where there is an even more extensive fauna. The fact that the primates on Cuba and Hispaniola have been suggested by some to be closely related to *Ateles*, *Alouatta*, and *Cebus* accords well with this view of a simple dispersal, perhaps relatively recently. However, detailed study of the Antillean primates has demonstrated some very distinctive monkeys—especially *Xenothrix*, but also *Paralouatta*, and *Antillothrix bernensis*. It seems more likely that the Caribbean primate may have been separated from other platyrrhines for many millions of years. In the absence of a better knowledge of platyrrhines from elsewhere, it is virtually impossible to calibrate the origin of the Caribbean platyrrhines, but a recent report of a Miocene talus from Cuba that resembles the *Dolichocebus* talus from the early Miocene of Argentina accords with a long period of endemism for the Caribbean monkeys (MacPhee and Iturralde-Vinent, 1995).

Summary of Fossil Platyrrhines

The current fossil record of platyrrhine evolution provides a number of insights into the history of New World monkeys as well as the limitations of the current record. Overall, the current record documents three phenomena: (1) an array of distinctive fossil monkeys from the late Oligocene and early Miocene of the southern part of the continent (Boli-

via, Chile, and Argentina) that are unquestionable platyrrhines, but cannot be clearly placed in modern subfamilies; (2) a great diversity of fossil platyrrhines from the middle-to-late Miocene (13.5–11.5 mya) of Colombia that are clearly attributable to extant subfamilies, or even genera; and (3) an increasing number of Pleistocene–Recent fossils from the Caribbean and Brazil that are very distinctive from either modern New World monkeys or the middle–late Miocene fossils. Thus, while the fossil record provides evidence that many aspects of the extant Platyrrhine radiation were present by the later part of the Miocene, it also provides evidence of a much greater diversity of New World monkeys from both earlier and later times in disparate geographic regions, dispelling any simple view that the evolution of New World monkeys has been largely static for the past 20 million years (e.g., Delson and Rosenberger, 1984). Among the outstanding questions begging to be answered are the relationships of the Patagonian and Caribbean primates to the extant radiation, and especially the Pleistocene history of Platyrrhines. Are the early Miocene monkeys from Patagonia “missing links” at the base of the extant (and later Miocene) radiation, or a “dead end” group of early, possibly geographically isolated monkeys, collateral to the modern radiation? Are the extinct monkeys from the Caribbean the remnants of an ancient endemic radiation on those islands or a collection of waif dispersals from the “Neotropical mainland”? How much more diverse were Pleistocene Platyrrhines than those alive today? In many ways the most striking feature of the fossil record of New World monkeys is the fact that it is quite clearly three geographically and temporally separated glimpses into a largely undocumented radiation of primates. To more fully appreciate platyrrhines in a broader evolutionary perspective, and to address the question of the origin of platyrrhines, it is instructive to compare the radiation of Platyrrhines with that of early anthropoids from the Old World.

Early Anthropoid Evolution in the Old World

Since the first decade of this century, most of our knowledge of early anthropoid evolution has come from the Eocene/Oligocene deposits in the Fayum of Egypt (Simons and Rasmussen, 1991). Until most recently, the fossil primates from the Fayum could be rather clearly allocated into one of two families of early anthropoids. Propliopithecids (*Aegyptopithecus* and *Propliopithecus*) are moderate-sized (4–6 kg) fruit and leaf-eating early catarrhines that have the dental formula (2.1.2.3/2.1.2.3) of later Old World monkeys and apes, but retain primitive platyrrhine features in their ear region and most aspects of their postcranial anatomy (Fleagle,

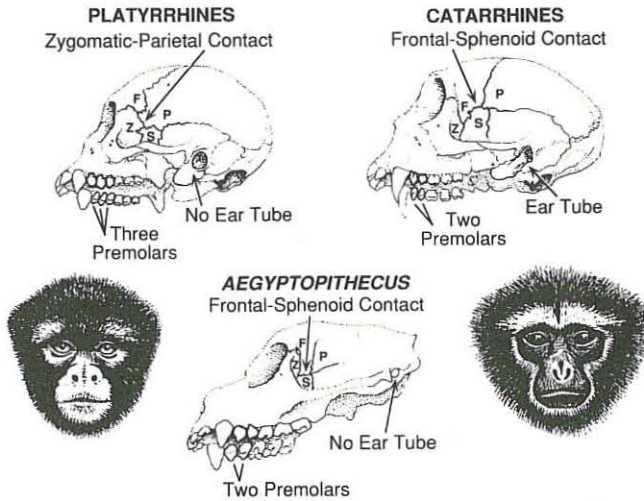


Figure 1.4. Comparison of the cranial features that characterize extant platyrrhines, extant catarrhines, and the early catarrhine *Aegyptopithecus*, showing the intermediate anatomical mosaic in *Aegyptopithecus*.

1988; Figure 1.4). Most authorities recognize them as stem catarrhines that postdate the platyrrhine/catarrhine split, but precede the divergence of hominoids and cercopithecoids (Fleagle and Kay, 1983; Figure 1.5).

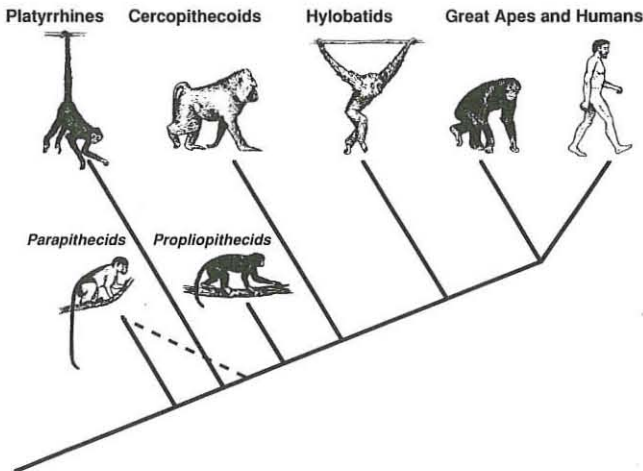


Figure 1.5. A cladogram showing the phyletic relationships of parapithecids and propliopithecids relative to extant anthropoid groups.

The parapithecids, the other family, are a much more primitive group. They are platyrrhine-like in many aspects of their anatomy including their dental formula and many aspects of cranial and dental anatomy, but also show a number of primitive "prosimian" features of the femur and dentition not found in any later anthropoids. Their exact phylogenetic position is less clear, but they probably precede the platyrrhine-catarrhine divergence or, alternately, are the most primitive catarrhines (Fleagle and Kay, 1987; Figure 1.5). Although distinct from all later Old World catarrhines, and in many ways intermediate between living prosimians, platyrrhines, and catarrhines, propliopithecids and parapithecids are nevertheless clearly anthropoid in most aspects of their anatomy (Figure 1.5). They blur the geographic and anatomical distinctions of platyrrhines and catarrhines, but do not stretch the "anatomical space" of anthropoids much beyond its present range.

In the past 5 years our understanding of early anthropoid evolution has changed in two ways: through the discovery of new, more primitive anthropoids from Egypt and from a diversity of early anthropoids from other localities, and, most recently, other continents. Propliopithecids and parapithecids are primarily known from the upper levels of the Jebel Qatrani Formation in the Fayum in deposits that are most probably early Oligocene in age. However, intense work at Quarry L-41 in the lowest, probably late Eocene, deposits of the same formation have yielded a totally different fauna of early anthropoids that greatly expands the diversity of the suborder and has muddled the issue of anthropoid origins (Simons, 1992; Simons and Rasmussen, 1995).

These new primates from the Eocene levels of the Fayum seem to fall into two major groups (Simons et al., 1994; Simons and Rasmussen, 1995). Best known are the oligopithecines, formerly represented only by the poorly known *Oligopithecus*. *Catopithecus*, a slightly smaller genus (1200 g) that resembles *Oligopithecus* in dental anatomy, is known from several complete skulls and various postcranial remains (e.g., Simons, 1990, 1995). These demonstrate that while *Catopithecus* is clearly anthropoid in having a fused frontal bone, postorbital closure, a platyrrhine-like ear region, and a catarrhine-like dental formula (2.1.2.3.), its dentition shows greater morphological similarities to adapid prosimians than to later anthropoids in molar and premolar anatomy (Rasmussen and Simons, 1992; Simons et al., 1994).

The oligopithecines are generally regarded as the lineal ancestors of the propliopithecids, but if so, they indicate that many dental features of platyrrhines, catarrhines, and probably parapithecids were acquired independently (e.g., Kay and Williams, 1994).

The other new Fayum primates show even more unusual features for early anthropoids. On the basis of their possession of three premolars and some striking postcranial similarities to later parapithecids, they have

been placed loosely in the suprfamily parapythecoidea (Simons et al., 1994). *Serapia eoacaena* is a tiny (200 g), generalized parapythecid that also shows some premolar similarities to oligopythecines and later anthropoids. *Arsinoea* is a tiny species with crenulated molars, perhaps related to seed-eating. *Proteopythecus* is yet another tiny anthropoid with extremely broad molars and a jaw that lacked a fused symphysis. Its phylogenetic affinities are unclear, but it shows many dental similarities to the early platyrrhine *Branisella* (Kay and Williams, 1995). Today there are no marmoset-sized anthropoids in the Old World, and it is generally thought that the tiny marmosets of the neotropics are secondarily "dwarfed" from much larger ancestors. However, the new Fayum remains suggest that tiny size may have been characteristic of the earliest anthropoids.

In addition to the new material from the Eocene levels of the Fayum, there are numerous other new early anthropoids from other parts of North Africa that present a similar picture (Figure 1.6). These include *Biretia*, a single lower molar from Bir el Ater in Algeria, as well as *Tabelia* and *Algeripythecus* from Glib Zegdou in Algeria (Godinot, 1994). In addition, there are abundant remains of anthropoids similar to those in the Fayum from several localities in Oman. All of these new taxa show dental similarities to later Fayum anthropoids, but are very much smaller. While only preliminary reports of these taxa are available at present, they suggest a very diverse adaptive radiation of anthropoids in the Eocene of Africa that was quite different in both body size and ecological adaptations from the anthropoids of the early Oligocene or today.

Most recently, Beard and colleagues (1994, 1996) described a new primate fauna, including adapid, omomyid, and tarsiid prosimians, as well as purported early anthropoids from the Eocene site of Shanghaung in China (Figure 1.5). The proposed anthropoid, *Eosimias*, is another tiny primate with primitive, tarsier-like molars and relatively large, possibly sexually dimorphic canines. They also noted dental similarities to platyrrhines.

EARLY ANTHROPOID FOSSIL LOCALITIES

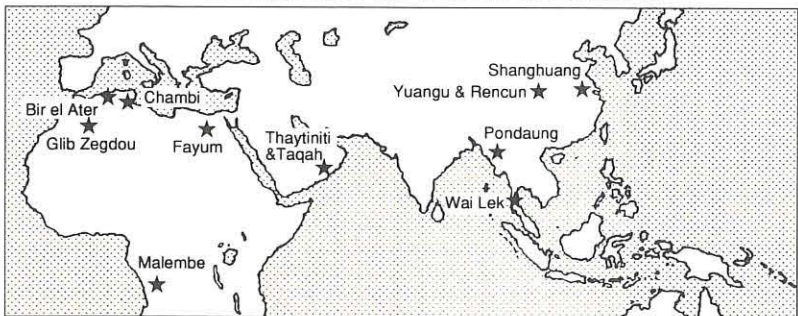


Figure 1.6. A map showing localities yielding fossil anthropoids or putative anthropoids from the Eocene and early Oligocene of Africa and Asia.

Overall, the most striking characteristics of the early anthropoids from the Old World are the many differences from either extant prosimians or extant catarrhines, and their persistent similarity to platyrrhines, in most nondenatal aspects of their anatomy (e.g., Fleagle and Kay, 1994). The anatomical similarities between Egyptian Oligocene anthropoids and platyrrhines were first noticed many years ago (e.g., Simons, 1967b; Fleagle et al., 1975) and this gave rise to the view that propliopithecids and parapithecids preceded the divergence of the modern catarrhines groups—Old World monkeys and apes (Fleagle and Kay, 1983; Fleagle, 1986). However, from a platyrrhine perspective, the morphological similarities between early African anthropoids and extant platyrrhines suggest that many aspects of platyrrhine cranial and postcranial anatomy are primitive retentions from an early anthropoid condition.

Platyrrhine Origins

Few topics in primate evolution are subject to more diverse hypotheses and unsatisfactory alternatives than the problem of platyrrhine origins (e.g., Ciochon and Chiarelli, 1980; Hoffstetter, 1980). For most of the Cenozoic Era, South America was an island continent, with its own fauna distinct from that on other continental areas (e.g., Simpson, 1980). Thus, edentates and marsupials were diverse and abundant, the ungulates were astrapotheres, pyrotheres, notoungulates, and litopterns rather than artiodactyls and perissodactyls, and the predators were marsupials and giant birds rather than creodonts and carnivores. Primates first appear in the fossil record of South America in the late Oligocene, with no evidence of the group prior to that time, despite an abundant fossil record of other mammals from the southern part of the continent (e.g., Hoffstetter, 1980; Simpson, 1980; Hartwig, 1994). The problem of platyrrhine origins is both a phylogenetic question and a biogeographical one. What did the last common ancestor of platyrrhines and catarrhines, or the first platyrrhine after the split look like and how did it get to South America? These issues are far from being resolved to everyone's satisfaction. However, the record of early anthropoid evolution in Africa and our present knowledge of primate evolution on other continents can be used to evaluate the alternatives.

The Phylogenetic Origin of Platyrrhines

In the early part of this century, it was generally believed that platyrrhines evolved from some group of North American prosimians; probably the notharctine adapids and catarrhines were evolved (probably independently) from some Old World prosimians (e.g., Gregory, 1922). Thus, the last common ancestor of platyrrhines would not be recognized

structurally as an anthropoid primate. This view still has some adherents, but seems most unlikely for several reasons. Almost all molecular studies indicate that platyrrhines and catarrhines shared a long period of common ancestry separate from any extant group of prosimians (Sarich and Cronin, 1980; Miyamoto and Goodman, 1990). Furthermore, all fossil and extant platyrrhines, all fossil and living catarrhines, and the Oligocene parapithecids of Africa show evidence of extensive postorbital closure, a striking derived feature uniting anthropoids (Cartmill, 1980; Ross, 1994). This feature was surely in the common ancestor of the group. Despite dental and some postcranial similarities shown by various Paleogene fossil prosimians to early anthropoids (Rasmussen, 1990, 1994), none shows any evidence of postorbital closure. Thus, if platyrrhines and catarrhines evolved independently from separate North American and European adapid ancestors, they must have evolved postorbital closure independently—a most unlikely event. It seems much more likely that the last common ancestor of platyrrhines and catarrhines was itself an anthropoid, with postorbital closure (Cartmill, 1980).

Moreover, the discovery that the earliest anthropoids in the Old World (and to a lesser degree the earliest catarrhines) are essentially platyrrhine-like in many aspects of cranial and postcranial morphology suggests that their common features are not parallelisms, but characteristics of the earliest anthropoids. This is also consistent with the platyrrhine fossil record, which suggests that platyrrhines have changed far less during the last 25 million years than have catarrhines (e.g., Delson and Rosenberger, 1984). On the basis of our understanding of both platyrrhine and catarrhine evolution, it seems most likely that the earliest platyrrhine and the last common ancestor of platyrrhines and catarrhines was an animal very much like a small platyrrhine or parapithecoid in both cranial and postcranial anatomy (e.g., Kay, 1980; Cartmill, 1980; Fleagle and Kay, 1987; Ford, 1990).

On the basis of our understanding of paleogeography, it is clear that the immigration of primates to South America must have involved some type of long distance rafting or island hopping across substantial water barriers, regardless of the ultimate source area. Such dispersal is almost certainly rare, but must have taken place if we are to account for the presence of land vertebrates on other islands, such as the Caribbean (e.g., MacPhee and Woods, 1982). North America and South America were separated throughout the Cenozoic until Central America slid into place about 5 million years ago to form the Panama Land Bridge and initiate the Great Faunal Interchange (Stehli and Webb, 1985). Africa and South America have been separated by the South Atlantic Ocean since the middle Cretaceous, well before the first appearance of primates (e.g., Tarling, 1980; Stehli and Webb, 1985). Even though the Atlantic Ocean has been increasing in width for the past 160 million years, the

distances in the Eocene between the west coast of Africa and the eastern coast of South America were not appreciably shorter than they are today (e.g., MacFadden, 1990). There was no obvious bridge to South America during the early Cenozoic; however it is probably significant that the lowest drop in sea level during the past 500 million years appears to have taken place during the early Oligocene, thus appreciably narrowing water barriers (Haq et al., 1987). However, given the isolation of South America and the rarity of immigration from other continents prior to 5 million years ago, our best available evidence for reconstructing the source of platyrrhines is our current understanding of the biogeography of the immigrants themselves.

For many years, paleontologists argued that Primates and most other groups of mammals in South America were immigrants that rafted from North America. Such a scenario is not unreasonable, for many of the early ungulates (e.g., condylarths) that are found in the early Cenozoic of South America have North American relatives. However, the two groups of mammals that first appear in South America in the Oligocene, higher primates and caviamorph rodents, are not known to have ever existed in North America prior to very recent times (Hoffsetter, 1980; Savage and Russell, 1983; Wyss, 1993). Thus, hypothesizing North America as the proximate source area for these groups requires a second unsubstantiated hypothesis that they were, in fact, on that continent, but have not yet been discovered in the fossil record, and that they immigrated to South America at a time when none of the mammalian groups known to have been in North America made the journey. The same is true for postulating any other continent, including Antarctica, as the source for platyrrhine origins. However, primitive anthropoids strikingly similar to platyrrhines, and caviamorph rodents are abundant in the fossil record of Africa 5 to 10 million years prior to their first appearance in South America (Hoffstetter, 1980; Fleagle et al., 1986; Simons and Rasmussen, 1995). Until early anthropoids are discovered on any other continent, Africa must be considered the most likely ultimate and proximate source of origin for platyrrhines (Hoffstetter, 1980; Simons and Kay, 1986; Fleagle and Kay, 1987; Fleagle, 1988; Wyss et al., 1993; Flynn et al., 1995).

Implications for the Study of Platyrrhine Biology

A broad consideration of the fossil record of platyrrhine and early anthropoid evolution raises a number of interesting questions about the modern platyrrhine radiation. Early African anthropoids are, in much of their anatomy, African platyrrhines; or, alternately, many of the characteristics of platyrrhine morphology and ecology seem to be features that characterized all anthropoids 30 million years ago. Attempts

to understand the functional anatomy and reconstruct the habits of these early anthropoids must be based on a knowledge of the extant species with the most similar anatomy, i.e., extant platyrrhines. However, aside from the practical problems of making functional sense of a fossil bone from the Oligocene of Egypt, and the biogeographic questions of how early anthropoids found their way between these two continents, there are some much broader issues raised by the similarities between early Old World anthropoids and living and fossil platyrrhines.

Why have platyrrhines retained the small size, frugivorous, arboreal habits of the Oligocene anthropoids while later catarrhines evolved larger size, more folivory, and terrestriality in several lineages? Are the differences due to environmental differences between the available habitats in South America and the Old World? Certainly the flora and range of habitats are more diverse and the gross geographic area is greater in Africa and Eurasia where catarrhine evolution has taken place than in South America where platyrrhines have evolved. Then too, there are differences in their mammalian competitors and predators. When platyrrhines first appeared in South America, the continent was filled with abundant insectivorous and frugivorous arboreal marsupials and insectivorous and folivorous edentates as well as large terrestrial predaceous birds. In addition, they seem to have arrived either contemporaneously with or slightly after the caviamorph rodents, which rapidly expanded into a very extensive array of arboreal and terrestrial species of all sizes (e.g., Simpson, 1980). In addition, there were no prosimians in the New World. Are the differences due to some intrinsic constraint in the nature of the early anthropoids themselves?

In the Old World, new discoveries from the Eocene of the Fayum have revealed an extraordinary diversity of Eocene early anthropoids, both more generalized and more specialized than the better known parapithecids and propliopithecids known from the Oligocene. According to current interpretations, the parapithecids appear to have gone extinct in the Old World while the propliopithecids gave rise to later catarrhines. On the other hand, the platyrrhines appear to be derived from a parapithecid-like ancestor. Is this just evolutionary serendipity? These are major issues in primatology that can be addressed only through comparative study of platyrrhines and the other major primate radiations using both neontological and paleontological perspectives.

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