

Eocene Adapidae, Paleobiogeography, and the Origin of South American Platyrrhini

6

P. D. GINGERICH

Introduction

The origin of South American platyrrhine monkeys or Ceboidea is among the most interesting problems in primatology. This problem is basically an historical one, and geological evidence has special importance for any solution. Fossil primates, mammalian faunas, and paleogeography have a direct bearing on the origin of South American monkeys. Fortunately, much has been learned in the past twenty years about the fossil record of primate evolution. Several recent discoveries are particularly important for understanding the origin of higher primates. Furthermore, new evidence about climatic history and faunal migration during the early Cenozoic provides an improved background for interpreting the primate fossil record. Much remains to be learned, but the evidence available at present is sufficient to suggest a reasonably detailed hypothesis of ceboid origins.

South American Faunas

Paleocene and Eocene mammalian faunas of South America (Riochican to Mustersan) include a diverse group of Marsupialia, edentates of the order

P. D. GINGERICH • Museum of Paleontology, University of Michigan, Ann Arbor, Michigan 48109.

or suborder Xenarthra, and a variety of ungulates representing the orders Condylarthra, Notoungulata, Litopterna, Trigonostylopoidea, Xenungulata, and Astrapotheria (Patterson and Pascual, 1972). The major Cenozoic faunal events in South America are summarized in Fig. 1.

Marsupials, edentates, condylarths, and a notoungulate are all known from the late Paleocene and early Eocene of North America (Jepsen and Woodburne, 1969; Rose, 1978). Thus some faunal exchange between North

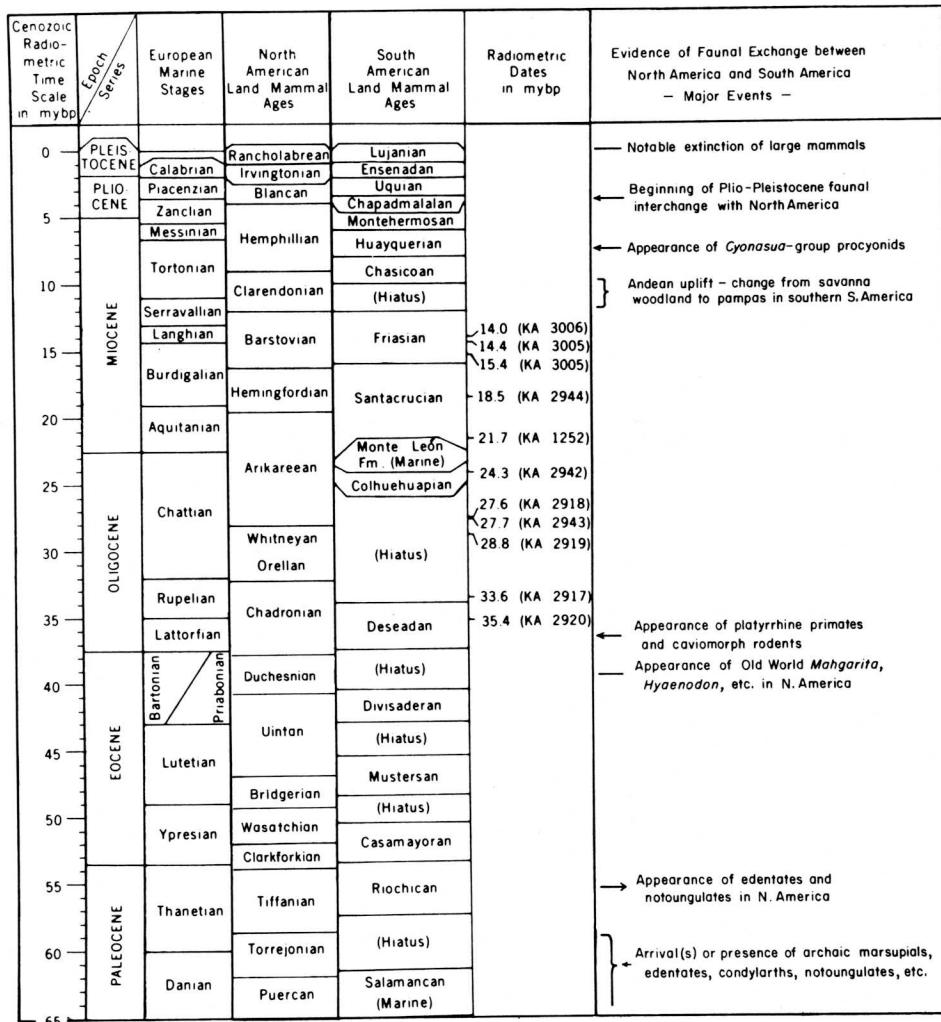


Fig. 1. Faunal succession and radiometric time scale for Cenozoic mammalian evolution in South America compared to sequences in North America and Europe. Major faunal events with a bearing on faunal migrations are indicated in the right-hand column. Data principally from Marshall *et al.* (1977) and Patterson and Pascual (1972), with additions from Wilson and Szalay (1976), Rose (1978), and others.

America and South America must have occurred during the Paleocene, filtered by a discontinuous land connection and/or the intermediate zone of tropical climate. This evidence contradicts statements by some recent authors that Paleocene and Eocene faunal migration between North America and South America was improbable or impossible, based on the Eocene position of South America relative to North America published by Frakes and Kemp (1972). Frakes and Kemp's Eocene reconstruction has been widely cited in discussing the origin of South American primate and rodent faunas, but it was constructed for another purpose and not tested against known faunal distributions before being published. A more reliable reconstruction of continental positions during the Eocene, taken from the recent book by Smith and Briden (1977), is shown in Fig. 4. Here the connection between North America and South America more closely resembles the filtered route suggested by the known distribution of Paleocene and Eocene land mammal faunas.

A major event in the history of South American mammalian faunas was the appearance of both platyrrhine primates and caviomorph rodents in the early Oligocene (Deseadan), dated at about 35–36 million years (m.y.) before present (Marshall *et al.*, 1977). The principal evidence of primates in this fauna is the type specimen of *Branisella boliviana* described by Hoffstetter (1969). Additional remains of primates from the Deseadan of Bolivia are fragmentary and all appear to represent *Branisella* as well. In contrast, the early caviomorph rodents known from the Deseadan are a diverse group including representatives of all five major suborders *Erethizontoidea*, *Chinchilloidea*, *Octodontoidea*, *Cavioidea*, and *Hydrochoeroidea* (Hartenberger, 1975). This diversity suggests that caviomorph rodents began radiating elsewhere before several different lines reached South America or, more probably, that they reached South America in the late Eocene. If primates arrived with rodents as part of the same faunal immigration, then primates too may have entered South America in the late Eocene. The late Eocene in South America, the "Divisaderan," is very poorly known and the Divisadero Largo fauna itself represents a peculiar facies difficult to date or relate to the mainstream of mammalian evolution (Simpson *et al.*, 1962). Thus there is no real evidence that rodents and primates were absent, and there is some slight evidence favoring their entry into South America during the late Eocene. Early and middle Eocene mammalian faunas (Casamayoran and Mustersan) are well known, include abundant microfauna, but lack primates or rodents, and it is therefore very unlikely that primates and rodents entered South America before the late Eocene.

Another filtered interchange occurred in the late Miocene with the appearance of the procyonid *Cyonasua* in South America in the Huayquerian. Subsequently, in the Montehermosan or Chapadmalalan, a land bridge between North America and South America was established through Central America and the great American mammalian interchange began (Webb, 1976). The documented occurrences of faunal interchange between North America and South America in the early Tertiary and again in the late Ter-

tiary and Quaternary, suggests that some limited faunal interchange in the middle Tertiary was at least a possibility.

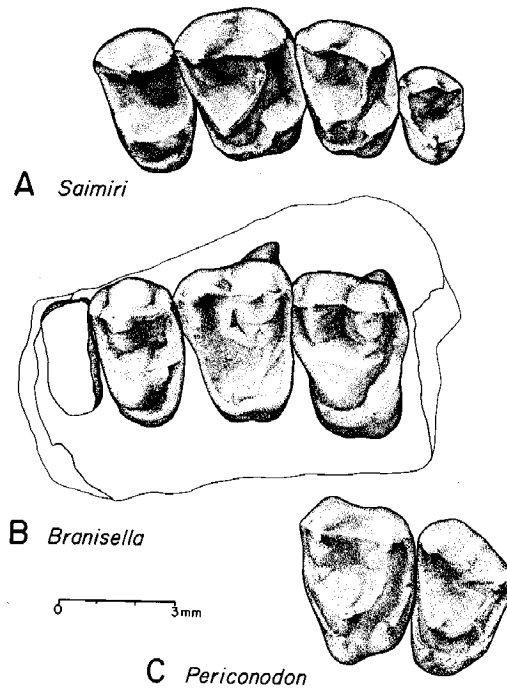
Branisella, Apidium, Aegyptopithecus, and the Origin of Simiiform Primates

Assuming that the earliest Platyrrhini and Caviomorpha entered South America in the late Eocene or earliest Oligocene, we can consider their relationship to primates and rodents in the late Eocene and early Oligocene elsewhere in the world. Descadan primates and rodents are often compared with the Fayum Oligocene rodents and primates of northern Africa (Hoffstetter, 1972; Lavocat, 1974; and others). Fayum primates and rodents are too young geologically to have given rise to Descadan elements of these orders in the South American fauna, but they show such similarity in structural grade that some reasonably close relationship is indicated. I am not sufficiently familiar with Eocene and Oligocene rodents to discuss the origin of Caviomorpha, but I have studied the original specimens of virtually all fossil primates relevant to the origin of Simiiformes (higher primates or "Anthropoidea"). I shall attempt to outline the nature of the paleontological evidence bearing on the origin of higher primates as simply as possible.

Branisella boliviana is known principally from the holotype maxillary fragment (Hoffstetter, 1969). In size and dental morphology this species corresponds closely to the living squirrel monkey (Fig. 2). The molars of *Branisella* in the holotype are somewhat worn, but they show the same trigon cusp and crest relationships, with a small hypocone on the internal cingulum, as seen in the living squirrel monkey. Virtually all of the fossil primates known from South America are similar to living genera and species of Cebidae, and it appears that living cebids do not differ greatly in general structure from their South American ancestors in the Oligocene.

At least five genera of primates are known from the Fayum Oligocene of Egypt. These fall naturally into three groups: (1) the adapoid *Oligopithecus*, (2) the parapathecoids *Apidium* and *Simonsius*, and (3) the hominoids *Propliopithecus* and *Aegyptopithecus* (Simons, 1965, 1972; Gingerich, 1978a). *Oligopithecus* is known only from a single mandible that resembles the Eocene adapid *Hoanghoni* from China (Gingerich, 1977c). The two genera that are best known anatomically and contribute most to our understanding of the morphology of Fayum anthropoids are *Apidium* and *Aegyptopithecus*. Cranially and postcranially *Apidium* and *Aegyptopithecus* resemble South American Cebidae to a remarkable degree (Simons, 1959, 1969, 1972; Gingerich, 1973; Conroy, 1976; Fleagle, 1978; Fleagle *et al.*, 1975; Fleagle and Simons, 1978). Thus, Oligocene *Branisella*, *Apidium*, and *Aegyptopithecus* taken together present a reasonably unified picture of the anatomy of a truly primitive simiiform primate. Among living primates, primitive Oligocene Simiiformes most closely resemble cebids and not callitrichids, tarsiids, or lemurids.

Fig. 2. Comparison of upper cheek teeth of primates related to the origin of South American primates, all drawn at same scale: (A) little worn left P^4M^{1-3} of the extant squirrel monkey *Saimiri sciureus*; (B) moderately worn left P^4M^{1-2} of the holotype of Oligocene *Branisella boliviana*; (C) little worn left M^{2-3} of the middle Eocene adapid *Periconodon huerzeleri*. Note close resemblance in overall size, and detailed similarity of trigon and hypocone cusps and crests in *Branisella* and *Saimiri*. *Periconodon* differs from these two principally in having a distinct pericone on the lingual cingulum, but otherwise it apparently represented an Eocene primate very similar in body size and dental adaptation to *Branisella* or even *Saimiri*. *Branisella* specimen is in the Muséum National d'Histoire Naturelle, Paris, and the *Periconodon* is in the Naturhistorisches Museum, Basel (Bchs. 640).



Two large families of primates of modern aspect are known from the Eocene: the tarsiiform Omomyidae and the lemuriform Adapidae. Anatomical characteristics seen in Oligocene higher primates are listed in Table 1 for comparison with the characteristics of Eocene omomyid and adapid primates possibly ancestral to the simiiform radiation.

Paleontology and comparative anatomy furnish two complementary approaches to understanding the adaptations and evolutionary history of primates. In a group like the primates for which the fossil record is reasonably well known, it is possible to outline the phylogenetic history of the group based on hard parts preserved in the fossil record (Gingerich and Schoeninger, 1977; Gingerich, 1978*b*). Interpreting the distribution of anatomical traits of living members in light of this phylogeny yields information about the probable evolutionary pathways of other hard parts and of soft anatomical characteristics not preserved in fossils. Many possible phylogenetic trees showing the relationships of primates can be suggested based on the comparative anatomy of living animals, but only one of these can reflect the actual historical pathway followed. Reversals, parallelism, and convergence are three well-documented evolutionary processes that cannot be detected by comparative study alone. For this reason, direct historical information about the actual stages of primate evolution is essential for reconstructing the evolutionary phylogeny of primates. In terms of the general question addressed in this chapter, the origin of higher primates, this reduces to two more specific questions: (1) What were the most primitive higher primates like?; and (2)

what were possible precursors at an earlier stage like, and to which of these are primitive anthropoids most similar? In other words the general problem of the origin of higher primates focuses on the question of whether Oligocene Simiiformes more closely resemble Eocene Omomyidae or Eocene Adapidae.

Table 1 lists 16 anatomical characteristics preserved as hard parts in Eocene Omomyidae and Adapidae, and in Oligocene simiiform primates. Four of these are indeterminate, being shared equally by all, by Eocene lower primates but not Oligocene anthropoids, or by Oligocene anthropoids but not Eocene lower primates. Of the remaining twelve characteristics, eleven are similarities shared by Eocene Adapidae and Oligocene Simiiformes but not Eocene Omomyidae. Only one of the twelve diagnostic characteristics, relative brain size estimated by the encephalization quotient, favors Eocene Omomyidae as the ancestors of higher primates.

Kay (1975) has shown that insectivorous and folivorous primates differ in body size, with the former usually being smaller than 500 g and the latter being greater than 500 g in body mass. This size threshold at about 500 g may appropriately be called "Kay's threshold." Omomyids radiated on the insectivorous side of Kay's threshold, whereas adapids radiated at larger body size on the folivorous side of the threshold (Fleagle, 1978; note that 500 g corresponds to an M_2 length of about 3.2 mm, or $\ln M_2$ length = 1.2, Gingerich, 1977a). The late Eocene and Oligocene radiation of simiiform primates was also on the folivorous side of Kay's threshold (Fleagle, 1978).

The dental formula of omomyids and adapids is variable and by itself does not suggest special affinity of either group to early simiiform primates. On the other hand, virtually all other dental characteristics distinguish Adapidae and Simiiformes from Omomyidae. The mandibular symphysis of omomyids is never fused. Fusion occurred independently at least five times in adapids. There also appears to be a trend toward fusion in progressively smaller adapids through the course of the Eocene. Thus by the late Eocene even *Mahgarita stevensi* with a body weight estimated at about 1 kg had a solidly fused mandibular symphysis (Wilson and Szalay, 1976) like that of early Simiiformes. As discussed elsewhere (Gingerich, 1977b), the anterior dentition of adapids and anthropoids differs from that of omomyids in having vertically implanted, spatulate incisors with the lower central incisors smaller than the lateral ones. Omomyids, on the other hand, typically have enlarged central incisors and reduced lateral incisors and canines, with the central incisors forming an almost bird-like beak (Fig. 3). Adapids have projecting, interlocking canines honed by an anterior premolar as in primitive Simiiformes (Gingerich, 1975). In addition, the canine teeth of some adapids appear to be sexually dimorphic (Stehlin, 1912; Gregory, 1920; Gingerich, 1979b) like those of primitive simiiform primates. Canine dimorphism has never been documented in Omomyidae, and in most omomyid genera, the canines are greatly reduced in size relative to the central incisors (Fig. 4).

The earliest Omomyidae and Adapidae have molars that are very similar in morphology, the only diagnostic differences in the dentition being in the

Table 1. Characteristics of Primitive Oligocene Simiiform Primates Compared to Those of Eocene Omomyidae and Adapidae^a

Morphological characteristics	Eocene Omomyidae	Oligocene Simiiformes	Eocene Adapidae
Body size			
Radiation ^d	Below Kay's threshold	Above Kay's threshold	Above Kay's threshold
Dentition	2.1.4.3 to 2.1.2.3 or 1.1.3.3	2.1.3.3 or 2.1.2.3	2.1.4.3 to 2.1.3.3
Dental formula ^b	Unfused Pointed $I_1 \geq I_2$ Limited Absent Absent Tritubercular On basal cingulum EQ = 0.42 to 0.97	Fused Spatulate $I_1 < I_2$ Interlocking Present Present Quadrate On basal cingulum EQ = 0.85 Partial-complete Free(?)—fused annulus Lost	Unfused to fused Spatulate $I_1 < I_2$ Interlocking Present Present Tritubercular to Quadrate On postproto- or basal cingulum EQ = 0.39 or 0.41 None Free annulus Large or small
Mandibular symphysis ^d			
Incisor form ^d			
Incisor size ^d			
Canine occlusion ^d			
Canine dimorphism ^d			
Canine/premolar hone ^d			
Molar form ^d			
Position of hypocone ^b			
Encephalization quotient ^c			
Postorbital closure ^b			
Ectotympanic ^d			
Stapedial artery ^b			
Postcranium			
Calcaneum/navicular ^d	Elongated	Short	Short
Tibia/fibula ^d	Fused	Unfused	Unfused

^aWhere there is variation and a clear direction of evolution documented by the fossil record, the trend is written as primitive-to-derived. Variation is indicated wherever it is known. The complete dental, cranial, or postcranial anatomy is not known for any genus, and future discoveries may show that presently known genera do not adequately represent Omomyidae, Adapidae, or primitive Simiiformes. See text for discussion.

^bCharacteristics in which Adapidae and Omomyidae share equal similarity or dissimilarity with primitive Simiiformes.

^cCharacteristics in which Omomyidae are more similar than Adapidae to primitive Simiiformes.

^dCharacteristics in which Adapidae are more similar than Omomyidae to primitive Simiiformes.

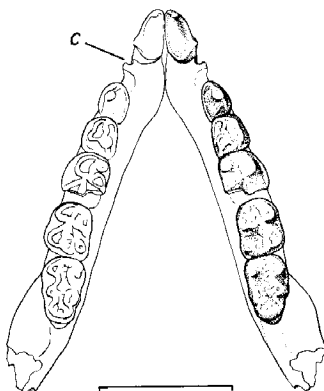


Fig. 3. Reconstruction of left and right mandibles of *Microchoerus erinaceus* showing the lower dentition in occlusal view. Note the large pointed central incisors (I_1), forming an almost birdlike beak. There are no second incisors (I_2) in *Microchoerus*, and the lower canine (labelled C in the figure) is greatly reduced in size relative to I_1 or P_2 . Specimen is in the British Museum of Natural History, London (M30345 and 30347). Scale bar is 1 cm.

morphology of the premolars and anterior dentition. Most omomyid genera retain a paraconid on the lower molars and a basically tritubercular molar structure (like that of *Tarsius*). Adapids, on the other hand, lost the paraconid on the lower molars relatively early and their molar structure is more quadrate than tritubercular. Oligocene simiiform primates have quadrate molars like those of adapids rather than omomyids. This is why genera like late Eocene *Amphipithecus* and *Pondaungia*, and early Oligocene *Oligopithecus* are difficult to classify. They have the molar structure of both Adapidae and Simiiformes (Szalay, 1970, 1972; Simons, 1971; Gingerich, 1977c). The hypocone in most representatives of all three groups, Omomyidae, Adapidae, and Simiiformes, is a so-called "true" hypocone on the basal cingulum.

In cranial structure, the relative size of the brain can be measured using Jerison's (1973) encephalization quotient (EQ). Radinsky (1977) calculated EQ values of .42, .79, and .97 for the omomyids *Tetonius*, *Necrolemur*, and *Rooneyia*, respectively. He gives EQ values of .41 and .39 for *Smilodectes* and *Adapis*, respectively. *Aegyptopithecus* had an EQ of about .85 (Gingerich, 1977a), so in relative brain size omomyids are closer to *Aegyptopithecus* than adapids are. Postorbital closure separates primitive Simiiformes from both Omomyidae and Adapidae, and thus does not indicate any affinity with one family or the other.

The structure of the ectotympanic in Omomyidae is tubular as it is in *Tarsius*. Adapidae have a free ectotympanic within the auditory bulla like that of living Malagasy lemurs. The ectotympanic of both *Aegyptopithecus* and *Apidium* was ringlike, and it undoubtedly filled much of the lateral wall of the auditory bulla like it does in living Ceboidea. It is possible that this primitive anthropoid condition could be derived from the tubular ectotympanic of an omomyid, but I am not aware of any other examples of loss of the tubular extension of the ectotympanic in primate evolution. In addition, the squamosal of *Apidium* has a small cup-shaped depression that received the distal end of the ectotympanic anulus. The anulus itself is not preserved, but the presence of a distinct depression where its free end articulated with the squamosal suggests that the anulus was not solidly fused to the auditory bulla

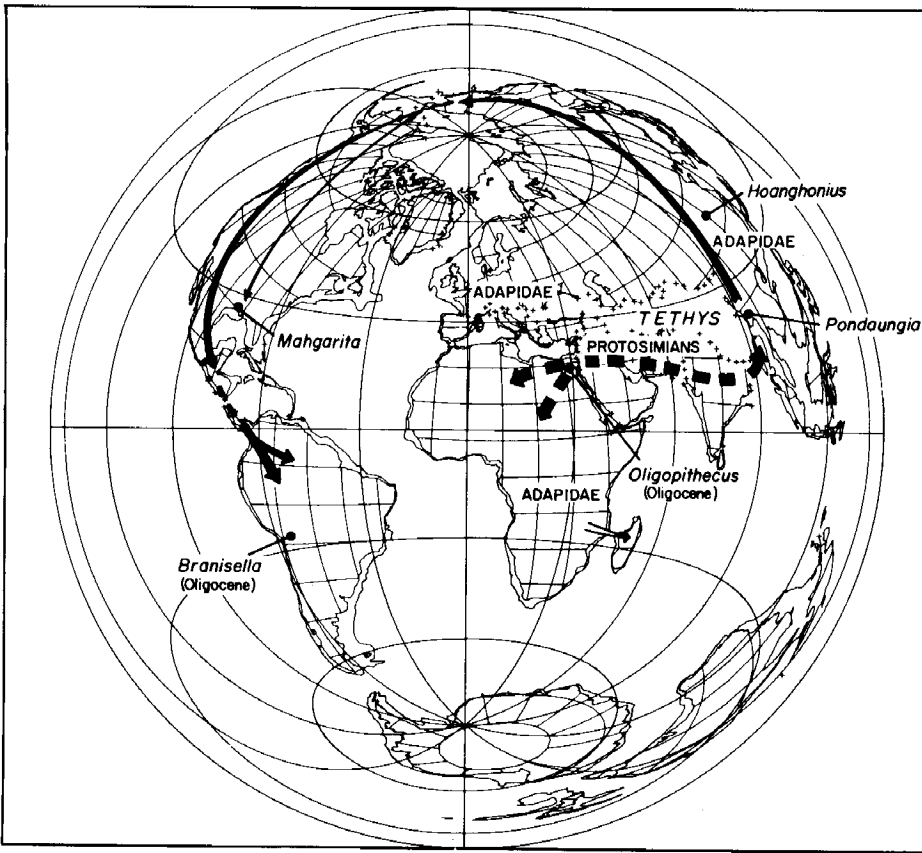


Fig. 4. Late Eocene paleocontinental map showing the position of South America relative to other continents. The geographic distribution of late Eocene adapid primates included Europe (*Adapis*, etc.), Asia (*Hoanghonius*), North America (*Mahgarita*), and almost certainly Africa and south Asia. By the middle or late Eocene the lemur fauna of Madagascar was probably isolated after derivation from African adapids. Late Eocene *Pondaungia* and *Amphipithecus* (both from the same general area of Burma) and early Oligocene *Oligopithecus* are transitional adapid-simiiform primates linking higher primates to an adapid origin. Early Oligocene *Branisella* is the earliest record of Ceboidea in South America. Note that the Burmese localities yielding *Pondaungia* and *Amphipithecus* were north of Tethys and part of Laurasia in the late Eocene. The evidence available at present favors origin of Simiiformes from an advanced adapid "protosimian" stock in south Asia or Africa or both. Part of the protosimian stock radiated in Africa, giving rise to the earliest Hominoidea by the middle and late Oligocene (*Propliopithecus*, *Aegyptopithecus*). Plausibly another part of the protosimian stock accompanied *Mahgarita*, *Hyaenodon*, and other Asian mammals across the Bering route into southern North America in the late Eocene. The protosimian stock then crossed from North America into South America by island-hopping via the route of present Central America or the West Indies. This hypothesis is shown by solid lines superimposed on the map. It is also possible that the adapid-protosimian stock ancestral to Ceboidea crossed the South Atlantic directly from Africa to South America. Base map is a Lambert equal-area projection from Smith and Briden (1977).

in *Apidium* (Gingerich, 1973). Hershkovitz (1974) has shown that the distal end of the ectotympanic sometimes does not fuse to the squamosal in *Tarsius* and in ceboids, but it is always solidly fused to the auditory bulla. The distal portion of the ectotympanic in *Tarsius* and ceboids is broad and flat, and it does not fit into a cup-like depression like that seen in *Apidium*. Obviously, more complete specimens of *Apidium* are required to determine the detailed relationship of the ectotympanic to the auditory bulla and squamosal, but evidence at hand indicates that neither *Apidium* nor *Aegyptopithecus* had an omomyid-like tubular ectotympanic fused to the auditory bulla. The facet for the distal articulation of the ectotympanic with the squamosal in *Apidium* suggests that the primitive simiiform configuration may have included a partially free ectotympanic anulus more similar to that of adapids.

Simiiform primates differ from all Eocene lower primates in lacking a stapedia branch of the internal carotid artery. Omomyids and at least some adapids have a relatively reduced stapedia and enlarged promontory branch of the internal carotid artery (Gingerich, 1973). Carotid circulation does not indicate any special similarity of either omomyids or adapids to early higher primates.

The postcranial skeleton of omomyids, adapids, and primitive Simiiformes is not yet sufficiently well described to permit a detailed comparison, but two aspects of hind limb anatomy deserve mention. The calcaneum is known in a number of different genera of omomyids, including *Hemiacodon*, *Teilhardina*, *?Tetonius*, *Necrolemur*, *Nannopithecus*, and *Arapahovius*, and in every case it is relatively elongated compared to generalized primates (Szalay, 1976; Savage and Waters, 1978). The tibia and fibula have been described in two omomyids, *Necrolemur* and *Nannopithecus* (Schlosser, 1907; Weigelt, 1933; see also Simons, 1961; Le Gros Clark, 1962), and in *Necrolemur* at least the fibula appears to be reduced in size and fused to the tibia. The conformation of the fibula in *Nannopithecus* is less certain (Simons, 1961). Calcaneal elongation and fibular fusion are resemblances of omomyids to living *Tarsius*, but they distinguish this group postcranially from both Adapidae and from Simiiformes.

Primitive Oligocene simiiform primates resemble Eocene Adapidae much more than they do Eocene Omomyidae. The most parsimonious interpretation of this evidence is that higher primates evolved from Adapidae and not from Omomyidae. It is generally accepted that living lemurs are derived from Eocene Adapidae and the living *Tarsius* from Eocene Omomyidae. Consequently, anthropoid primates and lemurs are probably more closely related to each other than either is to *Tarsius*. The implications for comparative anatomy are several. Anatomical characteristics such as the reduced rhinarium and nasal fossa (Cave, 1973), and the hemochorial placenta (Lukett, 1975) shared by *Tarsius* and Simiiformes but not Lemuriformes may be parallel evolutionary acquisitions (or possibly retained primitive states). The reliability of phylogenetic distances inferred from immunology and protein sequences (Goodman, 1975) appears somewhat questionable when these distances span a total temporal separation on the order of 80–100 million years

(40–50 m.y. in each lineage compared). I doubt that placing lemurs and lorises slightly closer to anthropoids than *Tarsius* is would significantly decrease the parsimony of the immunological or protein sequence result.

There is disagreement regarding the major phyletic relationships of Tarsiiformes, Lemuriformes, and Simiiformes, with different results depending on whether one attempts to trace phyletic groups through the fossil record or to infer history from the comparative anatomy of living forms. This means on the one hand that our evidence regarding primate phylogeny is still far from complete, and on the other hand that we need to take a more critical look at different methods being used to reconstruct primate history. Parallelisms and reversals are common evolutionary phenomena. For this reason I tend to trust a phylogeny based on closely spaced historical records preserved as fossils rather than one based on selected comparisons of animals living, so to speak, 40 or 50 m.y. after the fact.

Paleobiogeography

The approximate distribution of continental land masses during the late Eocene, when simiiform primates evolved from their adapid ancestors, is shown in Fig. 4. Superimposed on early Cenozoic paleogeography was a series of major worldwide climatic changes documented paleobotanically on the continents (Wolfe and Hopkins, 1967; Wolfe, 1978) and isotopically in the oceans (Savin *et al.*, 1975). The late Paleocene was generally a time of climatic cooling, followed by a definite warming trend at the end of the epoch that continued into the Eocene. After several fluctuations in the Eocene, there was a sharp drop in temperature worldwide at the end of the Eocene corresponding to Stehlin's (1909) "*grande coupure*" in European mammalian faunas. Climate strongly affects the distribution of mammalian faunas, and there is evidence that high latitude land bridges like the Bering route between Asia and North America were effectively opened or closed during the early Cenozoic by changes in climate as well as sea level.

Modern primates, more than most other orders of mammals, are sensitive to climate. Thus it is probably no accident that the introduction of Omomyidae and Adapidae into Europe and North America coincided with early Eocene climatic warming, and the reduction in diversity of both families on northern continents also coincided with climatic cooling. The *grande coupure* marks the final exit of both Eocene families from Europe. Simpson (1947) made an extensive analysis of mammalian faunal similarity between North America and Eurasia. He showed that the greatest faunal interchange between North America and Eurasia took place during the late Eocene just before the *grande coupure*.

The major faunal interchange between North America and Eurasia in the late Eocene assumes special importance in explaining the distribution of

Adapidae at this time. The principal radiation of adapids documented to date was in the Eocene of Europe, but finds in the poorly known early Cenozoic faunas of Asia (*Hoanghoni*) and Africa (*Oligopithecus*) suggest that major radiations of Adapidae may have taken place there as well. The notharctine adapid radiation in North America apparently became extinct early in the late Eocene, but one adapine genus, *Mahgarita*, is known from the late Eocene of Texas (Wilson and Szalay, 1976). It presumably reached North America as part of the late Eocene invasion from Asia that included the Old World creodont *Hyaenodon*, anthracotheres, etc. (Gingerich, 1979a). As a result, Adapidae apparently enjoyed a virtually worldwide distribution in the late Eocene.

Hoffstetter (1972, 1974) has advanced the hypothesis that tarsiiform primates radiated north of Tethys in Laurasia while their "sister-group" the simiiform primates radiated south of Tethys, initially in Africa and then in South America. It is true that omomyids are unknown outside of Laurasia, but it is difficult to see how Simiiformes could be derived from Tarsiiformes given this geographical exclusivity. A more reasonable hypothesis, I think, is that higher primates were derived from a group that shared a similar geographical distribution. For this reason, and all of the anatomical reasons discussed above, Adapidae as a group are a better candidate for simiiform ancestry than tarsiiform Omomyidae.

The most likely area of origin of higher primates, based on present evidence, appears to be Africa and/or South Asia. This is the region labelled "Protosimians" in Fig. 4, which lies between the known distribution of *Amphipithecus* and *Pondaungia* in Burma and *Oligopithecus* in Africa. All three of these genera have the distinction of being ambiguous adapid-simiiform intermediates at the time when simiiform primates were first differentiating.

The remaining problem is how the ancestors of Ceboidea reached South America if they originated in Africa or South Asia. There are two possibilities: (1) they crossed the Bering land bridge from Asia during a warm interval in the late Eocene and, with *Mahgarita*, colonized the southern part of North America, then crossed one of two possible volcanic island arcs bordering the Caribbean Plate (see Gingerich and Schoeninger, 1977) and entered South America (Fig. 4); or (2) they crossed the South Atlantic directly, either by rafting or by island-hopping across the Walvis-Rio Grande rise (see Tarling, this volume). Of these two hypotheses, I favor the former because of the difficulty primates would have crossing large tracts of open ocean on rafts. It was no doubt necessary to cross some ocean by island-hopping in either case, but this would be minimized in crossing from Central America to South America. Unfortunately, there is little evidence available as yet to test either hypothesized route.

A third possibility deserves mention, although I do not yet think the evidence is sufficient to warrant serious consideration. The new mandible of *Pondaungia* (Fig. 5) recently described by Ba Maw, *et al.* (1979) from the late Eocene of Burma bears a surprising resemblance to *Notharctus*. Pilgrim (1927)

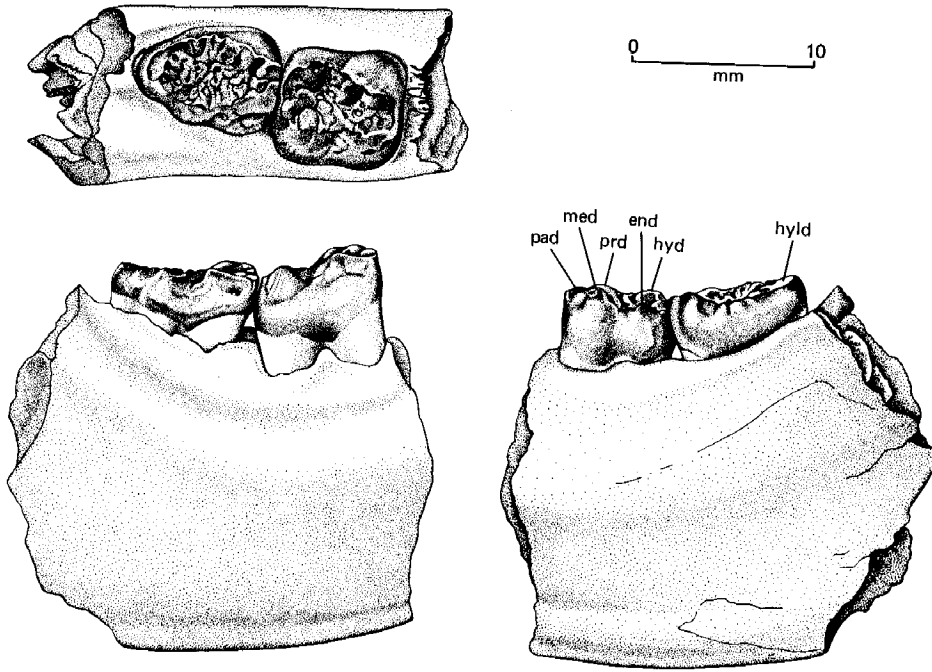


Fig. 5. Recently discovered right mandible of *Pondaungia* sp. with M_{2-3} from the late Eocene of Burma. Specimen resembles the adapid *Notharctus robustior* in size, placement of trigonid cusps and crests, development of talonid cusps and crests, and to some extent in enamel crenulation. The molars are relatively broader and flatter in *Pondaungia* indicating an anthropoid-like frugivorous adaptation similar to that of *Aegyptopithecus*, whereas *Notharctus* has more crested cheek teeth indicating a predominantly folivorous dietary adaptation. In spite of this difference in adaptation, among Eocene primates the molars of *Pondaungia* are most similar in structure to those of notharctine Adapidae, as Pilgrim (1927) stated over fifty years ago based on less well-preserved specimens. Figure reproduced from Ba Maw *et al.* (1979).

also compared *Pondaungia* extensively with *Pelycodus* and *Notharctus*. The dentition of the new specimen differs in being adapted for a more frugivorous diet, whereas *Notharctus* has more crested folivorous cheek teeth, but the basic plan of trigonid and talonid cusps is very similar. If *Pondaungia* is a notharctine, it is possible that higher primates originated in southern North America and subsequently migrated in the late Eocene from North America into South America and also from North America across the Bering route into south Asia and ultimately Africa. This is not a serious hypothesis at present, but it is a possibility.

Much has been learned in the past twenty years about the evolution and geographical development of primates, and continued recovery of new fossil specimens at the current rate will undoubtedly contribute in the next twenty years to a better understanding of the origin of South American primates. The most critical tests of phylogenetic hypotheses are new fossils.

ACKNOWLEDGMENTS

I would like to thank many museum curators for generous access to the fossil specimens discussed here, especially Drs. Elwyn L. Simons, Duke University Primate Center, Durham; D. E. Savage, University of California, Berkeley; M. C. McKenna, American Museum of Natural History, New York; R. Hoffstetter and D. E. Russell, Muséum National d'Histoire Naturelle, Paris; R. A. Reyment, Paleontologiska Institutionen, Uppsala; B. Engesser and J. Hürzeler, Naturhistorisches Museum, Basel; R. Wild and E. Heizmann, Staatliches Museum für Naturkunde, Stuttgart (Ludwigsburg); Darwish Alfar and Baher El-Kashab, Cairo Geological Museum, Cairo; and M. V. A. Sastry and A. K. Dutta, Geological Survey of India, Calcutta. I also thank Drs. R. L. Ciochon and D. E. Savage for permitting me to reproduce a figure of one of their most important new specimens from Burma in Fig. 5. Ms. Karen Payne drew the specimens in Figs. 2 and 3. Ms. Karna Steelquist assisted with photography and Ms. Anita Benson typed the manuscript.

This research has been supported principally by a NATO Postdoctoral Fellowship at the Université de Montpellier (1975), grants from the Smithsonian Foreign Currency Program for museum research in Egypt and India, and NSF grant DEB 77-13465 for research on Paleocene and Eocene faunas in North America.

References

- Ba Maw, Ciochon, R. L., and Savage, D. E., 1979, Late Eocene of Burma yields earliest anthropoid primate, *Pondaungia cotteri*, *Nature (London)* **282**:65-67.
- Cave, A. J. E., 1973, The primate nasal fossa, *Biol. J. Linnéan Soc.* **5**:377-387.
- Conroy, G. C., 1976, Primate postcranial remains from the Oligocene of Egypt, *Contrib. Primatol.* **8**:1-134.
- Fleagle, J. G., 1978, Size distribution of living and fossil primate faunas, *Paleobiology* **4**:67-76.
- Fleagle, J. G., and Simons, E. L., 1978, Humeral morphology of the earliest apes, *Nature (London)* **276**:705-707.
- Fleagle, J. G., Simons, E. L., and Conroy, G. C., 1975, Ape limb bone from the Oligocene of Egypt, *Science* **189**:135-137.
- Frakes, L. A., and Kemp, E. M., 1972, Influence of continental positions on Tertiary climates, *Nature (London)* **240**:97-100.
- Gingerich, P. D., 1973, Anatomy of the temporal bone in the Oligocene anthropoid *Apidium* and the origin of Anthropoidea, *Folia Primatol.* **19**:329-337.
- Gingerich, P. D., 1975, A new genus of Adapidae (Mammalia, Primates) from the Late Eocene of southern France, and its significance for the origin of higher primates, *Contrib. Mus. Paleontol. Univ. Mich.* **24**:163-170.
- Gingerich, P. D., 1977a, Correlation of tooth size and body size in living hominoid primates, with a note on relative brain size in *Aegyptopithecus* and *Proconsul*, *Am. J. Phys. Anthropol.* **47**:395-398.
- Gingerich, P. D., 1977b, Dental variation in early Eocene *Teilhardina belgica* with notes on the anterior dentition of some early Tarsiiformes, *Folia Primatol.* **28**:144-153.

- Gingerich, P. D., 1977c, Radiation of Eocene Adapidae in Europe, *Géobios, Mém. Spéc.* 1:165-182.
- Gingerich, P. D., 1978a, The Stuttgart collection of Oligocene primates from the Fayum Province of Egypt, *Paläontol. Z.* 52:82-92.
- Gingerich, P. D., 1978b, Phylogeny reconstruction and the phylogenetic position of *Tarsius*, in: *Recent Advances in Primatology*, Vol. 3, *Evolution* (D. J. Chivers and K. A. Joysey, eds.), pp. 249-255, Academic Press, New York.
- Gingerich, P. D., 1979a, Phylogeny of Middle Eocene Adapidae (Mammalia, Primates) in North America: *Smilodectes* and *Notharctus*, *J. Paleontol.* 53:153-163.
- Gingerich, P. D., 1979b, Sexual dimorphism in Eocene Adapidae: Implications for primate phylogeny and evolution, *Am. J. Phys. Anthropol.* 50:442.
- Gingerich, P. D., and Schoeninger, M. J., 1977, The fossil record and primate phylogeny, *J. Hum. Evol.* 6:482-505.
- Goodman, M., 1975, Protein sequence and immunological specificity, their role in phylogenetic studies of primates, in: *Phylogeny of the Primates: A Multidisciplinary Approach* (W. P. Luckett and F. S. Szalay, eds.), pp. 219-248, Plenum Press, New York.
- Gregory, W. K., 1920, On the structure and relations of *Notharctus*, an American Eocene primate, *Mem. Am. Mus. Nat. Hist.* 3:49-243.
- Hartenberger, J.-L., 1975, Nouvelles découvertes de rongeurs dans le Deseadien (Oligocène inférieur) de Salla Luribay (Bolivie), *C. R. Acad. Sci. Paris, Sér. D* 280:427-430.
- Hershkovitz, P., 1974, The ectotympanic bone and origin of higher primates, *Folia Primatol.* 22:237-242.
- Hoffstetter, R., 1969, Un primate de l'Oligocène inférieur sud-américain: *Branisella boliviana* gen. et sp. nov., *C. R. Acad. Sci. Paris, Sér. D.* 269:434-437.
- Hoffstetter, R., 1972, Relationships, origins, and history of the ceboid monkeys and caviomorph rodents: A modern reinterpretation, in: *Evolutionary Biology*, Vol. 6 (Th. Dobzhansky, M. K. Hecht, and W. C. Steere, eds.), pp. 323-347, Appleton-Century-Crofts, New York.
- Hoffstetter, R., 1974, Phylogeny and geographical deployment of the primates, *J. Hum. Evol.* 3:327-350.
- Jepsen, G. L., and Woodburne, M. O., 1969, Paleocene hyracothere from Polecat Bench Formation, Wyoming, *Science* 164:543-547.
- Jerison, H. J., 1973, *Evolution of the Brain and Intelligence*, Academic Press, New York.
- Kay, R. F., 1975, The functional adaptations of primate molar teeth, *Am. J. Phys. Anthropol.* 43:195-216.
- Lavocat, R., 1974, The interrelationships between the African and South American rodents and their bearing on the problem of the origin of South American monkeys, *J. Hum. Evol.* 3:323-326.
- Le Gros Clark, W. E., 1962, *The Antecedents of Man*, Edinburgh University Press, Edinburgh.
- Luckett, W. P., 1975, Ontogeny of the fetal membranes and placenta, their bearing on primate phylogeny, in: *Phylogeny of the Primates, a Multidisciplinary Approach* (W. P. Luckett and F. S. Szalay, eds.), pp. 157-182, Plenum Press, New York.
- Marshall, L. G., Pascual, R., Curtis, G. H., and Drake, R. E., 1977, South American geochronology: Radiometric time scale for middle to late Tertiary mammal-bearing horizons in Patagonia, *Science* 195:1325-1328.
- Patterson, B., and Pascual, R., 1972, The fossil mammal fauna of South America, in: *Evolution, Mammals, and Southern Continents* (A. Keast, F. C. Erk, and B. Glass, eds.), pp. 247-309, State University of New York Press, Albany.
- Pilgrim, G. E., 1927, A *Sivapithecus* palate and other primate fossils from India, *Mem. Geol. Surv. India* 14:1-26.
- Radinsky, L., 1977, Early primate brains: Facts and fiction, *J. Hum. Evol.* 6:79-86.
- Rose, K. D., 1978, A new Paleocene epoicitheriid (Mammalia), with comments on the Palaeonodonta, *J. Paleontol.* 52:658-674.
- Savage, D. E., and Waters, B. T., 1978, A new omomyid primate from the Wasatch formation of southern Wyoming, *Folia Primatol.* 30:1-29.

- Savin, S. M., Douglas, R. G., and Stehli, F. G., 1975, Tertiary marine paleotemperatures, *Bull. Geol. Soc. Am.* **86**:1499-1510.
- Schlosser, M., 1907, Beitrag zur Osteologie und systematischen Stellung der Gattung *Necrolemur*, sowie zur Stammesgeschichte der Primaten überhaupt, *Neues Jahrb. Mineral. Geol. Paläontol. Festsch.* **1807-1907**:197-226.
- Simons, E. L., 1959, An anthropoid frontal bone from the Fayum Oligocene of Egypt: The oldest skull fragment of a higher primate, *Am. Mus. Novit.* **No. 1976**:1-16.
- Simons, E. L., 1961, Notes on Eocene tarsoids and a revision of some *Necrolemurinae*, *Bull. Br. Mus. Nat. Hist. (Geol.)* **5**:45-69.
- Simons, E. L., 1965, New fossil apes from Egypt and the initial differentiation of Hominoidea, *Nature (London)* **205**:135-139.
- Simons, E. L., 1969, Recent advances in paleoanthropology, *Yearb. Phys. Anthropol.* **1967**:14-23.
- Simons, E. L., 1971, Relationships of *Amphipithecus* and *Oligopithecus*, *Nature (London)* **232**:489-491.
- Simons, E. L., 1972, *Primate Evolution, An Introduction to Man's Place in Nature*, Macmillan, New York.
- Simpson, G. G., 1947, Holarctic mammalian faunas and continental relationships during the Cenozoic, *Bull. Geol. Soc. Am.* **58**:613-688.
- Simpson, G. G., Minoprio, J. L., and Patterson, B., 1962, The mammalian fauna of the Divisadero Largo Formation, Mendoza, Argentina, *Bull. Mus. Comp. Zool.* **127**:237-293.
- Smith, A. G., and Briden, J. C., 1977, *Mesozoic and Cenozoic Paleogeographic Maps*, Cambridge University Press, Cambridge.
- Stehlin, H. G., 1909, Remarques sur les faunules de mammifères des couches éocènes et oligocènes du bassin de Paris, *Bull. Soc. Géol. Fr.* **9**:488-520.
- Stehlin, H. G., 1912, Die Säugetiere des schweizerischen Eocaens—*Adapis*, *Abh. Schweiz. Paläont. Ges.* **38**:1165-1298.
- Szalay, F. S., 1970, Late Eocene *Amphipithecus* and the origins of catarrhine primates, *Nature, (London)* **227**:355-357.
- Szalay, F. S., 1972, *Amphipithecus* revisited, *Nature (London)* **236**:170-180.
- Szalay, F. S., 1976, Systematics of the Omomyidae (Tarsiiformes, Primates): Taxonomy, phylogeny, and adaptations, *Bull. Am. Mus. Nat. Hist.* **156**:163-449.
- Webb, S. D., 1976, Mammalian faunal dynamics of the great American interchange, *Paleobiology* **2**:220-234.
- Weigelt, J., 1933, Neue primaten aus der mitteleozänen (oberlutetischen) Braunkohle des Geiseltals, *Nova Acta Leopold.* **1**:97-156.
- Wilson, J. A., and Szalay, F. S., 1976, New adapid primate of European affinities from Texas, *Folia Primatol.* **25**:294-312.
- Wolfe, J. A., 1978, A paleobotanical interpretation of Tertiary climates in the northern hemisphere, *Am. Sci.* **66**:694-703.
- Wolfe, J. A., and Hopkins, D. M., 1967, Climatic changes recorded by Tertiary land floras in northwestern North America, in: *Tertiary Correlations and Climatic Changes in the Pacific* (K. Hatai, ed.), *11th Pacific Sci. Symp.* **25**:67-76.