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

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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

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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

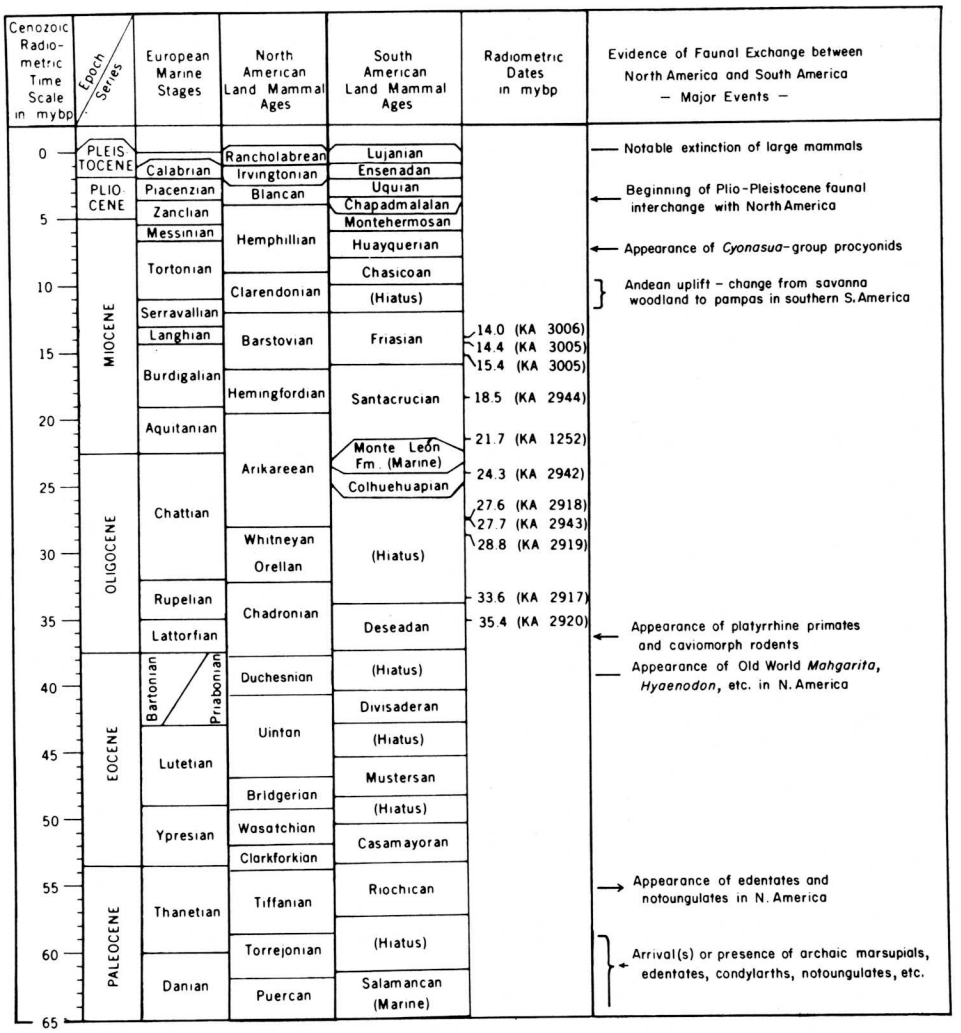

Fig. 1. Faunal succession and radiometric time scale for Cenozoic mammalian evolution in South America compared to sequences in North America and Europe. Major faunal events with a bearing on faunal migrations are indicated in the right-hand column. Data principally from Marshall *et al.* (1977) and 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. Deseadan 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 Deseadan 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 parapithecoids *Apidium* and *Simonsius,* and (3) the hominoids *Propliopithecus* and *Aegyptopithecus* (Simons, 1965, 1972; Gingerich, 1978*a*). *Oligopithecus* is known only from a single mandible that resembles the Eocene adapid *Hoanghonius* from China (Gingerich, 1977*c*). 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.