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Dentition of *Adapis parisiensis* and the Evolution of Lemuriform Primates

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The fossil record of Madagascar unfortunately sheds no light on the origin of its unique lemur fauna, nor does it assist in determining the relationships of the Malagasy lemurs to other primates. The known fossil forms are at most 3000–4000 years old (Tattersall, 1973*a*), which makes them virtual contemporaries rather than ancestors of the living species. The only adequately known fossil primates possibly related to the ancestry of the lemurs are found in sediments of Eocene age in North America, Europe, and Asia. The European genus *Adapis* includes species which deserve special attention in this regard.

A major problem in any consideration of lemur origins is biogeographical. Madagascar has apparently been an island since the Late Cretaceous, though previously it was joined on the west to Africa and on the east to India. (Cracraft, 1973, provides a good review of recent geophysical evidence bearing on this continental separation.) When and how did the ancestral lemurs get to Madagascar? Virtually all recent authors identify Africa as the source of the ancestral lemur stock, and their efforts to date the lemur invasion of

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Madagascar involve balancing a number of factors. The Mozambique Channel is believed to have widened gradually during the early Tertiary; thus the earlier the lemur invasion, the easier it would have been. On the other hand, the lemurs are advanced forms compared to the known Paleocene primates, suggesting that they probably did not evolve before the Eocene. For these reasons, the time of invasion of Madagascar by the ancestral lemur stock is usually considered to have been Early Eocene (McKenna, 1967; Cooke, 1968; Fooden, 1972; Tattersall, 1973*b*). Charles-Dominique and Martin (1970) suggest the possibility that numerous lemur types were present in the African region in the Paleocene, which they believe was possibly before Madagascar separated from Africa. Walker (1972) concludes that ancestral lemurs could have rafted across the Mozambique Channel from Africa until about the end of the Eocene, by which time the channel was probably about 240 km wide.

There are a number of problems with this theory. As Simons has pointed out (1972, p. 169), if Africa is the continent of origin of the lemur fauna, it is curious that lemurs have not been found in the primate-rich Oligocene and Miocene sediments of Africa. The paleogeography of Madagascar in the early Tertiary is not completely agreed on, but it appears certain that in the Eocene a considerable distance of ocean (100–200 km minimum) separated Africa and Madagascar. Prevailing winds and ocean currents make chance crossing of the Mozambique Channel extremely improbable today, and presumably had approximately the same effect in the Eocene. Finally, a satisfactory account of the origin of the lemur dentition has never been given. If the procumbent incisors and canines of lemurs are primitive, it is surprising that they do not appear in any of the Eocene lemuroids of Europe or North America. If they are not primitive, it is necessary to explain how the procumbent incisors and canines of lemurs isolated on Madagascar came to be shared with the lorises of Africa and Asia, which first appear in the Miocene. The purpose of this chapter is to present new observations on the dentition of Eocene lemuroids, and to discuss their implications for the origin of the lemur fauna of Madagascar.

DENTITION OF *ADAPIS*

All of the adequately known Paleocene primates are members of extinct side branches of early primate evolution, and the fossil record of lemuriform primates begins in the Eocene. All Eocene lemuroids are classified in the family Adapidae. Adapids share two diagnostic cranial characters with the living lemurs: they have a free ectotympanic annulus within the auditory bulla, and

the internal carotid artery divides into two branches, the promontory and the stapedial. Among fossil primates, this combination of characters is known only in the Adapidae.

Phylogeny of Adapidae

An outline phylogeny of adapid evolution is presented in Fig. 1. The earliest adapids, species of *Pelycodus*, first appear at the beginning of the Eocene in England (Blackheath beds), France (*Lignites de Soissonais*), and North America (Clark Fork beds). In North America, *Pelycodus* can be traced upward through the strata of the Lower Eocene and the advanced forms are placed in the genera *Notharctus* and *Smilodectes*. A skull of the Middle Eocene species *Notharctus "osborni"* is illustrated in Fig. 2, and the skull of *Pelycodus* undoubtedly was very similar. A Princeton University partial skull of *Pelycodus* (PU No. 14515) confirms that this primitive form had a fully developed postorbital bar as in *Notharctus*. The principal morphological difference between *Pelycodus* and *Notharctus* is the presence in the latter of well-developed mesostyles and hypocones on the upper molars.

In France, the *Sables à Unios et Térédines* are stratigraphically higher in the Lower Eocene than the *Pelycodus*-bearing *Lignites de Soissonais*, and yield a more advanced adapid, *Protoadapis*, a genus which persisted through the remainder of the Eocene (Russell *et al.*, 1967). Early species of *Protoadapis* resemble *Pelycodus*, differing chiefly in the replacement of the postprotocingulum by a hypocone on the upper molars, and reduction of the paraconid on the lower molars. Molars of *Protoadapis* are more sharply crested and have more open trigonids than do those of *Pelycodus*. Both *Pelycodus*

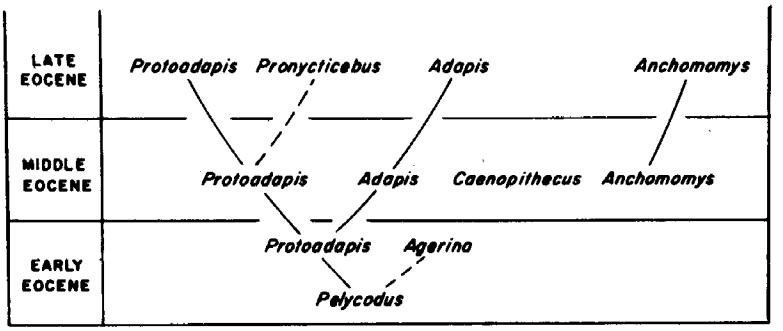

FIG. 1. Phylogeny of European genera included in the primate family Adapidae. *Adapis parisiensis* is a Late Eocene species of *Adapis*.

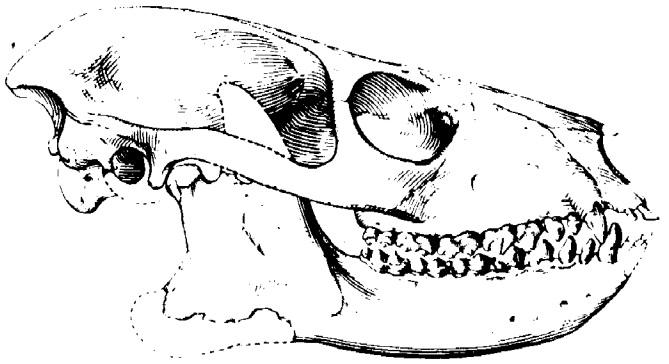

FIG. 2. Skull of *Notharctus "osborni,"* a closely related descendant of the earliest adapid *Pelycodus*. Drawing natural size, taken from Gregory (1920). This specimen may in fact be a female *Notharctus tenebrosus*.

and *Protoadapis* have small, vertically implanted incisors, large protruding canines, and premolars showing little molarization.

The Late Eocene *Pronycticebus* is known from a single skull and associated right mandible. The lower teeth of *Pronycticebus* are virtually identical to those of *Protoadapis*; however, the upper molars are relatively broader and have a more strongly developed hypocone. As its name implies, when first describing the skull of *Pronycticebus*, Grandidier (1904) considered it to be possibly related to the living lorisoid *Nycticebus*. Restudy by Le Gros Clark (1934), Simons (1962), and Szalay (1971) has led to agreement that *Pronycticebus* is an adapid. Simons dissected the bulla of *Pronycticebus* and demonstrated that this genus has a free tympanic ring, although the ring is located nearer to the external auditory meatus than is typical of lemuroid primates. This Simons (1962) interpreted as a possible indication of near fusion of the ring to the lateral wall of the bulla, suggesting that perhaps *Pronycticebus* is related in some way to lorisoid origins. Szalay (1971) interpreted the same evidence differently, as he believes the free tympanic ring of lemuroids to be derived from the lorisoid condition (Szalay, 1972). While Szalay's interpretation of tympanic evolution in Primates is theoretically possible, it is improbable and not supported by either ontogenetic development or the fossil record, a point that will be discussed in detail elsewhere.

The adapids *Agerina*, *Caenopithecus*, and *Anchomomys* (Fig. 1) are poorly known anatomically and as yet contribute little to our knowledge of primate evolution. They do, however, indicate that the European Eocene radiation of Adapidae was a broad one, with a minimum of four genera present in the Middle and Late Eocene.