Dentition of *Adapis* 5
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, 1973a), 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, 1973b). 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 post-protocingulum 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*
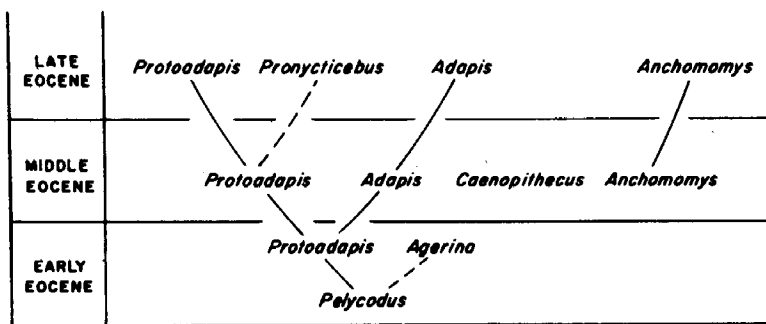

FIG. 1. Phylogeny of European genera included in the primate family Adapidae. *Adapis parisiensis* is a Late Eocene species of *Adapis*.
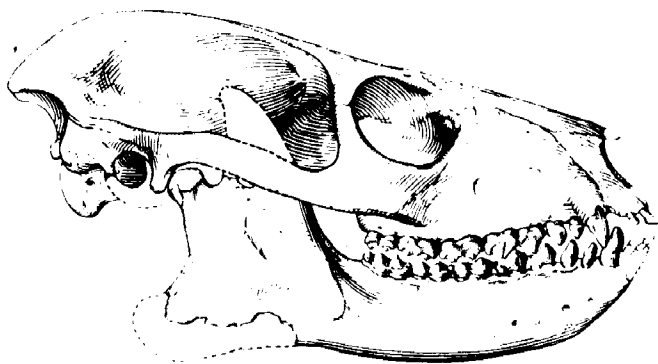
FIG. 2. Skull of *Notharctus "osborni,"* a closely related descendant of the earliest adapid *Pelycodus*. Drawing natural size, taken from Gregory (1920). This specimen may in fact be a female *Notharctus tenebrosus.*

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.

The remaining adapids, species of *Adapis*, have the greatest bearing on the origin of lemurs. These include some of the best-known fossil primates anatomically. Six species of *Adapis* are presently recognized (Schmidt-Kittler, 1971). These are, in the Middle Eocene: *A. sciureus*, *A. ruetimeyeri*, and *A. priscus*, and in the Late Eocene: *A. ulmensis*, *A. magnus*, and *A. parisiensis*. The type specimen of the genus *Adapis* was first figured and described by Cuvier in 1812 in the first edition of his *Recherches sur les Ossemens Fossiles*. The specimen is a badly crushed skull (Fig. 3), and it is not surprising that Cuvier was never able to determine its true affinities. In the second edition (1822) of his *Ossemens Fossiles*, Cuvier first named the specimen *Adapis*, a name sometimes used at that time for hyraxes, and classified it as a small pachyderm. No specific name was proposed for the taxon until publication of the section of de Blainville's *Ostéographie* dealing with *Adapis*. Cuvier's specimen was refigured by de Blainville (1849), who referred to it as *Adapis parisiensis*.

In 1859, Gervais described additional specimens as *Aphelotherium duvernoyi*, which he classified with *Adapis parisiensis* as an omnivorous pachyderm. The true affinities of these specimens were not recognized until Delfortrie (1873) described a nearly complete skull, which he named *Palaeolemur*
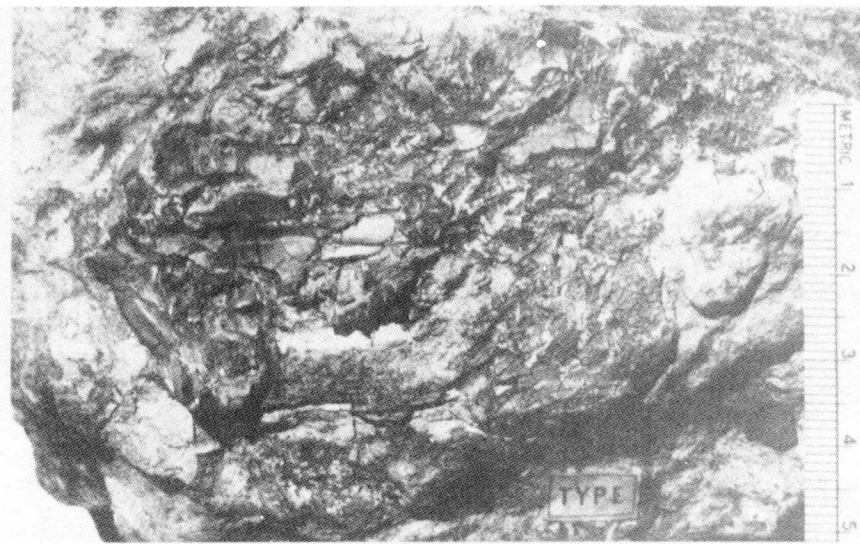

FIG. 3. Badly crushed palate and right mandible of the type specimen of *Adapis parisiensis*. This specimen was first figured and described by Cuvier in 1812. As with most early lithographs, Cuvier's figure is reversed left for right. Specimen is in Muséum National d'Histoire Naturelle in Paris.

betillei and correctly identified as a lemur-like primate. Gervais (1873) immediately recognized the identity of *Adapis parisiensis, Aphelotherium duvernoyi*, and *Palaeolemur betillei*, the first name having priority.

The following year Filhol (1874) described a new skull of a much larger primate as *Adapis magnus*. Gervais (1876) subsequently placed this species in a new genus *Leptadapis*. The canine teeth of *Adapis magnus* are significantly different in conformation from those of *A. parisiensis* (see below), and the name *Leptadapis* should probably be retained, at least as a subgenus. *Adapis parisiensis* and *A. (L.) magnus* are both now known from numerous skulls and jaws which were described in detail by Stehlin (1912) in a monograph on *Adapis*. The other four recognized species of *Adapis* were named by Stehlin (1912, 1916) and Schmidt-Kittler (1971), and remain inadequately known.

The phylogeny of Eocene adapids presented in Fig. 1 traces the evolution of *A. parisiensis* at the generic level from the earliest known ancestor *Pelycodus*, through the intermediate genus *Protoadapis*, leading in the Middle Eocene to species placed in *Adapis*. *Adapis parisiensis* is an advanced member of the genus, with important specialization of the lower canines, and first appears in the Late Eocene.

Dentition of *Adapis parisiensis*

The following description and discussion is based on the dentition of *A. parisiensis*. Comparison is made throughout with the dentition of the living lemur *Hapalemur griseus*. *Hapalemur* is approximately the same size as *A. parisiensis*, which eliminates problems of allometry when comparing the two. Considered together, the dentitions of all of the living lemurs exhibit a range of variation in morphology in which *Hapalemur* is, in most respects, intermediate. Because of its relatively generalized nature, the dentition of *Hapalemur* may closely approximate the condition of the ancestral lemur stock. Its resemblances to *Adapis* are thus of particular interest and importance.

Adapis parisiensis has a dental formula of $I_2^2C_1^1P_4^4M_3^3$. Its incisors above and below are broad and spatulate (Figs. 4 and 5), resembling those of anthropoid primates. The upper and lower canines are of medium size, protruding significantly beyond the premolars. The four premolars become progressively larger and more molariform, with the last being morphologically virtually molars. The upper and lower molars are all sharply crested. Small hypocones are present on M^1 and M^2, and M_3 is elongated, with a well developed hypoconulid, as in most primitive primates.

In *Hapalemur*, on the other hand, the upper incisors are very small teeth, placed close to the canine. The lower incisors are very narrow and styliform, forming part of a dental scraper or tooth comb. The upper canine in *Hapalemur* is a large sharply pointed tooth, but the lower canine is small and styli-
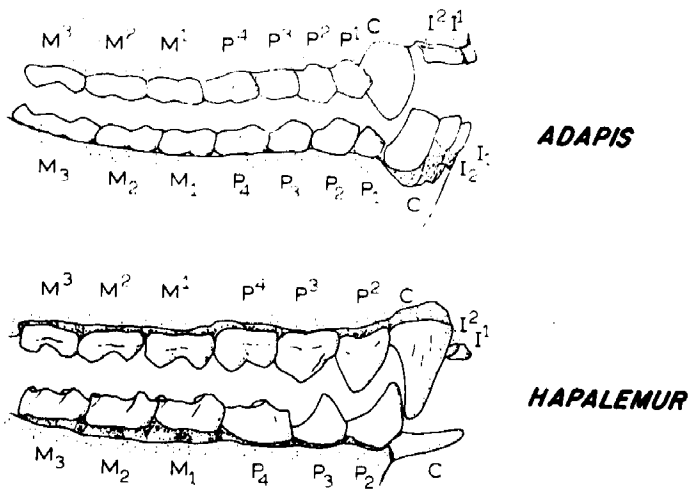
FIG. 4. Dentition of *Adapis parisiensis* and *Hapalemur griseus*, in lateral view. Note particularly the incisiform lower canine of *Adapis*, and the caniniform P_2 and procumbent lower canine of *Hapalemur*. Both to same scale, twice natural size. Drawing of *Adapis* based on specimens in Muséum National d'Histoire Naturelle in Paris and the Harvard Museum of Comparative Zoology.

form like the incisors and forms the lateral member of the dental scraper. The most anterior lower premolar (P_2) is enlarged and caniniform, and shears against the back of the upper canine. As in *Adapis*, $P_4{}^4$ are very molariform. In *Hapalemur*, the upper molars lack hypocones and M_3 does not have the hypoconulid lobe seen in *Adapis*.

Evolution of the Anterior Dentition

One of the most important characters distinguishing the lemurs and lorises from other primates is the tooth scraper formed by the lower incisors and canines. In the Indriidae, the scraper is formed by a single pair of lower incisors and the canines (or possibly two pairs of incisors and no canines), and was undoubtedly derived from the condition seen in the Lemuridae, where two pair of incisors plus the canines form the scraper (see *Hapalemur*, Fig. 5). The scraper of Lorisidae is virtually identical to that of the Lemuridae and undoubtedly shares common ancestry with it, as Martin (1972, p. 320) notes. In having the tympanic ring fixed in the lateral wall of the auditory bulla rather than free within it as in lemurs, the Lorisidae represent a "derived"
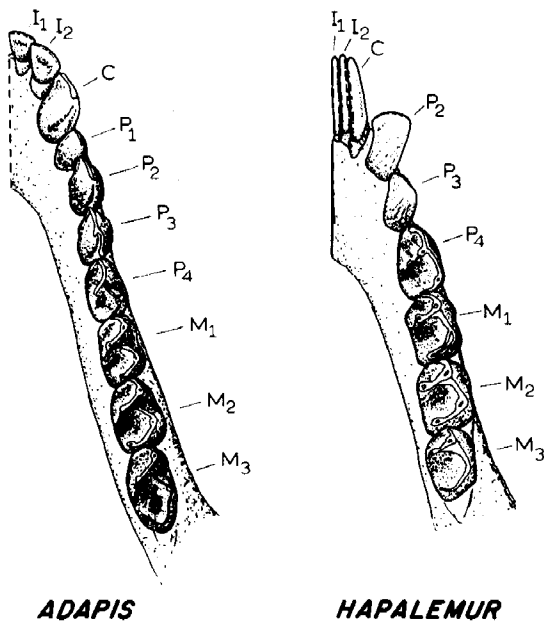
FIG. 5. Lower dentition of *Adapis parisiensis* and *Hapalemur griseus*, in occlusal view. Note incisor–canine functional unit, and the open, crested premolars and molars in both species. Both to same scale, twice natural size. Drawing of *Adapis* based on specimens in Muséum National d'Historie Naturelle, Paris.

group with respect to the ancestral lemur stock. The Lemuridae are primitive in both of these important characters and probably reflect the ancestral condition.

Two questions must be answered to explain the origin of the lemur dental scraper: what is its evolutionary history, and what is its functional basis? Regarding the evolutionary history of the dental scraper, it was previously thought that the pronounced procumbency of the lower incisors and canines in the tree shrews indicated a phase of evolutionary development preceding the more highly specialized dental comb of the living lemurs and lorises (Le Gros Clark, 1962). Van Valen (1965), Martin (1966, 1968), Campbell (1966), and others have recently restudied the relationships of the tree shrews, and concluded that the similarities between living tree shrews and Primates are based exclusively on retention of ancestral placental mammal characteristics and the convergent development of certain features in the two groups. If tree shrews are related to Primates at all, it would seem to be at the microsyopoid

level and, as Martin (1968, p. 390) notes, the "lemur-like" proclivity of the lower canines in some tree shrews represents a separate development convergently resembling (and not very closely at that) this character in lemurs.

An answer to the question of when the canine became incorporated into a functional unit with the incisors in the ancestral lemur/loris is provided by *Adapis*. *Adapis parisiensis* has spatulate, nearly vertically implanted lower incisors as is typical of the other adapids, and of anthropoids as well, but its canines differ in one important respect from those of all the other Eocene adapids. The lower canines of *A. parisiensis* are functionally incisors; the six lower anterior teeth in this species form a single functional unit (see Figs. 4 and 5, this chapter; Figs. 246 and 247 in Stehlin, 1912). Once the lower canines and incisors came to function as a unit, it is not difficult to understand how all six teeth were modified similarly to form a dental scraper.

Recent field studies have determined that a primary function of the tooth scraper in the wild is to scrape resin or gum from the bark of trees. This behavior has been reported in *Euoticus* by Charles-Dominique (1971), and in *Phaner* by Petter *et al.* (1971). The indriids include a significant amount of bark in their diet (Petter, 1962), which is pried loose with the dental scraper (Richard, 1973). It is entirely plausible that repeated use of the lower anterior teeth to scrape bark would, by natural selection, result in the modification of even vertically oriented incisors to form the procumbent scraper seen in lemurs and lorises. Incorporation of the lower canines into the scraper of lemurs and lorises suggests that the lower canines of the ancestral lemur/loris were functionally incisors. *Adapis parisiensis* is the only fossil primate known which had this configuration of canines, and it is thus the best candidate yet known for the common ancestor of lemurs and lorises.

One often cited character which supposedly bars *Adapis* from lemur ancestry is its fused mandibular symphysis. The reason for symphyseal fusion in Mammalia is not completely understood, but it is apparent that fusion of the mandibular rami is correlated with the development of sectorial incisors such as those seen in *Adapis* and in anthropoid primates. With modification of the sectorial incisors of *Adapis* to form a dental scraper, symphyseal fusion would no longer be necessary, and consequently the mandibles need no longer fuse during ontogeny. This is, if true, a relatively simple example of neoteny.

Evolution of the Cheek Teeth

No living lemurs or lorises have more than three premolars, while *Adapis* has four. Loss of one or more premolars is well documented in a number of fossil lineages. Loss of P_1 would pose no problem in the transition from *Adapis* to the ancestral lemur/loris, except that in *Adapis* there is already a well-developed functional relationship between the lower first premolar and

the upper canine. The lower first premolar (P_1) wears against the back of the upper canine in *Adapis*. The function of this wear in Anthropoidea is usually assumed to be to sharpen the upper canine (Every, 1970; Zingeser, 1969). It is also possible that a food-shearing mechanism is involved, and sharpening is not the principal function. Whatever the function of the lower premolar–upper canine relationship, the specimen illustrated in Fig. 6 shows how P_1 might have been lost without disturbing the premolar–canine wear pattern. In this specimen, P_1 is reduced and the upper canine wore against the back of the lower canine, P_1, and the front of P_2 simultaneously. In *A. parisiensis*, progressive enlargement of P_2 and reduction of P_1^1 would presumably have led to the stage illustrated by Fig. 6, and finally to that illustrated by *Hapalemur* (Fig. 4).

The cheek teeth of *Hapalemur griseus* exhibit a number of additional important derived characters which resemble, in detail, characters of the cheek teeth of *A. parisiensis*. P_3 in *Hapalemur* shows a peculiar pattern of ridging on the posterior surface of its principal cusp, which is very similar to that of *A. parisiensis*. *Hapalemur* has well-developed metastylids on P_4 and M_1, which is also a characteristic of *A. parisiensis*. These metastylids are very posteriorly placed, forming pseudoentoconids, in *Lepilemur*. Both *Adapis* and *Hapalemur* have sharply crested cheek teeth. On the lower molars of both genera, the paraconids are lost, being replaced by almost identical, sloping anterior cingulids. The result is a very open trigonid, and the talonids of the lower molars are also open on the lingual side. A functional analysis of tooth wear in *Adapis* and definitions of the terms used to describe *Adapis* molars were presented in an earlier paper (Gingerich, 1972).

One significant structural difference in the upper molars of *Adapis* and *Hapalemur* should be noted. The upper first and second molars of *A. parisiensis* usually have moderately developed hypocones, which are entirely lacking in *Hapalemur*. However, hypocones are well developed on the upper mo-
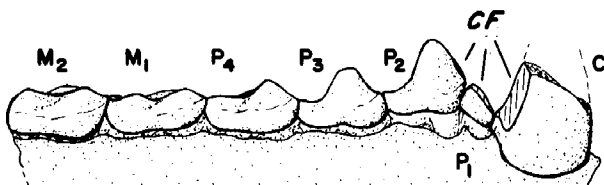

FIG. 6. Right mandible of *Adapis* (*Leptadapis*) *magnus*, in lateral view. *CF*, Wear facets formed by occlusion of upper canine. Apex of lower canine is broken. Twice natural size. Specimen in Muséum National d'Histoire Naturelle in Paris.

lars of indriids and lorisids, and may well have been present in the common ancestor of the lemurs and lorises.

The molars of *A. parisiensis* and *H. griseus* are so similar that if they were found together in the same fossil bed they would undoubtedly be placed together in the same primate family and possibly in the same genus. This could not be said for any of the other lemurs or lorises, except possibly *Lepilemur*, but it indicates the close relationship of the advanced adapid *A. parisiensis* to the living lemurs and lorises.

EVOLUTION OF LEMURIFORM PRIMATES

The phylogeny of Eocene adapids is outlined in Fig. 1. As was mentioned earlier, very little is known of the ancestor of *Pelycodus*. The presence of a free tympanic ring in adapids is a character linking them to Paleocene primates of the superfamily Microsyopoidea rather than Plesiadapoidea, and new specimens of the microsyopoid *Purgatorius unio* discovered by Clemens (1974) might be close to the ancestry of *Pelycodus*. Primitive members of the primate family Omomyidae have cheek teeth resembling those of *Purgatorius* and *Pelycodus* (Gingerich, 1973a), but enlargement of the anterior teeth and specializations of the ear region make it unlikely that omomyids are closely related to the origin of either Lemuriformes or Anthropoidea. Anthropoid primates were almost certainly derived from a primitive adapid (Gingerich, 1973b).

The dental scraper of lemurs and lorises is plausibly interpreted as a derivative of the anterior dentition of *A. parisiensis*, and the close resemblance of the cheek teeth of this species to those of the lemur *H. griseus* is additional evidence that *Adapis* is very closely related to the ancestry of the lemurs and lorises. Thus the phylogenetic relations of Lemuriformes (including Lorisidae) to other primates, and among themselves, are probably as represented in Fig. 7.

The proposed derivation of Lemuriformes from the advanced adapid *A. parisiensis* or a closely related contemporary species requires a reconsideration of the time and continent of origin of the ancestral lemur stock. The evolution of the lower canines in adapids can be traced in some detail through the Eocene. The first appearance of canines which are functionally a unit with the lower incisors is in the Late Eocene *A. parisiensis*, and it is unlikely that the tooth scraper of the lemur/loris ancestor evolved before the Early Oligocene, i. e., about 36–37 million years B.P.

At the beginning of the Oligocene, Walker (1972) estimates the Mozambique Channel to have been 250 km wide at its narrowest point, and estimates that the probability of animals making a chance crossing is about what it is
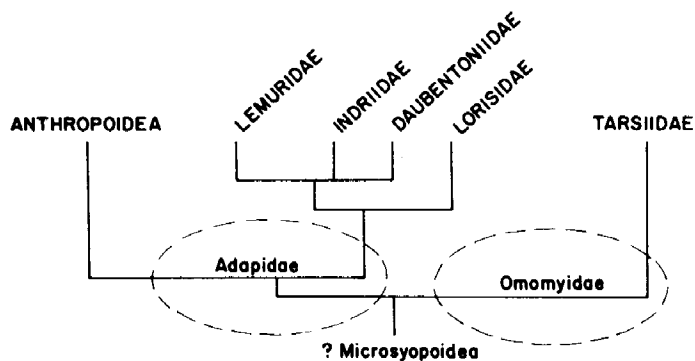
FIG. 7. Diagrammatic representation of the probable phyletic re-
lationships of living primates. Dashed ovals show approximate re-
lationships of the primitive Eocene families Adapidae and Omo-
myidae.

today—unlikely. This factor, plus the absence of lemurs in the Oligocene and
later fossil faunas of Africa, casts some doubt on the African origin of the le-
mur fauna of Madagascar.

The possibility of an Asian origin of the lemur fauna of Madagascar is
enhanced by the presence in Asia of lemuriform fossil primates, and by the
patterns of ocean currents and wind circulation. *Lantianius xiehuensis*,
named and described by Chow (1964) from the ?Late Eocene of China, is an
adapid.[1] *Amphipithecus mogaungensis* from the Late Eocene of Burma may
well, as Szalay (1970) believes, be a lemuroid (but see also Simons, 1971).
Simons (1972) noted that *Pondaungia cotteri*, also from the Late Eocene of
Burma, could, on the basis of tooth structure, be related to the adapid *Pely-
codus*, though it also resembles some Anthropoidea. Finally, *Indraloris lulli*
described by Lewis (1933) and Tattersall (1968) from the Late Miocene of In-
dia is clearly related to the adapid–lemurid–lorisid group, though its precise
affinities cannot yet be determined. These fossil forms, from a continent with
an as yet poorly sampled Tertiary mammalian microfauna, suggest the possi-
bility of a large Eocene and Oligocene radiation of Asian lemuriform pri-
mates.

Walker (1972) showed that the present fauna of Madagascar is more
similar to the Miocene African fauna than to the present-day African fauna.
A similar comparison could be made with the Miocene fauna of Asia. In fact,
the Early Miocene was a time of great faunal interchange between Africa and
Asia (Coryndon and Savage, 1973), and as Lorisidae first appear in Africa in
the Early Miocene (Walker, 1974), it is plausible that they first emigrated

[1]Recent careful study of Chow's figures and description suggests that *Lantianius* is an early
artiodactyl and not an adapid primate.

from Asia at this time. Of the three subfamilies of Viverridae in Madagascar, two are endemic and the other is most closely related to Asian forms (G. Petter, 1962). F. Petter (1962) suggests that the cricetid rodents of Madagascar are derived from African Oligocene forms. Cricetids are known from the Oligocene of Asia (Romer, 1966, p. 395), but not that of Africa (Wood, 1968). Thus an Asian origin may be the best explanation for the carnivores and rodents of Madagascar, as well as for the lemurs.

Fortunately, the paleogeography of the Indian Ocean at the beginning of the Oligocene has recently been reconstructed by geophysicists (McKenzie and Sclater, 1971), and a part of this reconstruction is reproduced in Fig. 8. Apart from Africa, the Asian continent is the only plausible area of origin for the ancestral lemur stock. It should be noted that at the beginning of the Oligocene, India and Ceylon were still south of the equator (Fig. 8). The Indian Ocean at this time was already large, and would almost certainly have contained a strong subtropical gyre and a strong south equatorial current. This current, together with southeast trade winds, could have carried rafts of drifting vegetation, including small mammals, from India to Madagascar. By the end of the Oligocene, India would presumably have moved entirely into the northern hemisphere, thereby greatly reducing the chances of subsequent rafting of mammals from Asia to Madagascar. Though the distance from
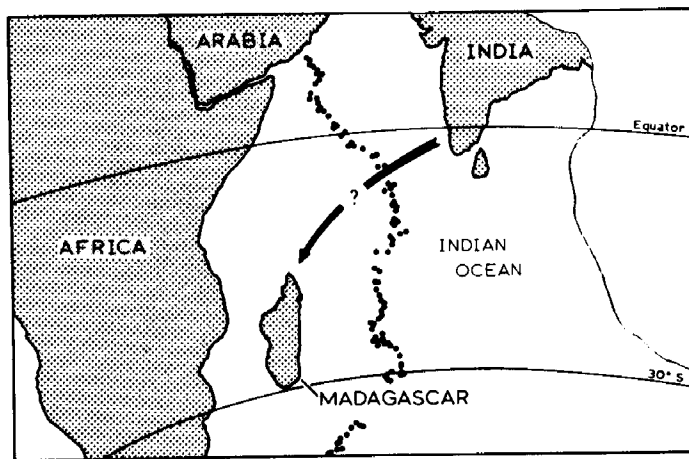

FIG. 8. Paleogeography of Indian Ocean at the beginning of the Oligocene, 36 million years B.P., showing suggested emigration of the ancestral Malagasy lemur stock from Asia rather than Africa. Solid circles are earthquake epicenters marking the boundary between the African and Indian crustal plates. Based on McKenzie and Sclater (1971).

Asia to Madagascar is considerably more than would be necessary for transport from Africa, the currents and winds appear to be more favorable, a point Matthew (1915) noted many years ago.

CONCLUSIONS

To summarize, the anterior dentition of *A. parisiensis* is unique among Eocene lemuriform primates in having the lower canines reduced in size and functioning as a unit with the lower incisors, a condition prestaging the incisor–canine dental scraper of lemurs and lorises. The detailed resemblances of the cheek teeth of *A. parisiensis* to those of *H. griseus* further support a close phyletic relationship of *Adapis* and the living Lemuriformes. It is postulated that increased use of the anterior lower teeth to procure resin or bark by *Adapis* or a close relative led to the well-developed anterior tooth scraper characteristic of both lemurs and lorises.

The phylogeny of Eocene lemuroids is relatively well known, and it is unlikely that the derived dental characters shared by *Adapis* and living lemurs evolved before the Late Eocene, or that the tooth scraper evolved before the Early Oligocene. For faunal and paleogeographic reasons, an Asian origin of lemurs and lorises in the Early Oligocene is suggested, with initial colonization of Madagascar by lemurs in the Oligocene presumably preceding the Miocene immigration of lorisids into Africa.

This evolutionary and migrational scheme is in a number of respects more plausible than those previously advanced to explain the origin of the lemur fauna of Madagascar; however, the conclusions must remain tentative until new fossil evidence from Africa and Asia is found to confirm them.

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