

RADIATION OF EOCENE ADAPIDAE IN EUROPE

by

PHILIP D. GINGERICH

RADIATION OF EOCENE ADAPIDAE IN EUROPE

by

PHILIP D. GINGERICH *

ABSTRACT

The fossil record of European *Adapidae* has been studied locality by locality, and each locality sample integrated into standard European faunal reference levels. It is possible to trace some lineages of species of *Adapidae*, and these show continuous gradual evolution in size and other morphological characteristics. Several examples of diminution in size, evolutionary reversal, and parallelism are discussed. *Adapidae* probably originated from a *Purgatorius*-like ancestor, and ultimately gave rise to both lemuriform and anthropoid primates.

RÉSUMÉ

La documentation fossile des *Adapidae* d'Europe a été étudiée gisement par gisement, et l'échantillon de chaque gisement intégré au sein de l'échelle des niveaux-repères d'Europe. Il est possible de reconstituer quelques lignées évolutives d'espèces d'*Adapidae*, et celles-ci montrent une évolution continue et graduelle de la taille ainsi que d'autres caractères morphologiques. Plusieurs exemples de réduction de la taille, de renversement évolutif, et de parallélisme sont discutés. Les *Adapidae* ont probablement leur origine chez un ancêtre comparable à *Purgatorius*, et pour finir ils donnent naissance à la fois aux lémuriformes et aux primates anthropoïdes.

MOTS-CLÉS : ÉVOLUTION BIOLOGIQUE, PROSIMIEN (ADAPIDAE), ÉOCÈNE, BIOMÉTRIE, PALÉOCLIMAT, EUROPE.

KEY WORDS : BIOLOGICAL EVOLUTION, PROSIMIAN (ADAPIDAE), EOCENE, BIOMETRICS, PALAEOCLIMATE, EUROPE.

* Museum of Paleontology, The University of Michigan Ann Arbor, Michigan 48109 (U.S.A.).

TABLE OF CONTENTS

I. - Introduction	166	V. - Origin of <i>Adapidae</i>	174
II. - Phylogeny reconstruction	167	<i>Purgatorius</i> and paleogene climatic	
Variation and recognition of biological		history	174
species	167	<i>Azibius</i> and adapid paleogeography	175
Biostratigraphy as temporal context	169	VI. - European <i>Adapidae</i> and later pri-	
Phenetic linking	169	mate evolution	176
Hypothesis testing	170	Origin of living Lemuriformes	176
III. - Phylogeny of European <i>Adapidae</i> ..	170	Origin and radiation of higher pri-	
IV. - Evolutionary change in <i>Adapidae</i> ..	171	mates	176
Size changes	171	VII. - Conclusions	179
Evolutionary reversal	171	Acknowledgments	179
Parallelism	172	References	180

I. — INTRODUCTION

The European *Adapidae* are of special interest and importance to the study of primate evolution for several reasons, both historical and phylogenetic: (1) *Adapis* was the first fossil primate genus to be described (although it was not recognized at the time as a primate) — a skull of *Adapis* being figured in G. Cuvier's first edition of the *Recherches sur les ossements fossiles* (1812). (2) *Caenopithecus lemuroides* was the first lemuriform fossil primate to be recognized as such and, interestingly, in describing it Rüttimeyer (1862) called attention also to its resemblance to some anthropoid primates (hence the name *Caenopithecus*). (3) *Adapidae* are common constituents of European Eocene mammal faunas, having a dense and continuous fossil record ideal for detailed evolutionary study. (4) Finally, recent comparisons of Eocene and Oligocene fossil primates have suggested that higher primates probably originated from an adapid ancestry.

The European *Adapidae* are ideal for detailed

evolutionary study because of their abundance in most Eocene stratigraphic intervals. This paper is a preliminary summary of some of the more interesting conclusions of a detailed analysis of the stratigraphic distribution and morphology of European *Adapidae*. Fortunately, it was possible to study virtually all important collections of these fossils, and the conclusions presented here have thus been tested against all of the evidence available to date. This evidence is considerable, and it is unlikely that the main outline of adapid evolution will be altered by future discoveries.

In this paper the methodology used to study phylogenetic history will first be outlined, and then the phylogeny of European *Adapidae* will be discussed. Some interesting examples of evolutionary change in *Adapidae* will be summarized. Finally, the origin of *Adapidae* and the relationship of European *Adapidae* to some Asian, African, and North American paleogene primates will be discussed.

II. — PHYLOGENY RECONSTRUCTION

Phylogeny is usually understood to mean the evolutionary history of the lines of descent of a group of organisms. Living mammals have only geographic and morphological attributes, whereas fossil mammals have geographic, morphological, and temporal attributes. Since fossil evidence is unique in including a temporal dimension, fossil evidence must always have special importance in reconstructing phylogenetic history. There is at present great interest in using « cladistic » analysis of morphological characters alone to reconstruct phylogeny. This approach necessarily ignores two fundamental attributes of fossils, their geographic and stratigraphic position, and an attempt has been

made to develop a rigorous, explicit method of phylogeny reconstruction based on all available attributes of the animals under study. This « stratophenetic » method is discussed in more detail elsewhere (Gingerich, 1976), and here it will only be summarized. Three steps are involved: (1) data organization, (2) linking, and (3) testing.

Variation and recognition of biological species

When specimens of living or fossil animals are collected from a given locality, they can usually

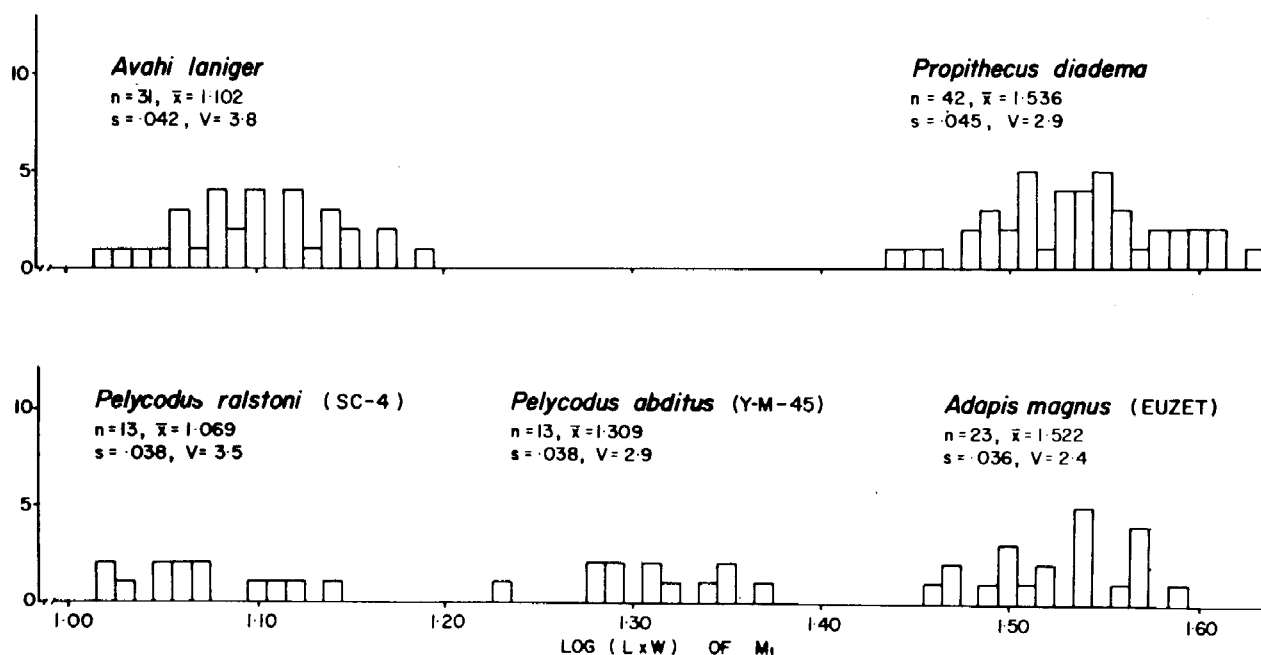


Fig. 1 — Comparison of variation in tooth size in two species of living Madagascar *Indriidae* (*Avahi* and *Propithecus*) with three species of extinct *Adapidae* from different stratigraphic levels in North America (*Pelycodus*) and Europe (*Adapis*). Localities of fossil samples are given in parenthesis. Justification for using size of the first lower molar to characterize tooth size in species samples is given in Gingerich (1974).

Comparaison de la variation de taille des dents chez deux espèces d'*Indriidae* actuels malgaches (*Avahi* et *Propithecus*) avec trois espèces d'*Adapidae* fossiles provenant de différents niveaux stratigraphiques de l'Amérique du Nord (*Pelycodus*) et d'Europe (*Adapis*). Les gisements des échantillons fossiles sont donnés entre parenthèses. La raison de l'utilisation de la taille de la première molaire inférieure pour caractériser la taille des dents chez les échantillons fossiles est donnée in Gingerich (1974).

be divided into a number of different natural groups. In the modern realm, these natural groups of « kinds » of animals are biological species. Each group shares close morphological similarity or phenetic resemblance, and each differs from the other groups by significant discontinuities in distributions of morphological variates. In a living mammal fauna from a given locality, specimens of twenty or more species may be found. Most of these will differ markedly in form (e. g. wolves and horses), others may differ only in size (e. g. wolves and coyotes), and a very few may be separable only after very detailed microscopic or biochemical examination. Similarly, a fossil fauna sampled from a given place and time will often include a dozen

or more species, most of which can be grouped easily into species on the basis of shared resemblances in form and size. In some cases size alone will be the only character distinguishing closely related species. It is unfortunately not possible to subject fossil tissues to the kind of detailed microscopic and biochemical examination used to distinguish some modern species — but these «problem» species constitute a relatively small percentage of the modern fauna and they probably cannot be reliably distinguished in the fossil record.

Variation is the raw material of natural selection, and its quantification is thus of fundamental importance for detailed evolutionary studies. Within each species there is usually a definite but

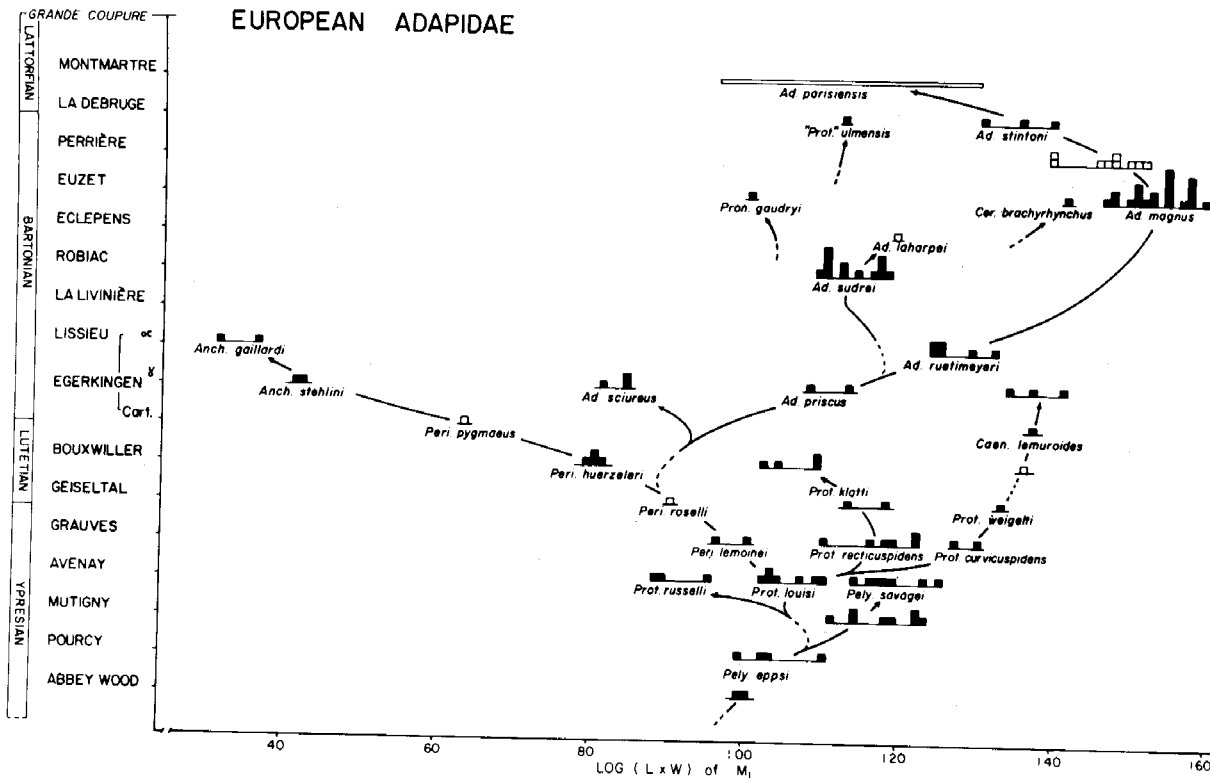


Fig. 2 - Adaptive radiation of European *Adapidae*. Phylogenetic relationships are indicated by lines on a plot of tooth size, but inferred relationships are based on overall similarity of adjacent samples in all available characters. Reproduced from Gingerich (1977).

Radiation adaptative des *Adapidae* d'Europe. Les relations phylogénétiques sont indiquées par les lignes qui relient les diagrammes de taille des dents, mais les relations supposées se fondent sur l'ensemble des ressemblances observées sur tout l'échantillon, pour la totalité des caractères disponibles. Repris d'après Gingerich (1977).

limited amount of variation in size and other characteristics. Considering the fauna from the late Eocene locality of Euzet described by C. Depéret (1917), a group of specimens of the primate species *Adapis magnus* can be distinguished easily from the other species present at Euzet. Within the species sample of *Adapis magnus* from Euzet, represented only by dental remains, there is clearly some variation in tooth dimensions (Table 1). This variation is comparable to that seen in living primates and other mammals in that the coefficients of variation (V) fall within the range characteristic of living species (Gingerich, 1974).

The existence of variation within species is important for evolution, but the limits of this variation and the existence of gaps in the distributions of variation are also important. Body size is a fundamental (perhaps the most important) attribute or aspect of an animal's adaptation. The size of the first lower molar is highly correlated with body size in mammals, and thus tooth size can be used to compare body size in related species. For example, the distributions of size of the first lower molar of the living indriid primates *Avahi laniger* and *Propithecus diadema* occur sympatrically in eastern Madagascar, and the most obvious and most important difference between them is a difference in body size, *Propithecus* being much larger than *Avahi*. This difference is accurately reflected in the plot of M_1 size in figure 1. It is often possible to separate sympatric fossil species in the same way (for example, *Protoadapis russelli* and *Protoadapis lousi* in fig. 2), and comparisons of tooth size thus provide a powerful tool for distinguishing biological species in the fossil record. Distributions of M_1 size in some fossil adapids from single localities, including *Adapis magnus* from Euzet, are plotted below *Avahi* and *Propithecus* in figure 1 to show that the distribution of variation in each is comparable to that seen in living primates.

Biostratigraphy as temporal context

Once the number of « biological » species in each locality sample is determined, based on grouping similar specimens and on studying the variation within each, it is desirable to relate these to each other. Relative temporal context is provided by stratigraphic superposition whenever possible, or by detailed analyses of faunal and lineage evolution in groups other than the one being studied. European *Adapidae* are found in isolated Eocene deposits, and it is not possible to relate them to each other on the basis of direct stratigraphic

superposition. However, studies of rodents and perissodactyls by L. Thaler (1966), J. L. Franzen (1968), J. L. Hartenberger (1973), J. Y. Crochet *et al.* (1975) and others provide a detailed series of reference levels (niveaux repères) for the European Eocene. These reference levels are listed in a column at the left of figure 2. Because the levels were established independently of any study of evolution in the *Adapidae*, they provide an independent biostratigraphic framework for studying adapid evolution.

Once the biostratigraphic sequence of all localities yielding fossils is established, it is possible to place these localities in relative temporal context. Distributions of variation in localities at each level can then be related to distributions in adjacent levels. If the reference levels are spaced closely enough (as in North American *Pelycodus*, Gingerich & Simons, 1977), it is possible to add time depth to the « biological » species identified in each level. The distributions of first lower molar size in European *Adapidae* in successive reference levels through the course of the Eocene are plotted in figure 2.

Phenetic linking

Following a study of variation of the *Adapidae* within each level, and ordering of these levels by independent stratigraphic or biostratigraphic criteria, it is possible to link species or species samples in one level to those in adjacent levels. This linking for European *Adapidae* is shown by solid and dashed lines in figure 2. Tooth size is a measure of body size, a fundamental attribute of any animal in an ecological and adaptational sense, and thus tooth size is plotted in figure 2. It must be emphasized, however, that all other characteristics of the fossils available have been studied, and *the linking is based on overall similarity with all morphological characters considered*. The pattern of linking is superimposed on a diagram showing distribution of tooth size because of the importance of size as an attribute of any specimen or species, but the linking is not based solely on size.

The resulting pattern of phenetic linking of species samples from adjacent stratigraphic levels is an hypothesis of relationship of the species of *Adapidae*, and an outline of the phylogeny of this group in Europe. Relationships that seems fairly certain are indicated by solid lines in figure 2, others that are less certain are indicated by dashed lines. Some lineages, like that from *Protoadapis* to *Anchomomys*, can be traced through a long

sequence of species, while others, like *Pronycticebus gaudryi*, remain as isolated distinctive species.

Hypothesis testing

It is sometimes claimed that a phylogenetic hypothesis constructed in this way is untestable,

and it is true that by incorporating all available information (morphological, geographical, and temporal) in its framing, the resulting hypothesis is usually a very robust one and not easily falsified. This does not, however, mean that it is untestable — new discoveries of fossil *Adapidae* are made every year, and the hypothesis will constantly be tested by the way in which new discoveries fit into it.

III. — PHYLOGENY OF EUROPEAN ADAPIDAE

A total of 28 valid species of *Adapidae* are now known from Europe, placed in eight genera (Gingerich, 1977). The earliest of these is *Pelycodus eppsi*, a species known from Abbey Wood in England and Pourcy in France (fig. 2). Interestingly, this European stem species *Pelycodus eppsi* is very similar and clearly very closely related to the earliest North American species of *Adapidae*, *Pelycodus ralstoni*. As will be discussed below in connection with the origin of *Adapidae*, these two species almost certainly shared a common ancestor before the two became isolated in Europe and North America, respectively. By comparison with the European radiation of *Adapidae*, North American *Pelycodus ralstoni* gave rise to a more modest radiation of some 15 species placed in four genera.

Pelycodus eppsi grades insensibly into a derived species *Pelycodus savagei* present at Mutigny, and up through this level a single lineage of *Pelycodus* is the only adapid lineage known from Europe. However at Avenay, the next highest reference level, three species of *Adapidae* are present. Small and medium-sized *Protoadapis* species are present at Avenay as well as *Pelycodus savagei*. The two species of *Protoadapis* differ slightly from earlier *Pelycodus* in having somewhat higher cusps with sharper crests connecting them, and in having a more strongly developed hypocone on the upper molars. It is, however, probable that *Protoadapis* evolved from a species of *Pelycodus* close to *Pely. eppsi*.

Three adapid species are common at Grauves: one species of *Periconodon*, and two closely related species of *Protoadapis*. In addition, a few teeth of *Pelycodus savagei* are known in the collection from Grauves. The three species making their first appearance at Grauves, *Periconodon lemoinei*, *Protoadapis recticuspidens*, and *Protoadapis curvicspidens* are most similar to *Protoadapis lousi*

from Avenay, and it is possible, if not probable, that all three evolved from that earlier species.

Periconodon lemoinei gave rise to a very distinctive lineage of small adapids that can be traced through the Lutetian to early Bartonian species of the genus *Anchomomys*. Until it can be better dated and shown to differ morphologically, *Anchomomys? quercyi* can be retained in the genus *Anchomomys* with a query. *Protoadapis recticuspidens* is very similar to slightly later *Prot. klatti* from Geiseltal and Bouxwiller, and *Prot. curvicspidens* may have given rise to *Caenopithecus lemuroides* via *Prot. weigelti*. The origin of Quercy *Protoadapis* and *Pronycticebus* is not known, but they may have been derived from a species like *Protoadapis lousi*. Because they retain a full complement of four premolars, it is unlikely that the Quercy species were derived from any known species of *Protoadapis* later than *Prot. lousi*, all of which show a tendency toward loss of P_1 and reduction of P_2 .

Cercamonius brachyrhynchus STEHLIN (Gingerich, 1975 b) is known from the type specimen, a mandible with P_4-M_2 , and from an undescribed edentulous mandible. Both specimens come from Prajous (= Memerlein) in Quercy, and both are in the collection of the Naturhistorisches Museum in Basel. The Basel collection from Prajous includes several molars of *Adapis magnus*, confirming reference of *Cercamonius* to the level of Euzet. Both specimens have the same premolar number and conformation, and both show partial symphyseal fusion, although the ramus of the edentulous mandible is somewhat shallower than the type specimen.

« *Adapis* » *ulmensis* described by N. Schmidt-Kittler (1971) appears to represent a new genus perhaps close to *Protoadapis*, but final placement

must await Schmidt-Kittler's analysis of new specimens he has collected from the type locality.

The remaining eight species of European *Adapidae* are all grouped in the genus *Adapis*. Two side branches from the central *Adapis* lineage apparently led to *Adapis sciureus* and *Adapis sudrei*, respectively, and there is a clear progression from more primitive forms in the lower levels to the most advanced *Adapis parisiensis* in the highest levels, but all form a natural group and it seems most reasonable to retain all in the genus *Adapis*. Of particular interest is the apparent derivation of *Adapis parisiensis* from *Adapis magnus* via the intermediate *Adapis stintoni* known from the Upper Headon beds, from Ehrenstein, and possibly from some Quercy localities. The only evidence possibly

contradicting the evolution of *Adapis parisiensis* from *Adapis magnus* comes from the fauna of Pont D'Assou (Tarn), listed by M. Richard (1946), where a large and small *Adapis* are both present (Sudre, pers. comm.). I have not yet been able to study this collection. As presently known, *Adapis parisiensis*, the type species of the genus is much more variable than any single species, and it probably includes at least two time successive species. New collections from single localities are at present insufficient to permit one to distinguish the species involved — practically all *Adapis parisiensis* specimens come from old Quercy collections where samples from many localities and stratigraphic levels have been mixed.

IV. — EVOLUTIONARY CHANGE IN ADAPIDAE

One of the objectives of reviewing the stratigraphic distribution and morphological characteristics of a group of animals is to see what perspective the group can give to our understanding of the evolutionary process. European *Adapidae* are important in providing some new evidence of size change, evolutionary reversals, and parallelism in stratigraphically documented sequences of fossils.

Size changes

Perhaps the most striking feature of the diagram presented in figure 2, showing size variation in species samples of European *Adapidae*, is the constant change seen in successive samples. No two levels have identical species samples. Even where two successive samples are retained taxonomically in the same species, the later sample usually differs slightly but significantly from the earlier one. The result is inescapably a dynamic conception of adapid species, rather than a static one. Competition and continuous adaptation to changing environments are presumably the cause of this observed pattern of continuous change through time.

Figure 2 also provides an important and interesting perspective on Cope's rule that animals tend to become larger during their evolution, or Deperet's « loi d'augmentation de taille dans les rameaux phylétiques » (1907, p. 199). First of all, the ancestral form *Pelycodus eppi* is almost

exactly intermediate in size compared to later size extremes. Secondly, of the seven segments of phyletic lineages where change can be traced with most confidence, four became larger :

- (1) *Pelycodus eppi* to *Pelycodus savagei*.
- (2) *Protoadapis curvicaudatus* to *Caenopithecus lemuroides*.
- (3) *Adapis priscus* to *Adapis magnus*.
- (4) *Adapis sudrei* to *Adapis laharpei*.

At the same time, three lineages clearly became smaller :

- (1) *Protoadapis louisi* to *Anchomomys gaillardi*.
- (2) *Protoadapis recticaudatus* to *Protoadapis klatti*.
- (3) *Adapis magnus* to *Adapis parisiensis*.

Thus there is no clear trend toward increasing size in the family, nor is there a clear predominance of lineages increasing in size over lineages decreasing in size. If anything the *Adapidae*, like other families of early mammals, suggest a general pattern of *radiation* toward both larger and smaller size from intermediate ancestral forms, a generalization given some theoretical justification by the phenomenon of character divergence.

Evolutionary reversal

The phylogeny of European *Adapidae* provides two interesting examples of evolutionary reversal.

Adapis became larger until the largest adapid species known, *Adapis magnus*, was reached. Then the lineage reversed and became progressively smaller in size. The reason for this abrupt reversal in the direction of evolutionary change in size is not known, but it is perhaps related to climatic deterioration preceding Stehlin's *Grande Coupure*. After the *Grande Coupure*, *Adapis* became extinct or withdrew to geographic areas not yet sampled paleontologically.

Evolutionary reversal of a different kind is seen in the gradual evolution of *Periconodon* and *Anchonomys* from *Protoadapis* (figure 3). In addition to the three major cusps on the upper molars of *Protoadapis lousi*, a hypocone is present on the posterointernal corner and a very small rudimentary « pericône » is present on the anterointernal corner. The hypocone remained about the same

relative size in later species, but the pericône gradually increased in *Periconodon lemoinei* and *Periconodon roselli*, reaching its largest size in *Periconodon huerzeleri* and *Periconodon pygmaeus*. Unfortunately, upper molars of *Anchonomys stehlini* are not yet known, but a pericône is completely lacking in *Anchonomys gaillardi*, suggesting an important evolutionary reversal in the development of the pericône in this lineage. Again the reasons for the reversal are not known, but in this case loss of the pericône may have been related to dietary shifts as the lineage became progressively smaller.

Parallelism

Several examples of parallel evolution are seen in the Adapidae. For example, P_1 was lost and P_2

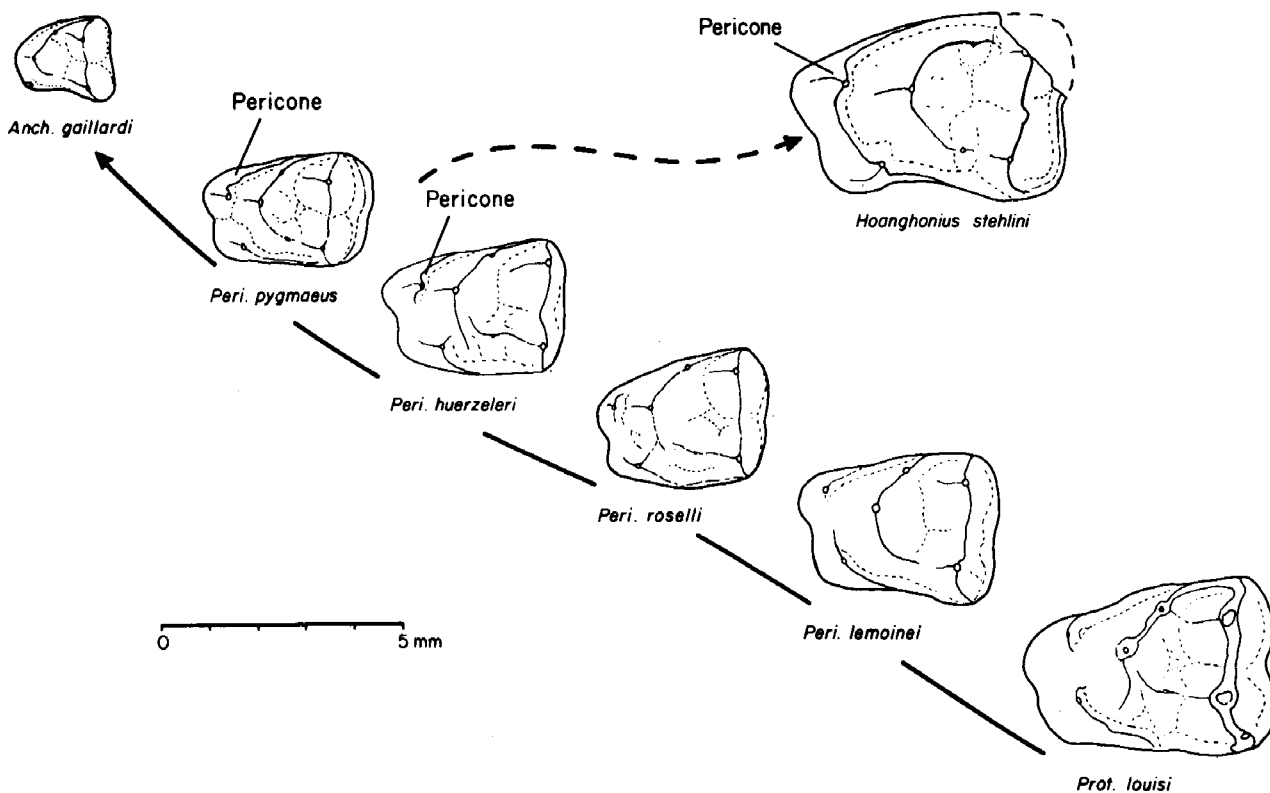


Fig. 3 — Diminution in size and evolutionary reversal in development of the pericône cusp on M^2 from *Protoadapis* to *Periconodon* to *Anchonomys* (compare with fig. 2). *Hoanghonius* is an Asian adapid primate possibly derived from *Protoadapis* or *Periconodon*.

Diminution de taille et renversement de l'évolution dans le développement de la cuspidé du péricône des M^2 de *Protoadapis* - *Periconodon* - *Anchonomys* (comparer avec la fig. 2). *Hoanghonius* est un adapidé asiatique peut-être dérivé de *Protoadapis* ou *Periconodon*.

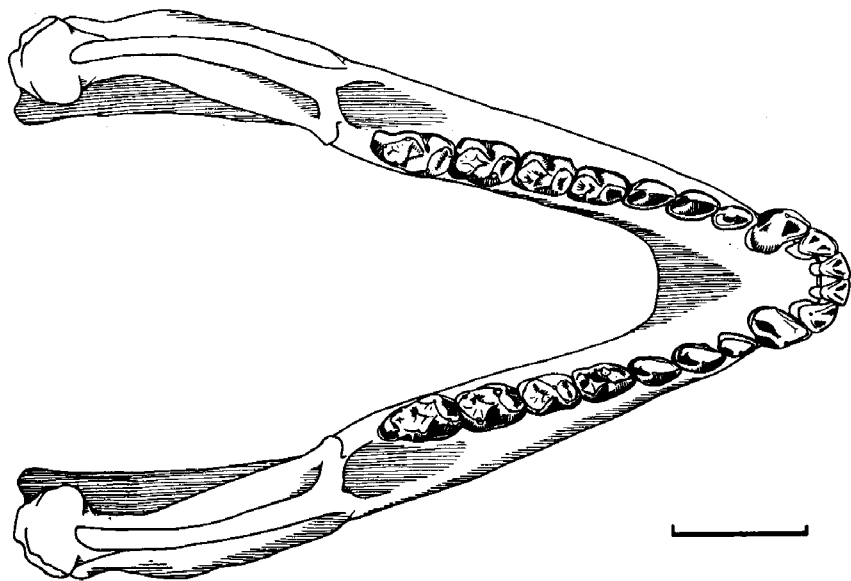
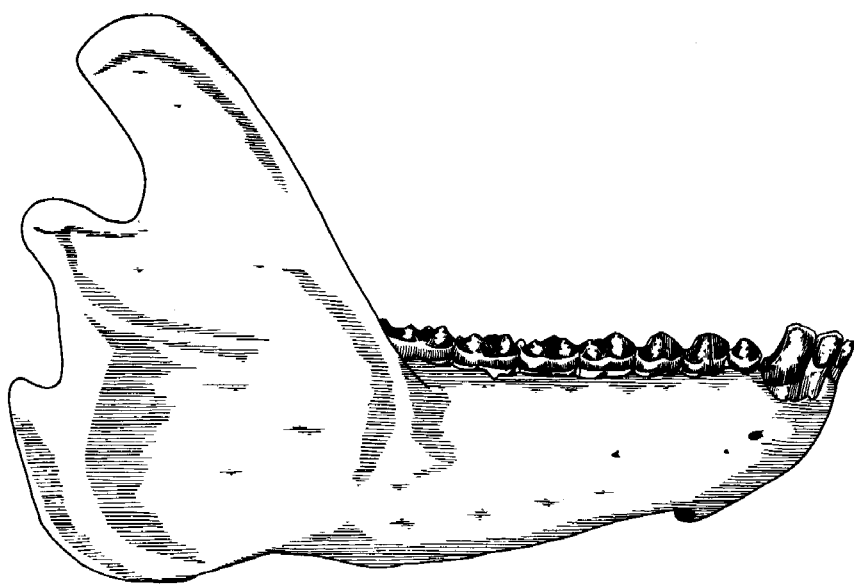


Fig. 4 — Reconstruction of the mandible of *Adapis parisiensis* based on Princeton University 11499 and specimens in the Muséum National d'Histoire Naturelle, Paris. Note particularly the anthropoid-like sectorial incisors and fused symphysis, and also the incisiform canines characteristic of this species. Scale : 1 cm.

Reconstitution de la mandibule d'*Adapis parisiensis* fondée sur le spécimen de l'Université de Princeton n° 11499 et le spécimen du Muséum d'Histoire Naturelle de Paris. On remarquera surtout les incisives sectoriales de type anthropoïde ainsi que la symphyse fusionnée ; les canines incisiformes sont caractéristiques de l'espèce. Echelle : 1 cm.

reduced in size independently in *Protoadapis klatti*, *Caenopithecus lemuroides*, and *Cercamonius brachyrhynchus*. Very similar reduction of the pre-molar region occurred, possibly independently, in the North American adapid of European aspect « *Margarita* » (Wilson & Szalay, 1976). This trend is related to shortening of the face in primates, and

characterized several early anthropoid primates as well as these advanced *Adapidae*.

Fusion of the mandibular symphysis furnishes an additional example of parallel evolution in *Adapidae*. Symphyseal fusion occurred independently in *Caenopithecus*, *Cercamonius*, and *Adapis* in Europe (fig. 4). Fusion also occurred independently

in North America in *Notharctus* and in Asia or North America in the ancestry of «*Margarita*». Thus symphyseal fusion occurred independently no fewer than five times in the Adapidae.

A metastylid cusp on the lower molars evolved independently in *Caenopithecus* and *Adapis*, and additional examples of independent parallel acquisition of morphological characteristics could be given. The common occurrence of evolutionary

reversals and parallel evolution documented here and in other detailed biostratigraphical studies should serve as a caution to those wishing to use key « derived » characters to reconstruct phylogeny using « cladistics ». Many detailed anatomical resemblances thought to be « shared, derived » characters are demonstrably not homologous in the sense they cannot be traced to a common presence in the last common ancestor.

V. — ORIGIN OF ADAPIDAE

As noted above, the earliest *Adapidae* appeared suddenly in Europe and North America in the early Eocene. All of the European *Adapidae* appear to have been derived from *Pelycodus eppsi* or some very closely related species, and all of the North American *Adapidae* appear to have been derived from *Pelycodus ralstoni*. *Pelycodus eppsi* and *Pelycodus ralstoni* are practically indistinguishable species, and either one could be the ancestor of the other. The question to be considered here is whether the *Adapidae* originated in the Old World or in the New World? Fortunately new evidence bearing on this questions has recently become available.

Purgatorius and paleogene climatic history

New collections made by W. A. Clemens (1974, and recent work) have improved our knowledge of the earliest *Purgatorius* considerably. Virtually all specimens of *Purgatorius* come from the early Paleocene of North America, but since mammal faunas of correlative age are unknown in Europe and Asia it is possible, perhaps probable, that *Purgatorius* enjoyed a Holarctic pangeographic distribution in the earliest Paleocene. *Purgatorius* appears to be sufficiently generalized to have given rise to all later primates, including what I have called Plesitarsiiformes on the one hand and Simiolemuriformes on the other (Gingerich, 1976).

A plausible hypothesis based on paleoclimates can be advanced to explain why intermediate forms linking a *Purgatorius*-like early Paleocene ancestor with *Pelycodus* are unknown. Paleocene and Eocene fossil mammals are known mostly from middle to high latitudes in North America, Europe,

and Asia. Hence only a portion of the available habitat for mammals during this time has been sampled paleontologically. In the early and middle Paleocene, paleobotanical evidence suggests that the areas where fossil deposits are known were in a belt of essentially subtropical climates, and diverse primate assemblages are known from this period in North America. During the late Paleocene, climates were cooler, the areas of known fossil deposits being in a warm temperate climatic belt, and known primate faunas appear less diverse (being dominated by plesiadapids). Subtropical climates returned to the latitudes of known fossil deposits in the early Eocene, and apparently brought with them a renewed diversity of primates, including the early adapid *Pelycodus* (Gingerich, 1976, p. 86-88).

This climatic history appears to have had two effects. First, it limited forms such as those directly ancestral to *Pelycodus* to equatorial areas (like central America, or southern Europe and Africa, or perhaps southern Asia) where fossil mammals have not yet been found. Thus the intermediate links between *Purgatorius*-like primates and *Pelycodus* are still unknown. Secondly, the distribution of land masses and oceans during the late Paleocene was such that when subtropical primate faunas were pushed southward, their original pangeographic distribution was disrupted. Characteristic endemic forms evolved in isolated American, European, and Asian faunas. Warming in the early Eocene again made high latitude land corridors connecting the northern continents accessible to subtropical mammals (McKenna, 1975), and many genera such as *Pelycodus* that originated in central America, southern Europe and Africa, or southern Asia assumed pangeographic Holarctic distributions.

Azibius and adapid paleogeography

The fact that Madagascar today contains a fauna dominated by lemuroid primates has led many authors to postulate an African origin for the Lemuriformes, including *Adapidae* (McKenna, 1967; Hoffstetter, 1974; and others). New evidence strengthens this view, although it must be noted that Paleocene and earliest Eocene mammals have not yet been found in Africa.

Of great interest and importance is the recent description of a new primate, *Azibius trecki*, from the Eocene of North Africa (Sudre, 1975). J. Sudre placed *Azibius* in the « Paromomyiformes », but, as figure 5 shows, it also resembles closely some Eocene *Adapidae* (I cannot agree with F. S. Szalay, 1975, p. 401, that *Azibius* is a hyopsodontid-like condylarth). As J. Sudre

(1975) suggested, the premolar enlargement and specialisation of *Azibius* are reminiscent of plesiadapiform primates such as *Elphidotarsius* and *Carpodaptus*. The morphology of M_2 , on the other hand, resembles much more closely the molar morphology of *Adapidae*. The squared preprotocristid and reduced paraconid are particularly important in this regard. Premolar enlargement and specialization are common in many mammalian groups, but the molar morphology of *Azibius* appears distinctly adapid, and for this reason I would refer *Azibius* to the *Adapidae* rather than any group of Plesiadapiformes.

Azibius and *Oligopithecus* (see below) give paleontological weight to an African origin of the *Adapidae*. My earlier suggestion that lemuriform primates may have colonized Madagascar from southern Asia (Gingerich, 1975a) should probably

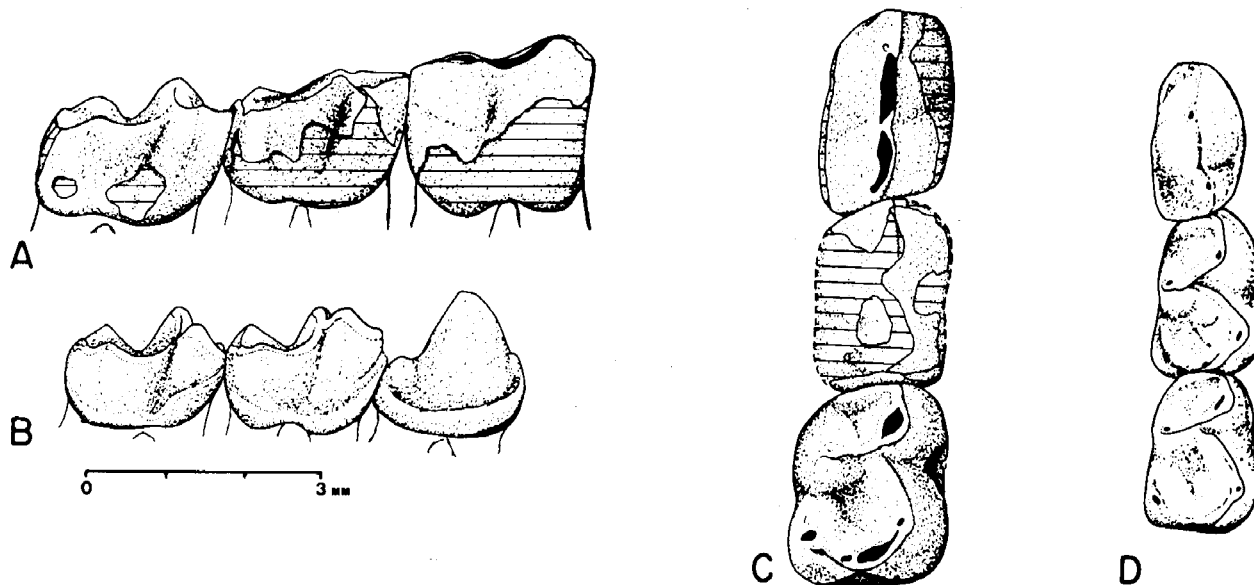


Fig. 5 — Comparison of the preserved dentition of the type specimen of *Azibius trecki* (A and C) with homologous teeth $P_4 - M_2$ in the type specimen of *Anchomomys stehlini* (B and D). Note particularly the open squared trigonids with reduced paraconids characteristic of *Adapidae*. Lines on *Azibius* specimen indicate areas of chemically eroded missing enamel, solid black indicates natural exposure of dentine.

Comparaison de la dentition conservée des spécimens type d'*Azibius trecki* (A et C) avec les dents homologues $P_4 - M_2$ du spécimen type d'*Anchomomys stehlini* (B et D). On remarquera surtout les trigonides ouverts en carré avec des paraconides réduits caractéristiques des *Adapidae*. Les hachures sur la figure d'*Azibius* indiquent la zone errodée chimiquement où manque l'émail, le figuré noir indique l'apparition naturelle de la dentine.

be abandoned in favor of an African origin. Arrival of *Pelycodus* in North America at the same time as the first hyaenodontid creodonts (Gingerich & Rose, 1977; hyaenodontids were the dominant

group of early African carnivores) is further circumstantial evidence favoring an African origin of *Adapidae*.

VI. — EUROPEAN ADAPIDAE AND LATER PRIMATE EVOLUTION

As stated in the introduction, part of the interest in Eocene Adapidae and in gaining a better understanding of their evolution stems from their importance for the origin of later primates, both lemuriform and simiiform or anthropoid.

Origin of living Lemuriformes

Living Lemuriformes are divided into two superfamilies, *Lemuroidea* and *Lorisoidea*, both of which are characterized by the presence of a distinctive mandibular dental scraper composed of incisors and canines. The *Lorisoidea* have a fossil record extending back to the Miocene in East Africa (Walker, 1974), but the *Lemuroidea* have only a subfossil and recent record in Madagascar. For a number of anatomical reasons, lemuroids are usually considered to more closely approximate the common ancestor of living lemuriform primates than lorisooids do. *Hapalemur* and *Lepilemur* are among the most generalized lemuriform primates, and they are thought possibly to be the most primitive for this reason.

When all living Lemuriformes are compared with European *Adapidae*, their closest resemblance is to *Adapis parisiensis*. *Adapis parisiensis* resembles both *Hapalemur* and *Lepilemur* in molar morphology (Gingerich, 1975a). *Adapis* lacks the dental scraper characteristic of living Lemuriformes, but it is unique among all adapids for which the anterior dentition is known in having the lower incisors and canines organized into a single functional unit (fig. 4). That is, the canines are not projecting teeth in *Adapis parisiensis*, but low crowned incisiform teeth that functioned as a single unit with the incisors. This conformation would appear to be an initial step required by the functional reorganization of the canines into a unit with the incisors, as is later seen in the dental scraper of Lemuriformes, thus *Adapis parisiensis* appears preadapted for the evolution of a dental scraper of the kind seen in living lemuriform primates.

Dental scrapers are used by living lemurs to

gather resin or gum, and to feed on tree bark (Martin, 1972). Once the lower canines were incisiform and functioning as a unit with the incisors, it is not difficult to see how their use to scrape resin and to prise bark might lead to modification of the unit into a procumbent dental scraper like that seen in living lemurs. Resin and bark are foods most important in the diet of living Lemuriformes during the dry season, and it should be noted that *Adapis parisiensis*, with its unique anterior dental conformation, evolved during a period of cooling and increased seasonality when resin and bark may have become increasingly important constituents in its diet.

Adapidae have long been regarded as the ancestors of living Lemuriformes because of dental and cranial resemblances, such as the free annular ectotympanic within the auditory bulla. *Adapis* itself is most similar to generalized living Lemuriformes, and probably the most closely related to them among known Eocene primates. The resemblances shared by *Adapis* with living genera like *Hapalemur* and *Lepilemur* can all be explained away as retained primitive characteristics or convergent specializations if one wishes, but the fact remains that *Adapis*, *Hapalemur*, and *Lepilemur* are remarkably similar in spite of a gap in the fossil record of some 35 my.

Origin and radiation of higher primates

Primitive Simiiformes or Anthropoidea can with confidence be traced back in the fossil record to the Oligocene. Primate fossils from the Fayum Province of Egypt, such as *Aegyptopithecus* discovered and collected by Simons' expeditions, are sufficiently complete to establish beyond any doubt that they represent primitive anthropoids (Simons, 1972). These fossils are particularly important in studying the origin of higher primates for two reasons: (1) they demonstrate that the ancestry of Simiiformes is probably at least as old as the late Eocene, and (2) they demonstrate many features of the osteology of truly primitive anthro-

poids in a way that comparative analysis of living forms could not. Undoubted higher primates are to be found first in the Quarry G level of the Fayum where the genera *Apidium* and *Propliopithecus* are first found. Before the time represented by Quarry G, several primates are known from the late Eocene and early Oligocene that are equivocally placed in either the *Adapidae* or the anthropoid Simiiformes, for example *Oligopithecus* and *Hoanghoni* (figure 6), *Amphipithecus* (Szalay, 1970; Simons, 1971), and *Cercamoni* (Gingerich, 1975b). These forms all share some combination of molar morphology, symphyseal fusion, canine honing, premolar crowding, and deep mandibular rami that make some advanced *Adapidae* virtually indistinguishable from primitive anthropoids. As was outlined in discussing phylogeny reconstruction above, the intermediate morphological characteristics and intermediate stratigraphic position of these equivocal late Eocene and early Oligocene genera makes them very strong evidence that higher primates evolved from *Adapidae*. Stratophenetically they link the *Adapidae* even more closely to Simiiformes than the former are linked to living Lemuriformes.

Assuming that lemuroids and lorisooids are derived from a species close to *Adapis parisiensis*, and anthropoids are derived from a form like *Hoanghoni* or *Cercamoni*, the last common ancestor of living Lemuriformes and Simiiformes probably lived in the early Eocene, or about 50 my ago. Primates confused with anthropoids do not appear in the fossil record until the late Eocene, and it is unlikely that they evolved before that time. The late Eocene was a time of broad intercontinental migration when a number of Eurasian genera invaded North America (*Hyaenodon*, etc.; see Simpson, 1947). Presence of an adapid of Eurasian aspect, «*Margarita*», in Texas in the late Eocene indicates that primates were part of this migration and provides very suggestive evidence that the ancestral Ceboidea may have followed the same route to South America. The last common ancestor of cebooids and Old World higher primates was probably a late Eocene species, and the separation can thus be dated at about 40 my.

An outline of the phylogenetic history of primates suggested by the fossil evidence is reproduced in figure 7, where the last common ancestor of living *Tarsius* and other primates is interpreted as an early Paleocene *Purgatorius*-like form. Thus the separation between *Tarsius* and other living primates occurred about 60 to 65 my ago. I am aware that the geometry of the phylogeny in figure 7 and the dates of divergence between Tar-

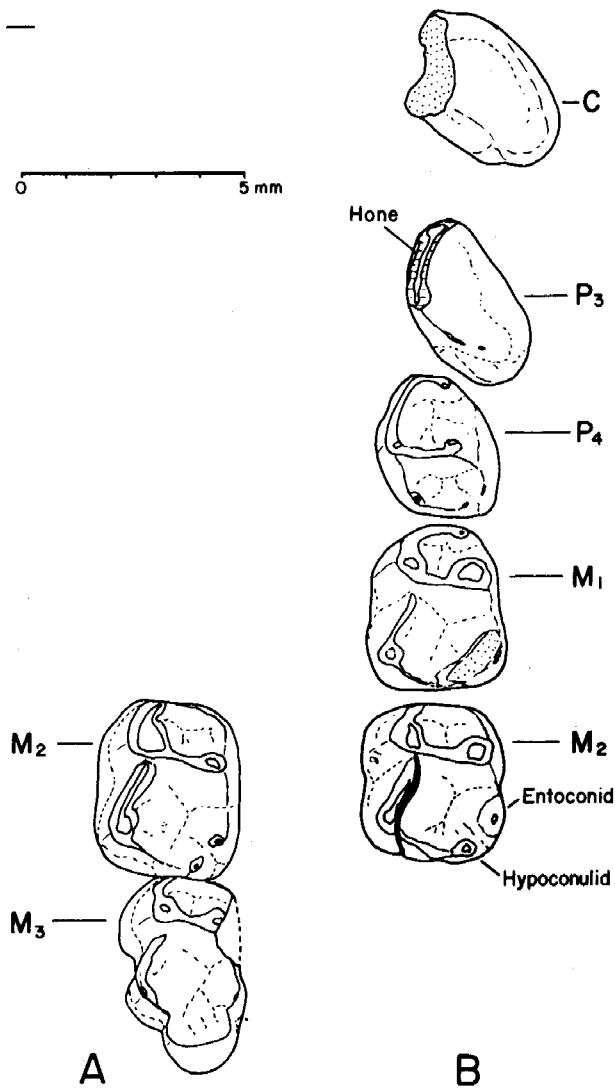


Fig. 6 — Comparison of the type specimen of *Hoanghonius stehlini* (A) with the type specimen of *Oligopithecus savagei* (B). Both show teeth only, in occlusal view. Note particularly the open squared trigonid with reduced paraconid of *M₂* characteristic of *Adapidae*, and the distinctive notch between closely approximated hypoconulids and entoconids in both. *Oligopithecus*, like some advanced *Adapidae*, has a distinctive *P₃* hone for the upper canine.

Comparaison des spécimens types d'*Hoanghonius stehlini* (A) avec le spécimen type d'*Oligopithecus savagei* (B). Ces deux figures sont seulement des vues occlusales des dents. On remarquera surtout le trigonide ouvert en carré avec un paraconide réduit caractéristique des *Adapidae* et l'encoche caractéristique entre les hypoconulides et entoconides assez rapprochées, qui est présente chez les 2 formes. *Oligopithecus*, comme quelques *Adapidae* évolués, possède une *P₃* caractéristique avec facette d'usure pour la canine supérieure.

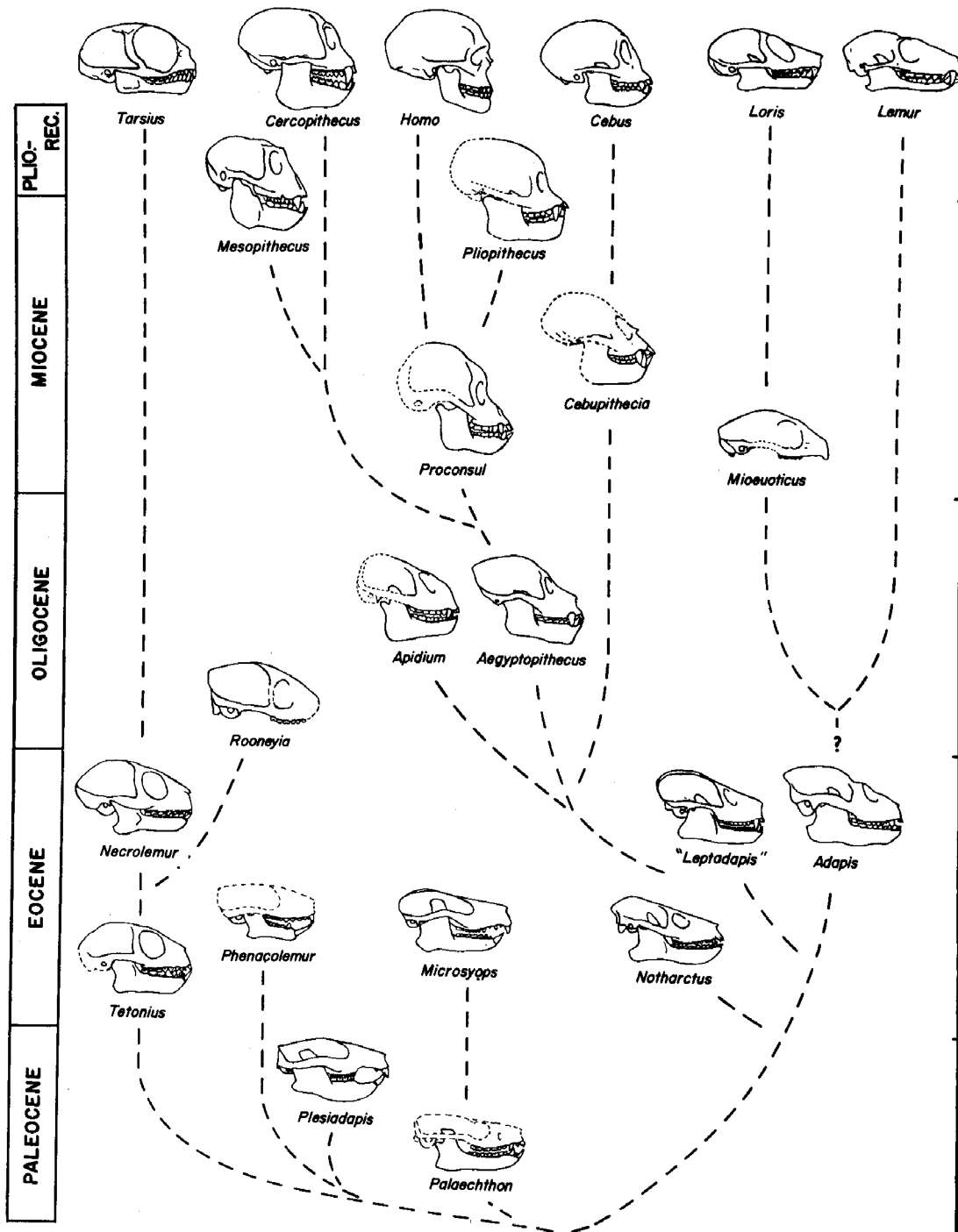


Fig. 7 - General outline of the phylogeny of Primates, based on a stratophenetic analysis of available fossil specimens. Figures of primate skulls are not to scale. Higher primates can be traced to an adapid ancestry in the late Eocene (probably from a Eurasian stock). Lorisoids and lemuroids probably also originated from *Adapidae*. This figure is discussed at greater length by Gingerich and Schoeninger (1977).

Tableau général de la phylogénie des Primates, fondée sur une analyse stratigraphique et phénotypique des spécimens fossiles disponibles. Les schémas des crânes de primates ne sont pas à l'échelle. Les primates évolués peuvent être issus d'une ascendance adapidienne à l'Eocène supérieur (probablement d'un stock eurasiatique). Les lorisoides et lémuroides s'enracinent aussi probablement chez les *Adapidae*. Ce schéma est discuté plus longuement dans Gingerich et Schoeninger (1977).

siiformes, Lemuriformes, and Simiiformes given here differ significantly from those suggested by some cladistic analyses of biochemical and anatomical systems in living primates (for example, see Goodman, 1975; Luckett, 1975; and others). One problem to which attention might be directed is the question of how good a representative the sole living genus *Tarsius* is of the whole infraorder Tarsiiformes? The evidence on primate phylogeny provided by the fossil record is now sufficiently

complete and detailed that it deserves to be analyzed independently, and the results stated without bias from studies limited to living primates. The phylogeny presented in figure 7 is an hypothesis of relationships that will continually be tested in the future by the extent to which newly discovered fossil primates fit into it, but it is an hypothesis based on an increasingly dense and continuous fossil record suggesting that it may well prove to be a robust theory of primate phylogeny.

VII. — CONCLUSIONS

Phylogeny reconstruction is basically an historical and thus paleontological problem that requires accurately dated fossil specimens for any but the most tentative solutions. Reconstructing phylogeny from the fossil record requires first (1) a study of variation and determination of the number of « biological » species in each collection of fossils from each locality sampled, then (2) relating localities sampled to each other on the basis of superposition and/or biostratigraphical correlation, (3) linking of samples in adjacent stratigraphic intervals based on overall similarity or phenetic resemblance, and finally (4) continued testing by the extent to which new fossil discoveries conform to the hypothesis suggested by the pattern stratophenetic linking.

The phylogeny of European *Adapidae* and the phylogeny of Primates have been studied using this stratophenetic method. Evolutionary lineages of European *Adapidae* show several interesting examples of diminution as well as increase in size, several evolutionary reversals, and a number of examples of parallelism. The best documented lineages of *Adapidae* show continuous gradual evolutionary change through time.

Adapidae probably originated in Africa from a *Purgatorius*-like ancestor during the middle or late Paleocene, and the first adapid species appeared in Europe and North America early in the Eocene as immigrants. Eocene *Adapidae* probably gave rise to both living Lemuriformes and living anthro-

poid primates, some of which colonized South America from Asia by migrating through North America in the late Eocene. Judging from the fossil record, the divergence of Tarsiiformes from the Lemuriformes-Simiiformes group happened about 60-65 my ago. Lemuriformes separated from Simiiformes about 50 my ago, and the divergence of Platyrrhini and Catarrhini dates to about 40 my ago.

Acknowledgments

The research reported here was made possible by a NATO Postdoctoral Fellowship at the Université de Montpellier, and I am particularly grateful to Professor L. Thaler, Dr. J. Sudre, and other colleagues in Montpellier for making my stay there so rewarding and enjoyable. I also wish to thank Drs. D. E. Russell in Paris, P. Louis in Cormicy, P. Mein in Lyon, M. Crusafont-Pairo in Sabadell, B. Engesser in Basel, N. Schmidt-Kittler in Munich, and many other curators of European collections of *Adapidae* for access to specimens. Some travel and research funds for this project were provided by the Rackham School of Graduate Studies and by the Turner Fund for geological research, University of Michigan. Krystyna Swirydzuk drew figure 4, Karna Steelquist copied the figures, and Mrs. Gladys Newton typed the manuscript.

		n	Range	\bar{x}	s	v
C ₁	L	7	6.6 – 8.2	7.20	.54	7.5
	W	7	4.7 – 5.5	5.21	.25	4.9
	H	6	8.1 – 9.2	8.85	.45	5.1
P ₁	L	2	3.6 – 3.8	3.70	.14	3.8
	W	2	2.3 – 2.6	2.45	.21	8.7
P ₂	L	12	5.8 – 6.9	6.43	.34	5.3
	W	12	3.5 – 4.2	3.93	.20	5.1
P ₃	L	15	5.6 – 6.8	6.42	.32	4.9
	W	15	3.6 – 4.4	4.01	.22	5.4
P ₄	L	21	5.9 – 7.0	6.48	.31	4.8
	W	21	4.0 – 5.3	4.67	.33	7.0
M ₁	L	23	6.3 – 7.4	6.80	.26	3.8
	W	24	4.5 – 5.4	4.90	.25	5.1
M ₂	L	24	6.7 – 8.1	7.50	.37	4.9
	W	24	5.0 – 6.2	5.62	.36	6.3
M ₃	L	19	9.0 – 10.7	10.12	.46	4.6
	W	18	4.4 – 6.1	5.39	.37	6.8
M. Depth		23	15.0 – 20.2	17.64	1.34	7.6
C ¹	L	4	7.3 – 8.7	7.78	.63	8.1
	W	4	5.4 – 6.4	5.83	.51	8.7
	H	3	10.0 – 10.7	10.30	.36	3.5
P ¹	L	2	3.3 – 4.2	3.75	.64	17.0
	W	2	2.2 – 2.5	2.35	.21	9.0
P ²	L	4	6.1 – 7.0	6.50	.37	5.8
	W	4	3.6 – 4.2	3.95	.30	7.6
P ³	L	5	4.7 – 7.0	5.44	.93	17.1
	W	5	5.9 – 6.4	6.22	.21	3.3
P ⁴	L	6	5.7 – 6.3	6.00	.23	3.8
	W	6	6.9 – 7.6	7.32	.26	3.6
M ¹	L	8	6.4 – 7.1	6.86	.25	3.6
	W	7	7.7 – 8.7	8.36	.34	4.1
M ²	L	8	6.5 – 7.5	7.21	.36	5.1
	W	7	7.7 – 9.5	8.86	.66	7.4
M ³	L	6	6.4 – 6.8	6.55	.18	2.7
	W	5	7.7 – 9.1	8.48	.61	7.2

Tabl. 1 – Summary of dental measurements of *Adapis magnus* from Euzet. L : length; W : width; M. depth: mandibular depth below M₁; n : sample size; Range : range of variation; \bar{x} : sample mean; s : standard deviation; V : coefficient of variation.

Résumé des mensurations des dents d'*Adapis magnus* d'Euzet. L : longueur; W : largeur; M. Depth : hauteur de la mandibule au niveau de M₁; n : nombre d'échantillons; Range : amplitude de la variation; \bar{x} : moyenne; s : standard déviation; v : coefficient de variation.

