

# 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

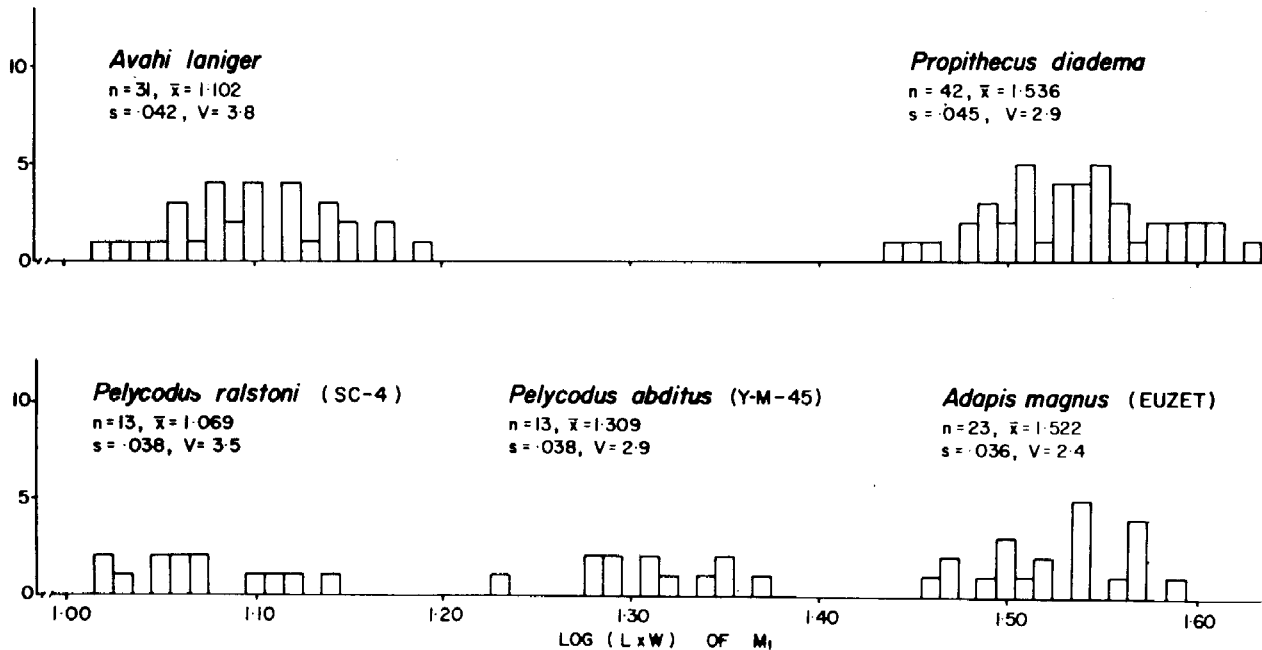


Fig. 1 — Comparison of variation in tooth size in two species of living Madagascar *Indriidae* (*Avahi* and *Propithecus*) with three species of extinct *Adapidae* from different stratigraphic levels in North America (*Pelycodus*) and Europe (*Adapis*). Localities of fossil samples are given in parenthesis. 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

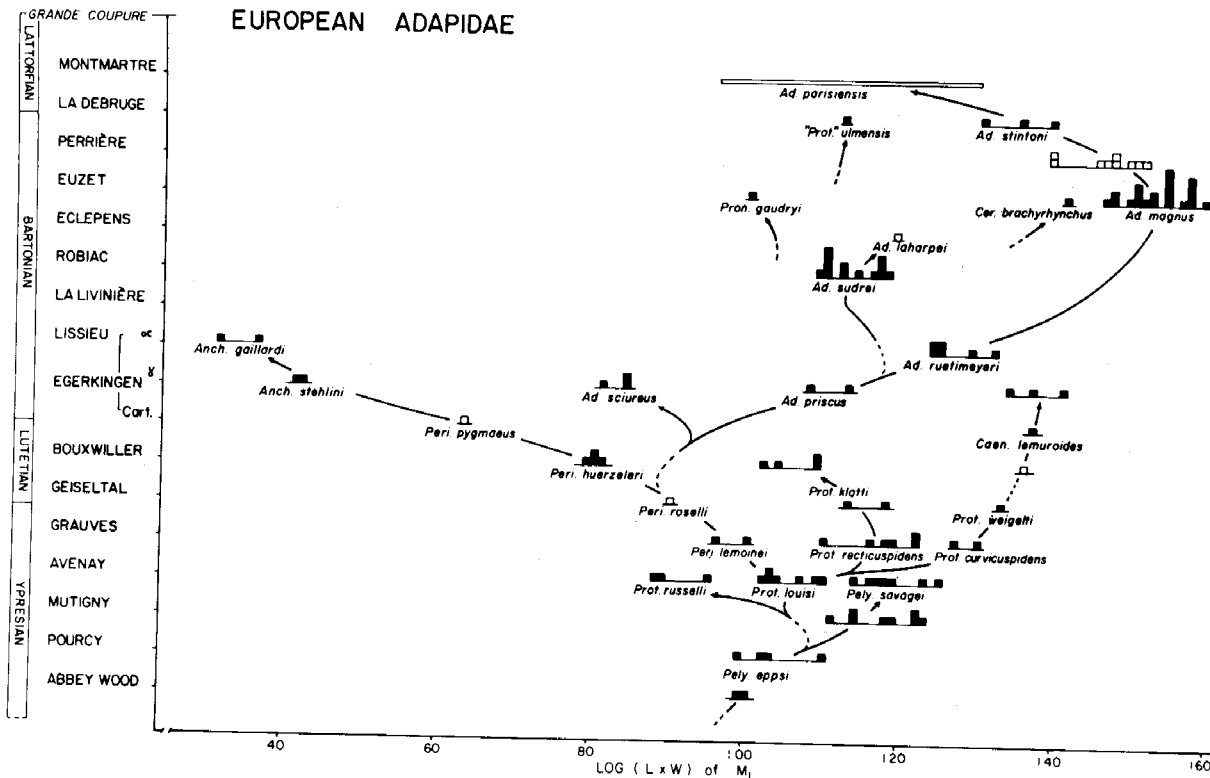


Fig. 2 - Adaptive radiation of European *Adapidae*. Phylogenetic relationships are indicated by lines on a plot of tooth size, but inferred relationships are based on overall similarity of adjacent samples in all available characters. Reproduced from Gingerich (1977).

**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 louisi*

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 louisi*. 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. louisi*, 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  $P_2$

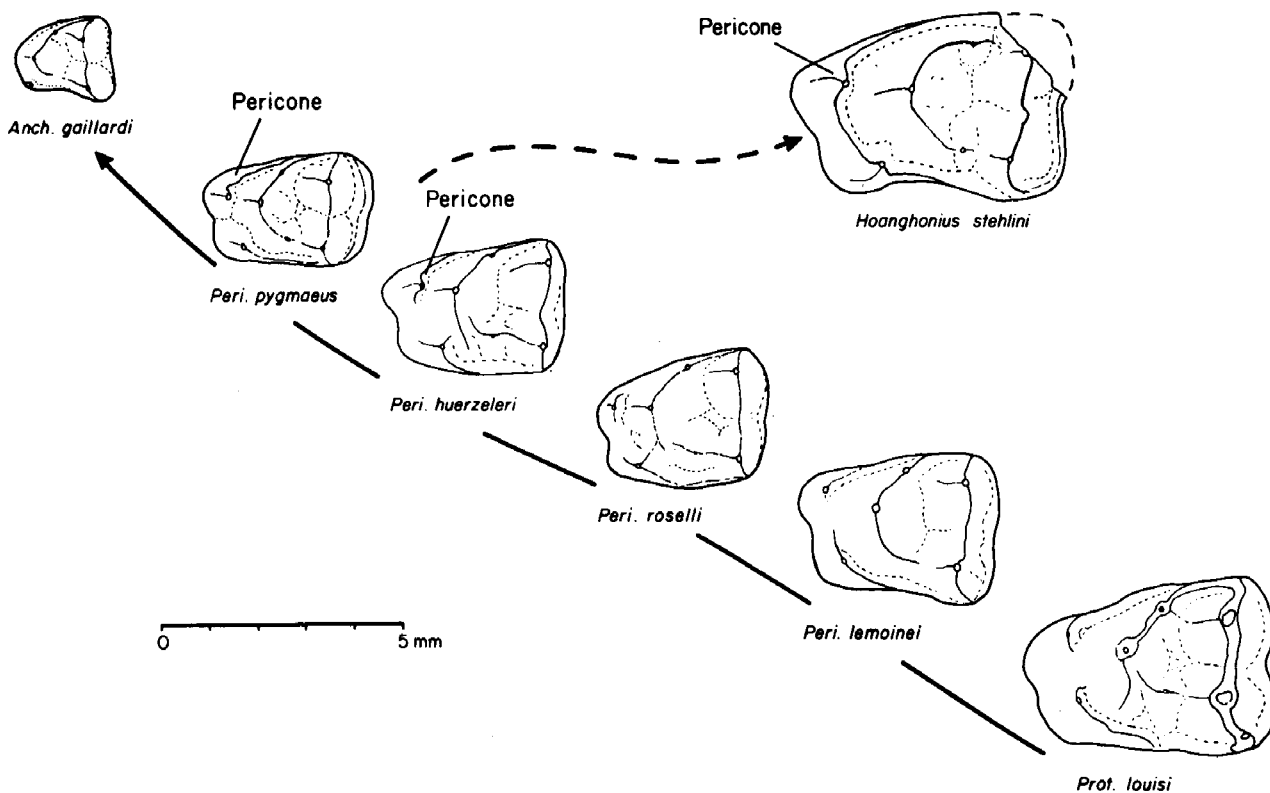


Fig. 3 — Diminution in size and evolutionary reversal in development of the pericône cusp on  $M^2$  from *Protoadapis* to *Periconodon* to *Anchonomys* (compare with fig. 2). *Hoanghonius* is an Asian adapid primate possibly derived from *Protoadapis* or *Periconodon*.

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*.

