

New Species of Eocene Primates and the Phylogeny of European Adapidae

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Abstract. Restudy of virtually all of the important collections of European Eocene primates of the family Adapidae indicates that 28 valid species in 8 genera are now known, spanning a time period of nearly 20 million years. The biostratigraphic distribution of each species has been studied in the context of established reference levels, and a maximum of four evolutionary lineages are known from any one locality. Ten new species are proposed in the genera *Pelycodus* (1 sp.), *Protoadapis* (4 sp.), *Periconodon* (2 sp.), *Anchomomys* (1 sp.), and *Adapis* (2 sp.). Phylogenetic relationships among the species, based on stratophenetic linking, are indicated whenever possible.

Introduction

The first illustration and description of a fossil primate was published by CUVIER in 1812. Ten years later he named the specimen *Adapis*, thinking that it was a small pachyderm perhaps related to hyraxes. Exactly 50 years after CUVIER'S first description of *Adapis*, RÜTIMEYER [1862] described a fossil specimen from slightly older sediments as *Caenopithecus lemuroides*. This was the first species to be recognized as a fossil lemuriform primate, although RÜTIMEYER emphasized the possibility that it might at the same time be related to higher primates. Fifty years later STEHLIN [1912] described the cranial anatomy of *Adapis* in one of the most complete descriptions of a fossil primate genus ever published. At the end of still another 50-year period, SIMONS [1962] reviewed the Eocene lemuriform primates of Europe.

Since 1962, an enormous quantity of new adapid material has been collected and described in Europe by RUSSELL *et al.* [1967], SUDRE [1969],

SCHMIDT-KITTLER [1971], CRAY [1973], CRUSAFONT-PAIRÓ and GOLPE-POSSE [1975], and others. In addition, the relative biostratigraphic position of many of the European localities yielding Adapidae is now well established, following detailed studies by THALER [1966], FRANZEN [1968], HARTENBERGER [1973], CROCHET *et al.* [1975], and others [see especially FAHLBUSCH, 1976]. As a result, it is now possible to discuss the phylogenetic history of the Adapidae in much more detail than was possible previously. The purpose of this paper is to record a number of new species, and to outline the phylogenetic relationships of the genera and species of European Adapidae.

Institutional abbreviations used in this paper are as follows: Basel – Naturhistorisches Museum, Basel (Switzerland); BMNH – British Museum (Natural History), London (England); Halle – Geiseltal Museum, Halle (GDR); Louis – Private collection of P. LOUIS in Cormicy near Reims (France); Louvain – Laboratorium voor Actuepaleontologie, Katholieke Universiteit, Louvain (Belgium); Lyon – Université Claude Bernard, Lyon (France); MNHN – Institut de Paléontologie, Muséum National d'Histoire Naturelle, Paris (France); Montpellier – Laboratoire de Paléontologie, Université de Montpellier, Montpellier (France); Munich – Universitätsinstitut für Paläontologie, Munich (FRG); Sabadell – Instituto Paleontología, Sabadell (Spain); UCM – Museum of Paleontology, University of California, Berkeley, Calif. (USA).

Species of European Adapidae

The family Adapidae, as now known, includes 28 European species placed in 8 genera. The valid genera and species of European Adapidae are listed in table I. Of these 28 species, 9 are here newly described, and a replacement name is proposed for one preoccupied species name. SZALAY [1974] recently proposed that *Anchomomys* (?) *quercyi* be placed in the new genus *Huerzeleris*, that *Adapis sciureus* be placed in the new genus *Microadapis*, and that *Adapis magnus*, *A. priscus*, and *A. ruetimeyeri* be placed in GERVAIS' genus *Leptadapis*. WILSON and SZALAY [1976] also placed *Protoadapis klatti* in WEIGELT's genus *Europolemur*. The result is that the genera *Huerzeleris*, *Microadapis*, *Adapis*, and *Europolemur* are all monotypic, each including but a single species. These four genera are not recognized in this study because, given present knowledge of phylogenetic relationships, their recognition obscures rather than clarifies the unified nature of the adapid radiation. However, it is necessary to retain *Caenopithecus* [RÜTIMEYER, 1862], *Pronycticebus* [GRANDIDIER, 1904], and

Table I. The European species of Eocene Adapidae

Species	Type locality (reference level)
<i>Protoadapis</i> group	
1. <i>Pelycodus epsi</i> [COOPER, 1932]	Abbey Wood (Dormaal)
2. <i>Pelycodus savagei</i> sp. nov.	Avenay (Mutigny-Avenay-Grauves)
3. <i>Protoadapis russelli</i> sp. nov.	Avenay (Avenay)
4. <i>Protoadapis louisi</i> sp. nov.	Avenay (Avenay)
5. <i>Protoadapis recticuspidens</i> [LEMOINE, 1878]	? (Grauves)
6. <i>Protoadapis curvicuspidens</i> [LEMOINE, 1878]	? (Grauves)
7. <i>Protoadapis klatti</i> [WEIGELT, 1933]	Geiseltal (Geiseltal-Bouxwiller)
8. <i>Protoadapis weigelti</i> sp. nov.	Geiseltal (Geiseltal)
9. <i>Protoadapis filholi</i> nom. nov.	'Quercy' (?)
10. ' <i>Protoadapis</i> ' <i>ulmensis</i> [SCHMIDT-KITTLER, 1971]	Ehrenstein 1A (La Debruge)
11. <i>Periconodon lemoinei</i> sp. nov.	Grauves (Grauves)
12. <i>Periconodon roselli</i> [CRUSAFONT-PAIRÓ, 1967]	Las Saleres (Geiseltal)
13. <i>Periconodon huerzeleri</i> sp. nov.	Bouxwiller (Bouxwiller)
14. <i>Periconodon pygmaeus</i> [RÜTIMEYER, 1890]	Egerkingen-Cartier (Egerkingen I)
15. <i>Anchomomys stehlini</i> sp. nov.	Egerkingen-γ (Egerkingen II)
16. <i>Anchomomys gaillardi</i> [STEHLIN, 1916]	Lissieu (Lissieu)
17. <i>Anchomomys</i> (?) <i>quercyi</i> [STEHLIN, 1916]	'Quercy' (?)
18. <i>Caenopithecus lemuroides</i> [RÜTIMEYER, 1862]	Egerkingen-Cartier (Bouxwiller-Egerkingen I & II)
19. <i>Pronycticebus gaudryi</i> [GRANDIDIER, 1904]	Memerlein (Euzet)
20. <i>Cercamomys brachyrhynchus</i> [STEHLIN, 1912]	Prajous (Euzet)
<i>Adapis</i> group	
21. <i>Adapis sciureus</i> [STEHLIN, 1916]	Egerkingen-γ (Egerkingen II)
22. <i>Adapis priscus</i> [STEHLIN, 1916]	Egerkingen-γ (Egerkingen II)
23. <i>Adapis ruetimeyeri</i> [STEHLIN, 1912]	Egerkingen-α (? Lissieu)
24. <i>Adapis sudrei</i> sp. nov.	Robiac (Robiac)
25. <i>Adapis laharpei</i> [PICTET and HUMBERT, 1869]	Eclépens (Le Bretou)
26. <i>Adapis magnus</i> [FILHOL, 1874]	'Quercy' (Euzet)
27. <i>Adapis stintoni</i> sp. nov.	Headon Lignite Bed (La Debruge)
28. <i>Adapis parisiensis</i> ¹ [BLAINVILLE, 1849]	Montmartre (Montmartre)

¹ It may eventually be necessary to recognize *Adapis angustidens* [FILHOL, 1883] and *Adapis betillei* [DELFORTRIE, 1873] as species distinct from *Adapis parisiensis*.

Cercamomius [GINGERICH, 1975] as monotypic genera because of their distinctive specializations.

New species of Adapidae are briefly diagnosed and figured in this paper. More complete data on dental variation, cranial anatomy, and evolutionary

trends will be presented in a monograph on the family Adapidae now being prepared. An outline of the phylogeny of European Adapidae is presented here, following description of the new species.

***Pelycodus savagei*, New Species (fig. 1B)**

Cantius cf. eppsi (in part), RUSSELL *et al.* [1967, p. 18].

Type. MNHN Av-5757, a right M₁ from Avenay measuring 4.1 mm in length, and 3.5 mm in width.

Diagnosis. *Pelycodus savagei* differs from *Pelycodus eppsi* in being significantly larger, but it is otherwise very similar to that species. The European *Pely. savagei* resembles *Pely. trigonodus* from North America in size, but differs from that species in having the hypocone, where present, developed from the basal cingulum and not from the postprotocingulum. In addition, *Pely. savagei* differs from contemporary species of *Pelycodus* in North America in having relatively broader and flatter molars with slightly lower and more rounded cusps.

Etymology. Named for Professor D.E. SAVAGE, University of California at Berkeley, in recognition of his contribution to the discovery, collection, and study of European Adapidae from Avenay and elsewhere.

Discussion. European Adapidae (subfamily Adapinae) are usually distinguished from North American Adapidae (subfamily Notharctinae) by the formation of the hypocone. In Adapinae the hypocone appears on the basal cingulum, whereas in Notharctinae the hypocone is developed on the postprotocingulum. It is interesting that correlation of this morphological distinction with geographic distribution holds even within the genus *Pelycodus*, where a 'true' hypocone on the basal cingulum evolved in the European forms, and a 'pseudohypocone' on the postprotocingulum evolved in the North American species. This might be considered evidence for placing the European species of *Pelycodus* in SIMONS' [1962] genus *Cantius*, but such a move would obscure the fundamental unity of the ancestral stock of both Adapinae and Notharctinae.

Hypodigm. Numerous isolated teeth from Avenay and Mutigny in the Louis, MNHN, and UCMP collections. A few isolated teeth from Grauves are also referred to this species.

***Protoadapis russelli*, New Species (fig. 1C)**

Prosimii, family, genus, and species indet., RUSSELL *et al.* [1967, p. 42].

Type. Louis Av-183, a right M₁ from Avenay measuring 3.1 mm in length and 2.5 mm in width.

Diagnosis. *Protoadapis russelli* differs from contemporary *Prot. lousi* and all other known *Protoadapis* in being significantly smaller.

Etymology. Named for Dr. D.E. RUSSELL, Muséum National d'Histoire Naturelle in Paris, in recognition of his contribution to the discovery, collection, and study of European Adapidae from Avenay and elsewhere.

Discussion. This species is at present known from only a small number of isolated teeth, but these specimens are sufficient to demonstrate that a very small species of *Protoadapis* is present at Avenay.

Hypodigm. The type and two additional lower first molars [described by RUSSELL *et al.*, 1967, p.42], and some additional isolated teeth, all from Avenay.

***Protoadapis lousi*, New Species (fig. 1D)**

Cantius cf. epsi (in part), RUSSELL *et al.* [1967, p. 18].

Cf. *Protoadapis* sp., RUSSELL *et al.* [1967, p. 41].

Type. Louis Av-118, a right M₁ from Avenay measuring 3.8 mm in length and 2.9 mm in width.

Diagnosis. *Protoadapis lousi* differs from *Prot. russelli* in being significantly larger, and it is smaller than all later species of *Protoadapis*. *Prot. lousi* resembles closely the slightly later species *Periconodon lemoinei*, but differs from it in being significantly larger.

Etymology. Named for M. PIERRE LOUIS of Cormicy near Reims, in recognition of his contribution to the discovery, collection, and study of European Adapidae from Avenay and elsewhere.

Discussion. As suggested previously [GINGERICH, 1974, p.900] two species, not one, are included in the Avenay sample of isolated teeth that RUSSELL *et al.* [1967] included in *Cantius cf. epsi*. In addition, the specimen described by RUSSELL *et al.* as Cf. *Protoadapis* sp. clearly belongs to the new species *Protoadapis lousi* described here. It would appear from study of specimens collected at the localities of Condé-en-Brie and Sézanne, and briefly described by LOUIS [1966, 1970], that *Prot. lousi* probably represents the common ancestor of *Periconodon* and later species of *Protoadapis* as well, but confirmation of this relationship must await full description of these specimens.

Hypodigm. Type and numerous teeth from Avenay in the Louis, MNHN, and UCMP collections.

***Protoadapis weigelti*, New Species (fig. 2C)**

Type. Halle 10209 – H/14 (1949), a right mandible from Geiseltal (Neu-mark-West, Trichter VI) with M₁₋₂ preserved. The enamel on these teeth is

