Folia Primatologica
Editor: J. BIEGERT, Zurich
Publishers: S. KARGER, Basel
SEPARATUM (Printed in Switzerland)
Folia primatol. *28:* 60–80 (1977)

New Species of Eocene Primates and the Phylogeny of European Adapidae

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Key Words. Eocene primates · Lemuriformes · European Adapidae · *Pelycodus* · *Protoadapis* · *Periconodon* · *Anchomomys* · *Adapis*

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

Cercamonius [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 M_1 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 M_1 from Avenay measuring 3.1 mm in length and 2.5 mm in width.

Diagnosis. Protoadapis russelli differs from contemporary *Prot. louisi* 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 louisi, New Species (fig. 1D)

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

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

Type. Louis Av-118, a right M_1 from Avenay measuring 3.8 mm in length and 2.9 mm in width.

Diagnosis. Protoadapis louisi differs from *Prot. russelli* in being significantly larger, and it is smaller than all later species of *Protoadapis. Prot. louisi* 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. *eppsi*. In addition, the specimen described by RUSSELL *et al.* as Cf. *Protoadapis* sp. clearly belongs to the new species *Protoadapis louisi* 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. louisi* 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 (Neumark-West, Trichter VI) with M_{1-2} preserved. The enamel on these teeth is

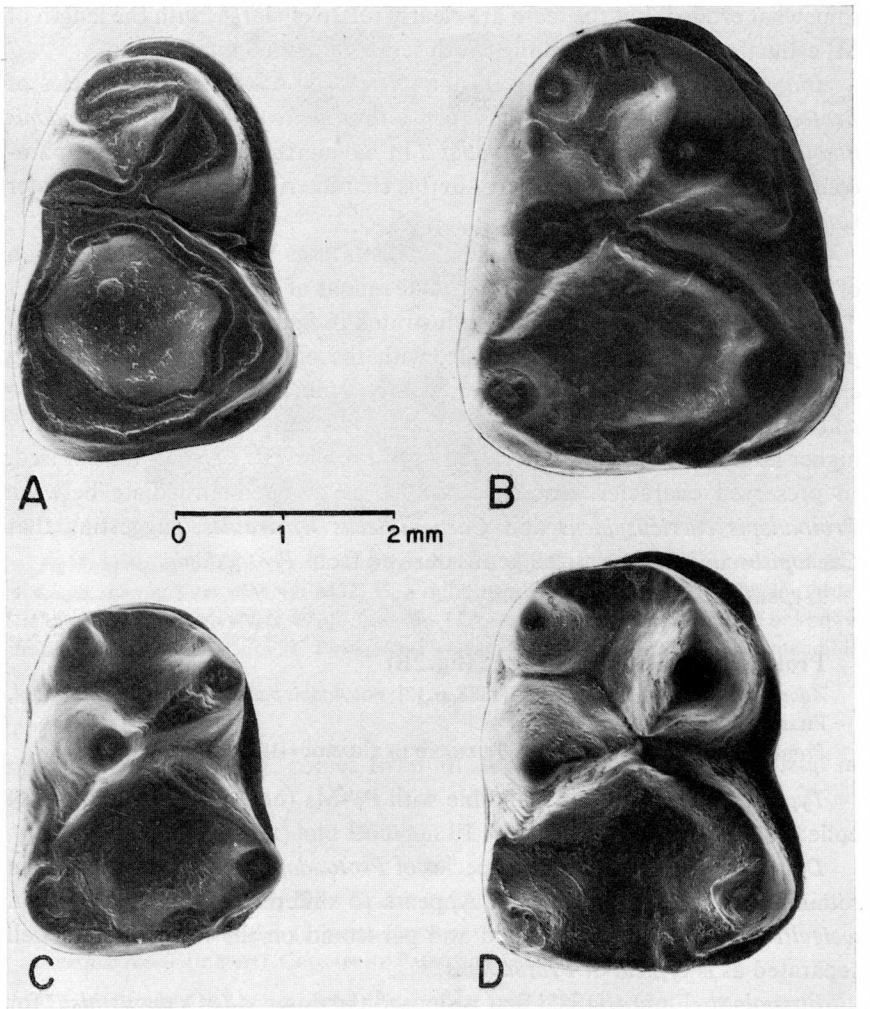


Fig. 1. Type specimens of four new species of European Adapidae. All are right M_1, in occlusal view, and printed at the same scale. *A Periconodon lemoinei* TYPE, Louis Gr-106, from Grauves. *B Pelycodus savagei* TYPE, MNHN Av-5757, from Avenay. *C Protoadapis russelli* TYPE, Louis Av-183, from Avenay. *D Protoadapis louisi* TYPE, Louis Av-118, from Avenay.

somewhat eroded, but the teeth are clearly relatively large, with the length of M_1 estimated as 5.4 mm and the width estimated as 4.0 mm.

Diagnosis. *Protoadapis weigelti* differs from all contemporary species of *Protoadapis* in being significantly larger. It appears to differ from *Protoadapis filholi* and other species of *Protoadapis* in having the protoconid and paraconid more closely approximated – in this characteristic it resembles the later *Caenopithecus lemuroides.*

Etymology. Named for Professor Dr. JOHANNES WEIGELT, in recognition of his contribution to study of the primate faunas of Geiseltal.

Discussion. The type mandible, illustrated in figure 2C, is relatively complete but unfortunately very fragile, with the enamel on the teeth being chemically eroded. This is, however, clearly a much larger species of *Protoadapis* than *Protoadapis klatti*, also known from Geiseltal (from a slightly higher level). The mandibular symphysis in *Protoadapis weigelti* was unfused. In preserved characters this species appears to be intermediate between *Protoadapis curvicuspidens* and *Caenopithecus lemuroides*, suggesting that *Caenopithecus* is a specialized genus derived from *Protoadapis.*

Hypodigm. Type specimen only.

Protoadapis filholi, New Name (fig. 2B)

Adapis angustidens Filhol, FILHOL [1888, p. 12]; not *Adapis parisiensis angustidens* Filhol, FILHOL [1883, p. 21].

Protoadapis angustidens (in part), TEILHARD DE CHARDIN [1922, p. 96].

Type. Unnumbered left mandible with P_3–M_3 (now lost) in the MNHN collection from Quercy.

Diagnosis. Differs from most species of *Protoadapis* in being larger, and in retaining four lower premolars. Appears to differ from the earlier *Prot. weigelti* in having the protoconid and paraconid on the lower molars well separated as is typical of *Protoadapis.*

Etymology. FILHOL [1888] first proposed the name *Adapis angustidens* for the species discussed here, however that species-group name is preoccupied by the senior species-group homonym *Adapis parisiensis angustidens* proposed by FILHOL [1883] himself 5 years earlier. As a result, it is necessary to replace this junior primary homonym with a new specific name, for which *filholi* is proposed. Unfortunately, the type specimen of *Protoadapis filholi* is now lost, but good photographs of the specimen were published by TEILHARD DE CHARDIN [1922]. The only specimen of *Protoadapis filholi* known to the author is a left mandible with M_{2-3} in the collection of the Laboratorium voor Actuopaleontologie, Katholieke Universiteit, in Louvain (fig. 2B). This

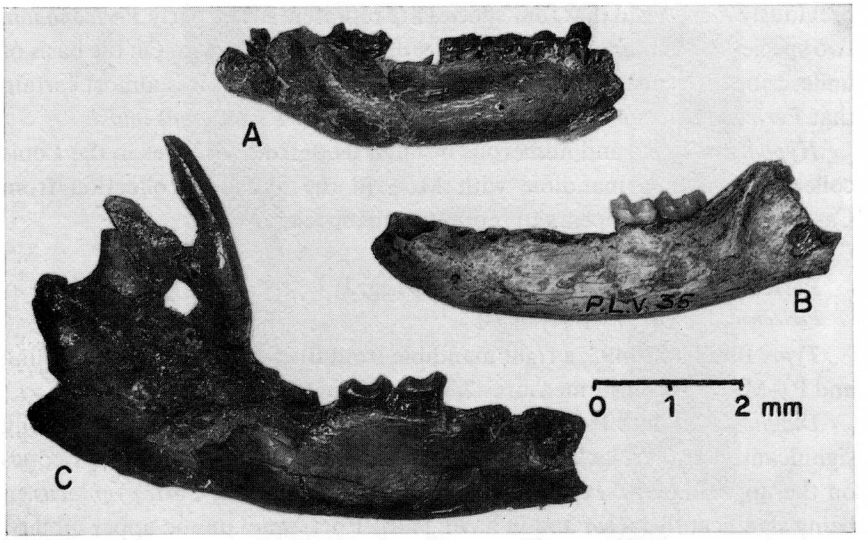


Fig. 2. Specimens of European *Adapis* and *Protoadapis*, all in lateral view, natural size. *A Adapis stintoni* TYPE, BMNH M32135, a right mandible from the Upper Headon beds, Isle of Wight. *B Protoadapis filholi*, Louvain PLV-35, a left mandible from an unknown stratigraphic level in Quercy. *C Protoadapis weigélti* TYPE, Halle 10209, a right mandible from Geiseltal.

specimen, like the type, comes from an unknown stratigraphic horizon in Quercy.

Hypodigm. Type (lost) and Louvain PLV-35.

Periconodon lemoinei, New Species (fig. 1A)

Protoadapis curvicuspidens (in part), RUSSELL *et al.* [1967, p. 36].

Agerinia roselli (in part), CRUSAFONT-PAIRÓ and GOLPE-POSSE [1974, p. 29].

Type. Louis Gr-106, a right lower first molar from Grauves, measuring 3.5 mm in length and 2.6 mm in width.

Diagnosis. Differs from all later species of *Periconodon* in being larger. Differs from contemporary species of *Protoadapis* in being significantly smaller, and in lacking or having a much reduced paraconid on M_1.

Etymology. Named for V. LEMOINE in recognition of his contribution to the discovery and description of early Eocene Adapidae in Europe during the 19th century.

Discussion. LOUIS [1970] and GINGERICH [1974] both presented evidence that at least two species of Adapidae were present at Grauves, but it was not

previously recognized that four species are represented: an early *Periconodon*, two species of *Protoadapis*, and a few teeth of a rare *Pelycodus*. On the basis of undescribed specimens from Sézanne and Condé-en-Brie, it is almost certain that *Periconodon lemoinei* is a direct descendant of *Protoadapis louisi*.

Hypodigm. Type, and numerous isolated teeth from Grauves in the Louis collection. Also, a mandible with M_{1-2} in the Sabadell collection from Castigaleu in Spain appears to represent this species.

Periconodon huerzeleri, New Species (fig. 3)

Periconodon sp., JAEGER [1971, p. 94].

Type. Basel Bchs-495, a right mandible from Buchsweiler with P_3 erupting and P_4–M_3 in place. M_1 measures 2.8 mm in length, and 2.3 mm in width.

Diagnosis. Differs from *Periconodon lemoinei* and *Peri. roselli* in being significantly smaller, lacking a paraconid on P_4, and having larger pericones on the upper molars. *Periconodon huerzeleri* differs from *Peri. pygmaeus* in being significantly larger and in having larger pericones on the upper molars.

Etymology. Named for Professor JOHANNES HÜRZELER of Basel, who collected the type and most of the hypodigm of this species, in recognition of his contributions to the study of Eocene primates.

Discussion. Two fossiliferous levels are known at Bouxwiller, the type and other specimens in the older collection at Basel coming from the upper level, and the newer collections of HAMMEL, JAEGER, and FISCHER coming from a slightly lower level (Marnes vertes inf.). The specimens from the lower level appear to be slightly larger than those from the upper level, but both samples are easily accommodated within *Periconodon huerzeleri*.

Hypodigm. The type and other mandibles, maxillae, and isolated teeth from the upper level at Bouxwiller are in the 'Naturhistorisches Museum' in Basel, as is the FISCHER collection of teeth from the lower level. JAEGER's collection of isolated teeth is in the Laboratoire de Paléontologie in Montpellier. HAMMEL'S private collection (not seen) is now in the University Department of Geology in Strasbourg.

Anchomomys stehlini, New Species (fig. 4)

Anchomomys cf. *gaillardi*, STEHLIN [1916, p. 1412].

Anchomomys pygmaeus (in part), SZALAY [1974, p. 123].

Type. Basel En-1, a right mandible with P_4–M_3 from Egerkingen γ. M_1 in the type specimen measures 2.0 mm in length, and 1.3 mm in width.

Diagnosis. Anchomomys stehlini differs from *Anchomomys gaillardi* in being significantly larger and in having relatively broader lower molars. *Anchomomys*

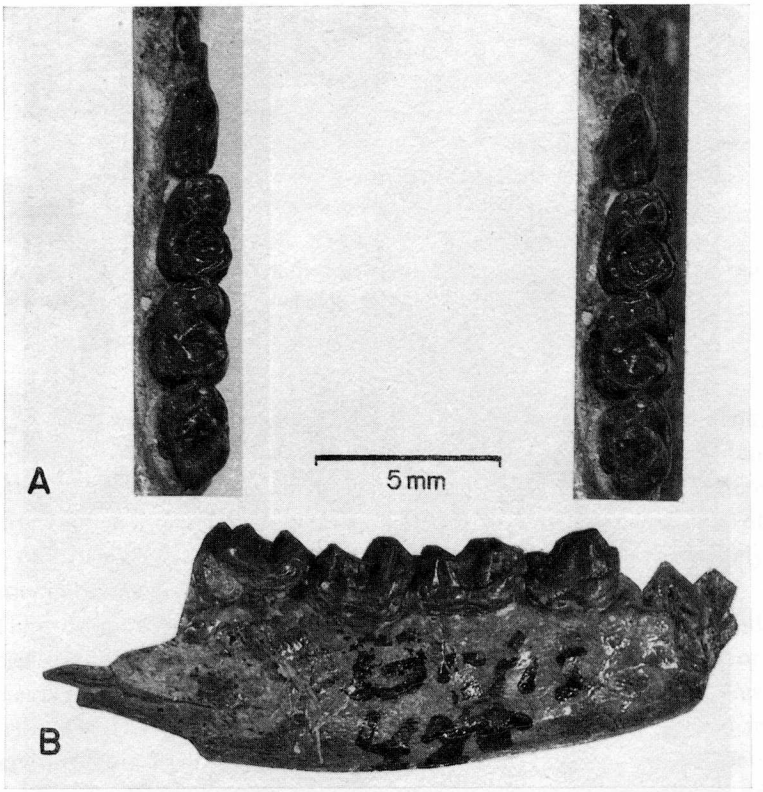


Fig. 3. Periconodon huerzeleri TYPE, Basel Bchs-495, a right mandible from Buchsweiler. *A* Stereophotograph in occlusal view. *B* Lateral view. Note P_3 erupting after P_4 and molars have erupted.

stehlini differs from earlier species of *Periconodon*, from which it appears to have evolved, in being smaller and in having relatively longer and narrower lower molars.

Etymology. Named for Professor H.G. STEHLIN in recognition of his enormous contribution to the discovery, collection, and description of Eocene primates from Egerkingen and elsewhere.

Discussion. In a recent paper, SZALAY [1974] stated that the specimen here designated as the type of *Anchomomys stehlini* came from the locality 'Horn'. Labels with the type and other specimens of this species, as well as their color and preservation, clearly indicate that they were collected at the Egerkingen γ

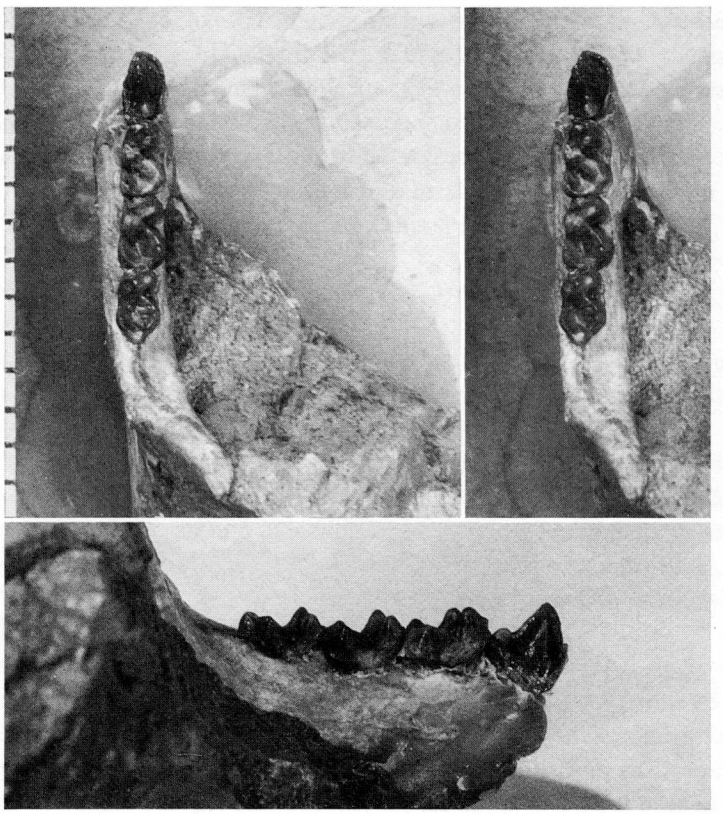


Fig. 4. Anchomomys stehlini TYPE, Basel En-1, a right mandible from Egerkingen γ, in occlusal stereophotograph (top) and lateral view (bottom). Scale is in mm.

locality. No fossil locality 'Horn' is known in Switzerland [HÜRZELER and ENGESSER, personal commun.].

A different problem, also requiring consideration of the correct locality of origin of specimens, concerns reference of the species *pygmaeus* to *Anchomomys* by SZALAY [1974] and others. Virtually all of the primate fossils from Egerkingen come from one or another of three collections, which contain faunas of slightly different ages: (1) the first discovered and oldest is the Cartier collection from the Huppersand, (2) STEHLIN's last discovered but intermediate in age collection from Egerkingen γ, and (3) STEHLIN's collection from Egerkingen α, which contains the youngest fauna of the three. The type specimens of both '*Anchomomys*' *pygmaeus* [RÜTIMEYER, 1890] and *Peri-*

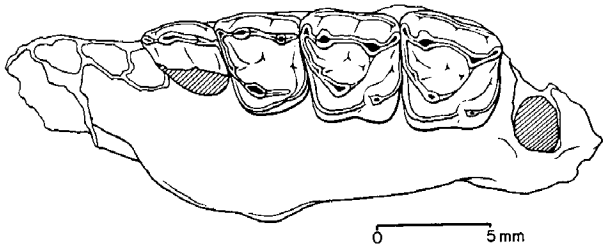


Fig. 5. Adapis sudrei TYPE, Montpellier RBN-5120, a left maxilla with P^3 (broken) and P^4–M^2 intact from Robiac. Drawing of occlusal view, from SUDRE [1969].

conodon helveticus [RÜTIMEYER, 1891] are in the Cartier collection from the Huppersand. The type of the former species, an upper M^1 is virtually identical to M^1 in the type specimen of the latter species, except that the pericone is slightly less well developed. SZALAY's [1974] very detailed drawing of the type of '*Anchomomys*' *pygmaeus* is inaccurate in omitting completely the distinct pericone present on this tooth.

There is no evidence to suggest that more than a single small adapid species is present in the Cartier collection, and the correct name for this species is *Periconodon pygmaeus* [RÜTIMEYER, 1890] (= *Periconodon helveticus* [RÜTIMEYER, 1891]). Only a single very small adapid is represented in the collections from Egerkingen γ – this species is intermediate in size between *Periconodon pygmaeus* and *Anchomomys gaillardi* (see fig. 6, 8), but appears to be closer to *Anch. gaillardi*, and it is thus placed in *Anchomomys*.

Hypodigm. Type, Basel Eh-748 a left mandible with M_{1-2}, and Eh-749 an M_3 (now lost).

Adapis sudrei, New Species (fig. 5)

Adapis cfr. *parisiensis*, STEHLIN [1912, p. 1274].

Adapis aff. *parisiensis*, SUDRE [1969, p. 111].

Type. Montpellier RBN-5120, a left maxilla with P^3–M^2 from Robiac (Nord). Dental measurements of the type sample of *Adapis sudrei* from Robiac are summarized in table II.

Diagnosis. Adapis sudrei differs from *Ad. laharpei*, *Ad. ruetimeyeri*, *Ad. magnus*, and *Ad. stintoni* in being significantly smaller. It differs from *Adapis sciureus* in being significantly larger. *Adapis sudrei* is close in size to *Ad. priscus*, but differs from that species in having relatively longer and narrower lower molars. *Adapis sudrei* resembles closely some *Ad. parisiensis*, but differs

from that species in having slightly more molarized premolars, especially P^3, and in lacking symphyseal fusion.

Etymology. Named for Dr. J. SUDRE of Montpellier, in recognition of his contributions to the discovery, collection, and description of Eocene primates.

Discussion. This species has rightfully been compared by previous authors with *Adapis parisiensis*, which it resembles closely in size and dental morphology. While both clearly belong in the genus *Adapis*, it now appears that their close similarity is largely a result of parallel evolution. The absence of symphyseal fusion in all specimens of *Ad. sudrei* preserving this region, and the presence of fusion in all specimens of *Ad. parisiensis* with a fully erupted dentition is probably the most important diagnostic difference between these species at present.

Hypodigm. The type and numerous other maxillae and mandibles from Robiac in Montpellier, Basel, Lyon, and the private collection of P. GIGASE in Antwerp.

Adapis stintoni, New Species (fig. 2A)

Adapis magnus, SCHMIDT-KITTLER [1971, p. 173].

Adapis parisiensis, CRAY [1973, p. 71].

Type. BMNH M32135, left and right mandibles and isolated upper teeth of a single individual from the Lignite bed, Upper Headon beds, Headon Hill, Isle of Wight. M_1 in this specimen measures 5.6 mm in length, and 4.0 mm in width.

Diagnosis. Differs from early species of *Adapis* in having a fused mandibular symphysis and the elongated molars with large metastylids characteristic of *Ad. magnus* and *Ad. parisiensis*. *Adapis stintoni* differs from *Ad. magnus* in being significantly smaller, and from *Ad. parisiensis* in being significantly larger (see fig. 8).

Etymology. Named for Mr. F.C. STINTON of Bournemouth, Hampshire, who collected the type specimen of this species.

Discussion. Adapis stintoni is an especially important species because it is intermediate both temporally and morphologically between the well-known *Adapis magnus* and *Adapis parisiensis*, and it provides almost certain evidence that the latter is a descendant of the former. Given these phylogenetic relationships, continued use of the name *Leptadapis* as a genus or subgenus for *Ad. magnus* and other species does not appear justified.

Hypodigm. Type, specimens from Ehrenstein in the Munich collection referred to *Adapis magnus* by SCHMIDT-KITTLER [1971], and possibly some specimens from Quercy.

Table II. Summary of dental measurements of *Adapis sudrei* from Robiac, based on specimens in Montpellier, Basel, Lyon, and the private collection of P. GIGASE[1]

		n	Range	$\bar{x}$	s	V
P_1	L	1	2.9	–	–	–
	W	1	1.6	–	–	–
P_2	L	1	3.9	–	–	–
	W	1	2.2	–	–	–
P_3	L	4	3.7– 4.4	4.10	0.29	7.1
	W	4	2.3– 2.7	2.48	0.17	6.9
P_4	L	7	4.3– 4.6	4.41	0.12	2.7
	W	7	2.9– 3.3	3.07	0.16	5.2
M_1	L	12	4.1– 4.6	4.35	0.17	3.9
	W	12	3.0– 3.3	3.15	0.13	4.1
M_2	L	11	4.6– 4.9	4.76	0.12	2.5
	W	11	3.3– 4.0	3.56	0.22	6.2
M_3	L	9	5.8– 6.6	6.28	0.27	4.3
	W	10	3.1– 3.6	3.24	0.16	4.9
M. depth		4	9.0–10.6	9.85	0.77	7.8
C^1	L	4	3.5– 4.3	3.90	0.34	8.7
	W	4	2.3– 2.6	2.45	0.17	6.9
	H	4	4.0– 4.7	4.43	0.31	7.0
P^2	L	1	4.4	–	–	–
	W	1	2.8	–	–	–
P^3	L	1	3.7	–	–	–
	W	1	3.5	–	–	–
P^4	L	5	3.7– 4.0	3.88	0.13	3.4
	W	5	4.5– 4.9	4.64	0.15	3.2
M^1	L	5	4.5– 4.6	4.54	0.05	1.1
	W	5	5.2– 5.5	5.38	0.13	2.4
M^2	L	4	4.6– 5.1	4.88	0.22	4.5
	W	4	5.4– 6.2	5.88	0.34	5.8
M^3	L	3	3.8– 4.1	4.00	0.17	4.3
	W	3	4.9– 5.4	5.07	0.29	5.7

[1] L = Length; W = width; M. depth = mandibular depth below M_1; n = sample size; Range = range of variation; x = sample mean; s = standard deviation; V = coefficient of variation. H is crown height of upper canine.

Phylogenetic Relationships

In order to study the phylogenetic relationships of a group of fossil species, one must have an understanding of variation within each species sample, and an independently established stratigraphic or biostratigraphic context ordering the available samples temporally [see GINGERICH, 1976, for discussion of this stratophenetic approach to phylogeny reconstruction]. All morphological characteristics of each species sample available for study should be analyzed. Which of these characters will prove most interesting cannot always be predicted in advance, although tooth size (and by inference body size) is usually one of the most informative.

An example of data organization for a selected group of species is presented in fig. 6, where tooth size (length of M2) is plotted for each of seven successive stratigraphic intervals. Even though the number of specimens in each sample is relatively small, a very clear pattern of change emerges. Beginning with the species *Protoadapis louisi*, each successive species is slightly but significantly smaller than the previous one. Because there is a dense and continuous record of species in successive intervals differing only slightly from species in adjacent intervals, one is justified in concluding that a single evolutionary lineage from *Protoadapis louisi* to *Anchomomys gaillardi* is represented. Other continuous trends seen in this lineage but not documented here are a gradual increase, then decrease, in the size of the pericone, a gradual reduction in the size of the paraconid on P_4, and a gradual increase in the ratio of length to width of the lower molars.

The variation in length of M2 in each successive sample of the lineage leading to *Anchomomys gaillardi*, shown in figure 6, is well within the variation typical for a single species of primate (see table II, for example). However, when dental size variation is studied for a large sample of what is called *Adapis parisiensis*, it is clear that the variation in this 'species' exceeds that typical of a single species by a factor of two or more (fig. 7). The great variability in *Adapis* '*parisiensis*' in this case is undoubtedly a result of mixing collections from different stratigraphic intervals spanning a significant period of time. The type specimen of *Adapis parisiensis* is about the same size as *Adapis crassa*, and the latter is probably a synonym of the former. Similarly, *Ad. mutans* is probably a synonym of *Ad. betillei*. Thus, when the stratigraphic record of *Adapis* '*parisiensis*' becomes better known, it may be necessary to recognize both *Ad. angustidens* and *Ad. betillei* in addition to *Ad. parisiensis*.

A diagram showing histograms of first lower molar size for samples from each stratigraphic interval yielding European Adapidae is presented in figure

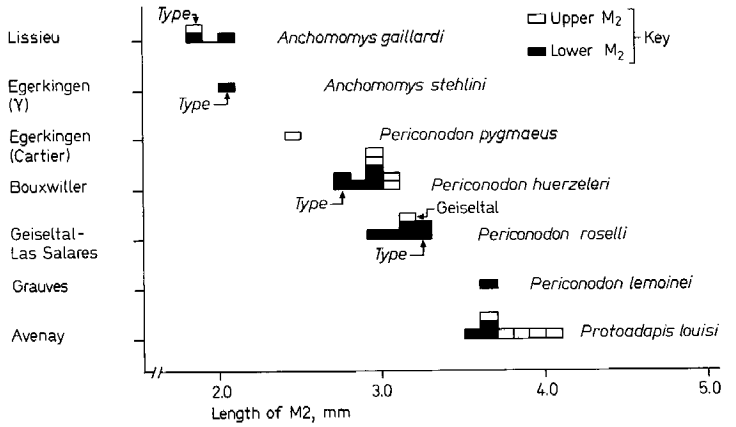


Fig. 6. Histograms of M2 length for species samples from seven consecutive biostratigraphic intervals. Each species sample resembles closely samples in adjacent intervals but differs significantly from them. Plot shows gradual decrease in size of M2 in a single evolutionary lineage from *Protoadapis louisi* to *Anchomomys gaillardi*. Patterns of change in other characters are similarly gradual. See figure 8 for position of this lineage in European adapid radiation. Note that *Periconodon (= Agerinia)* from Geiseltal and Las Salares are of similar size, justifying placement of both in *Periconodon roselli*.

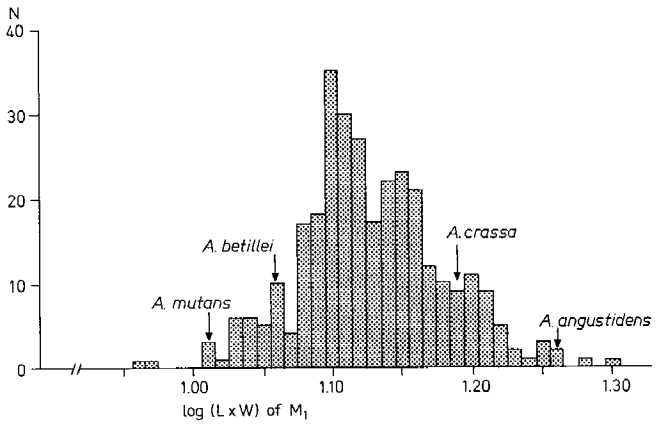
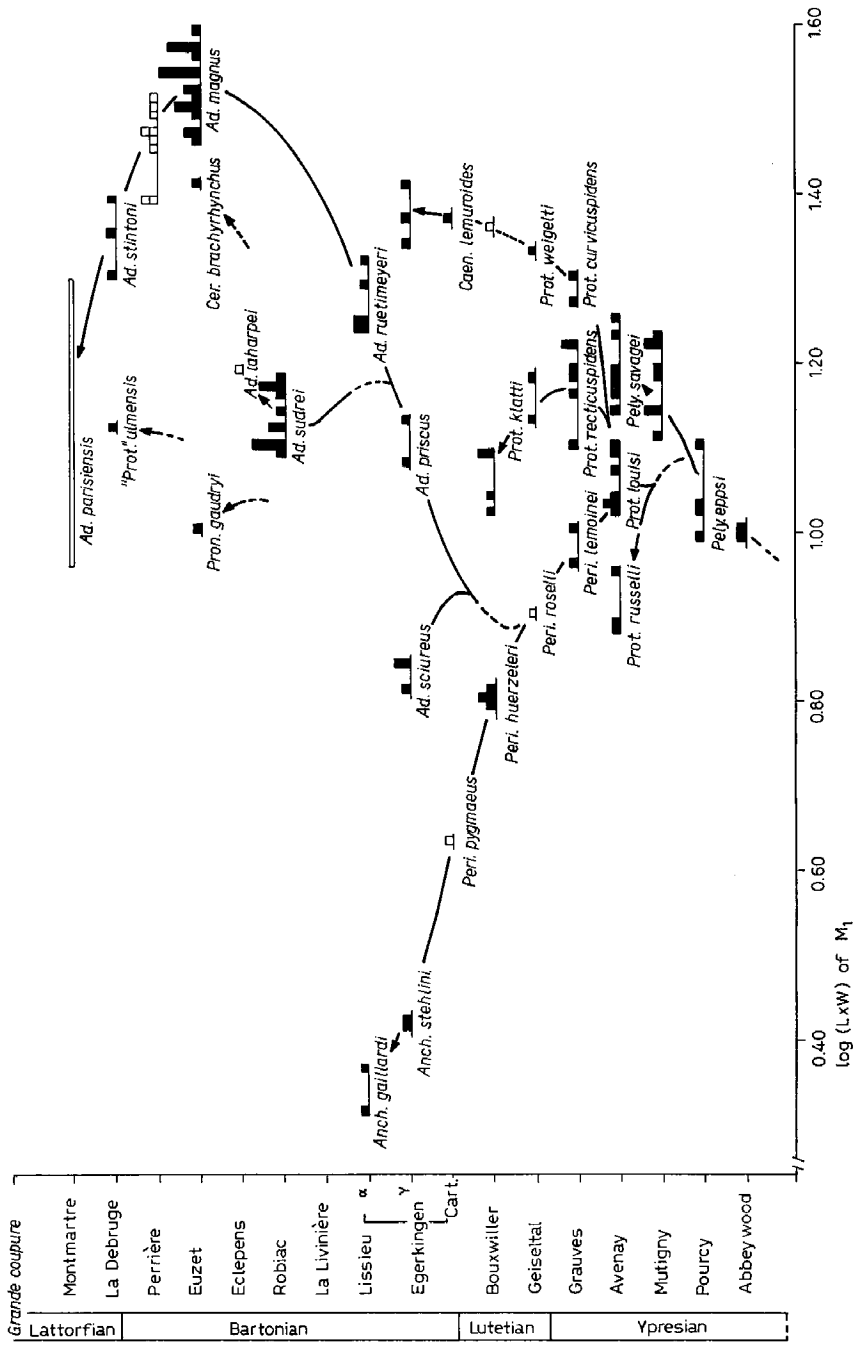


Fig. 7. Histogram of the size of M_1 in N = 313 specimens of *Adapis* '*parisiensis*' from Quercy. Positions of types of available species-group names are indicated by arrows. The type specimen of *Adapis parisiensis*, from the Gypse de Montmartre, is similar in size to *A. crassa*, and the latter is probably a synonym of the former. The range of variation in this sample is about twice that to be expected in a large sample of a single species from one locality, and the increased variability is almost certainly due to mixing of samples from many stratigraphic levels. See figure 8 for the position of this sample relative to other European Adapidae. Specimens plotted here are in collections in Basel, Paris, Louvain, Montauban, and Montpellier.

8. Solid lines show reasonably certain pathways linking similar species into phyletic lineages. The dashed links are less certain, but appear to be the most probable pathways given the evidence now available. Two species, *Anchomomys (?) quercyi* and *Protoadapis filholi*, come from unknown stratigraphic intervals in Quercy, and their age and relationships are thus uncertain. The phylogenetic relationship of three species of known age, *Pronycticebus gaudryi*, '*Protoadapis*' *ulmensis*, and *Cercamonius brachyrhynchus*, are also unclear because suitable ancestors are as yet unknown in immediately preceding stratigraphic intervals.

Some final comments can be added to the above discussion, based on the information presented in figure 8. During the Eocene, the European Adapidae appear to have radiated from a single ancestral species, *Pelycodus eppsi*. A maximum of four species are known from any one locality or stratigraphic interval. Four species occur together at the locality of Grauves (including the rare *Pelycodus savagei*), and at the locality of Egerkingen γ. Judging from their tooth and body size, the European Adapidae radiated to fill a range of ecological niches that appears comparable to the range of niches occupied today by lemuroid primates in Madagascar or ceboid primates in South America. Most were probably fruit and leaf eaters, but the small *Anchomomys* may well have supplemented its diet with a significant quantity of insects. The adaptive similarity of Eocene Adapidae to Lemuroidea on the one hand, and Ceboidea on the other, suggests that the common ancestral stock of both of these modern groups may be found in the Adapidae, and a detailed examination of this question is now in progress.

Fig. 8. Histograms of the size of M_1 and stratophenetically based phylogenetic relationship of the 26 dated species of European Adapidae. *Anchomomys (?) quercyi* and *Protoadapis filholi* come from unknown levels in the Quercy phosphorite deposits of France and cannot be accurately placed on the diagram. The diagram shows the size distribution of specimens of each species known from each of the biostratigraphic reference levels (*'niveaux repères'*) listed at the left of the figure. The vertical scale represents approximately 18 million years (from 53 to 35 million years before present) spanning most of the Eocene and part of the early Oligocene [BERGGREN, 1972; some authors include the Lattorfian in the Eocene]. Solid lines link species whose phylogenetic relationship is fairly well established. Dashed lines indicate uncertainty about the precise origin of certain lineages or clades. Links between related species are based on phenetic consideration of all characters available for study in each species in each stratigraphic interval, but only tooth size can be shown on this diagram. Note several evolutionary reversals, common parallel evolution, and general pattern of character divergence in tooth size (and by inference body size). Maximum rates of change in tooth size in incremental and decremental lineages shown here are comparable to those in other Paleocene and Eocene primates [GINGERICH, 1976, p. 68].


Ad. parisiensis
"Prot." ulmensis
Ad. stintoni
Cer. brachyrhynchus
Ad. magnus
Pron. gaudryi
Ad. sudrei
Ad. laharpei
Ad. priscus
Ad. ruetimeyeri
Caen. lemuroides
Prot. weigelti
Prot. curvicuspidens
Prot. klatti
Prot. tecticuspidens
Pely. savagei
Peri. lemoinei
Prot. louisi
Peri. roselli
Prot. russelli
Ad. sciureus
Peri. huerzeleri
Peri. pygmaeus
Anch. stehlini
Anch. gaillardi
Pely. eppsi
Grande coupure
Montmartre
La Debruge
Perrière
Euzet
Eclepens
Robiac
La Livinière
Lissieu
α
γ
Egerkingen
Cart.
Bouxwiller
Geiseltal
Grauves
Avenay
Mutigny
Pourcy
Abbey wood
Lattorfian
Bartonian
Lutetian
Ypresian
0.40
0.60
0.80
1.00
1.20
1.40
1.60
log (LxW) of M1

Acknowledgements

I thank the many curators of collections of European Adapidae for unrestricted access to virtually all important specimens of this extinct family. This research was undertaken during a NATO Postdoctoral Fellowship at the Université de Montpellier, and I thank Professor L. THALER for facilities, and J. SUDRE and others for much helpful discussion. J. DAVID ARCHIBALD, University of California at Berkeley, kindly provided a copy of his notes on Adapidae. At the University of Michigan, KARNA STEELQUIST printed the figures, A. RYAN helped compile figure 7, Mrs. GLADYS NEWTON typed the manuscript, and the Scott Turner Fund, Department of Geology and Mineralogy, and a Faculty Research Grant, Rackham School of Graduate Studies, provided funds for some travel expenses.

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