Z. Morph. Anthrop.	71	2	135—142	Stuttgart, August 1980

Dental and cranial adaptations in Eocene Adapidae

By **Philip D. Gingerich**, Ann Arbor

With 2 figures in the text

Summary: There is no animal living today that makes an ideal model for what an Eocene adapid was like in terms of its behavior and adaptations. Nor can one living model adequately represent a group as diverse as the Adapidae. Adapids possessed a mosaic of anatomical features, some primitive and some relatively advanced for their time. They share a few specializations (chiefly postcranial) with lemuroids, and at the same time share a number of advanced specializations with anthropoids. Most adapids weighed between 0.6 and 8.0 kg, they had relatively small brains by modern standards, their dentition indicates a range in dietary adaptations from frugivory to folivory for most species, and at least one genus *(Adapis)* was sexually dimorphic. Considering all of these features, an average adapid may have resembled the hypothetical combination of a gentle lemur and a squirrel monkey.

Zusammenfassung: Die Adapidae besaßen ein Mosaik primitiver und relativ evoluierter anatomischer Merkmale. Besonders im postcranialen Skelett weisen sie zum einen einige Spezialisationen der Lemuriformes auf, zum anderen evoluiertere Merkmale der Simier. Das Körpergewicht der meisten Adapiden lag zwischen 600 und 8000 g. Sie hatten relativ kleine Gehirne, ihre Bezahnung läßt auf eine frugi- bis folivore Ernährung schließen. Zumindest ein Genus *(Adapis)* verfügte über einen Sexualdimorphismus. Unter Berücksichtigung aller Merkmale könnte der durchschnittliche Vertreter der Adapidae einer hypothetischen Primatenform aus der Kombination von Totenkopfaffe und einer kleinen Lemurenspezies geähnelt haben.

The primate family Adapidae is first known from the lower Eocene of Europe and North America. At first appearance, the European radiation is more diverse (including *Donrussellia*, *Protoadapis*, and *Pelycodus*) than that in North America (where only *Pelycodus* is represented). This suggests that Europe was possibly closer to the center of origin of the family than North America was. Other circumstantial evidence suggests that the origin and initial radiation of Adapidae was probably in Africa and/or South Asia during the late Paleocene or earliest Eocene. Some 17 genera and 48 species of adapids are known from the Eocene of Europe, Asia, Africa(?), and North America, compared with a single Oligocene genus *(Oligopithecus)* with one species from Africa, and two relict genera *(Indraloris* and *Sivaladapis)* with three species in the Miocene of South Asia (Gingerich & Sahni, 1979).

The phylogenetic relationships of Adapidae in Europe and North America have been reviewed recently (Gingerich, 1977, 1979; Gingerich & Simons, 1977). In this paper I would like to discuss in general terms some of the dental and cranial adaptations of Eocene Adapidae.

0044-314X/80/0071-0135 $ 2.00

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Body size

Body size is perhaps the most fundamental component of an animal's general adaptation. Morphological, ecological, behavioral, and life history parameters are influenced, if not determined, by body size. Fortunately body size is highly correlated with tooth size, and it can thus be estimated even from fragmentary fossil remains. The lower first molar is one of the teeth most commonly represented in fossil primate specimens. In a sample of 43 non-human living primates, ranging systematically from *Tarsius* to *Gorilla*, the log of crown area of M_1 has a coefficient of correlation $r = .95$, and coefficient of determination $r^2 = .90$. In other words, 90 % of the variance observed in tooth size can be explained simply as a result of variation in body size in different species of primates. The following regression equation can be used to predict body size given tooth size:

$$\text{Body weight} = \frac{[L \times W]^{1.62}}{48.4}$$

where body weight is measured in kg, and M_1 length (L) and M_1 width (W) are measured in mm (based mostly on data in HARVEY et al., 1978; and SWINDLER, 1976). The evolution of body size in European Adapidae is illustrated in Fig. 1. Adapids were relatively small (200–1,000 g) when they first appeared in the European fossil record, but this distribution of body size in the family as a whole shifted rapidly to larger size. Most later adapids in Europe ranged from 600 g to 7–8 kg. All of the known radiation of Adapidae in North America was in the 600 g to 8 kg range.

KAY (1975; see also KAY & HYLANDER, 1978) demonstrated that insectivorous and folivorous primates can be separated morphologically from frugivorous primates by the more crested structure of their molar teeth. Furthermore, insectivorous primates can be distinguished from folivorous primates on body size alone. The largest primate insectivore weighs about 300 g, whereas the smallest folivore weighs about 700 g. There is thus a threshold between the two adaptive zones at around 500 g body weight. Even frugivorous primates tend to fall on one or the other side of this threshold, depending on their secondary specialization for insects or leaves (KAY, 1975). The 500 g threshold between insectivorous-frugivorous and folivorous-frugivorous adaptive zones is shown in Fig. 1. This figure shows clearly that the European adapid radiation took place within the folivorous-frugivorous adaptive zone. Some adapids, such as *Cercamonius*, have relatively flat teeth indicating that they were feeding predominantly on fruit,

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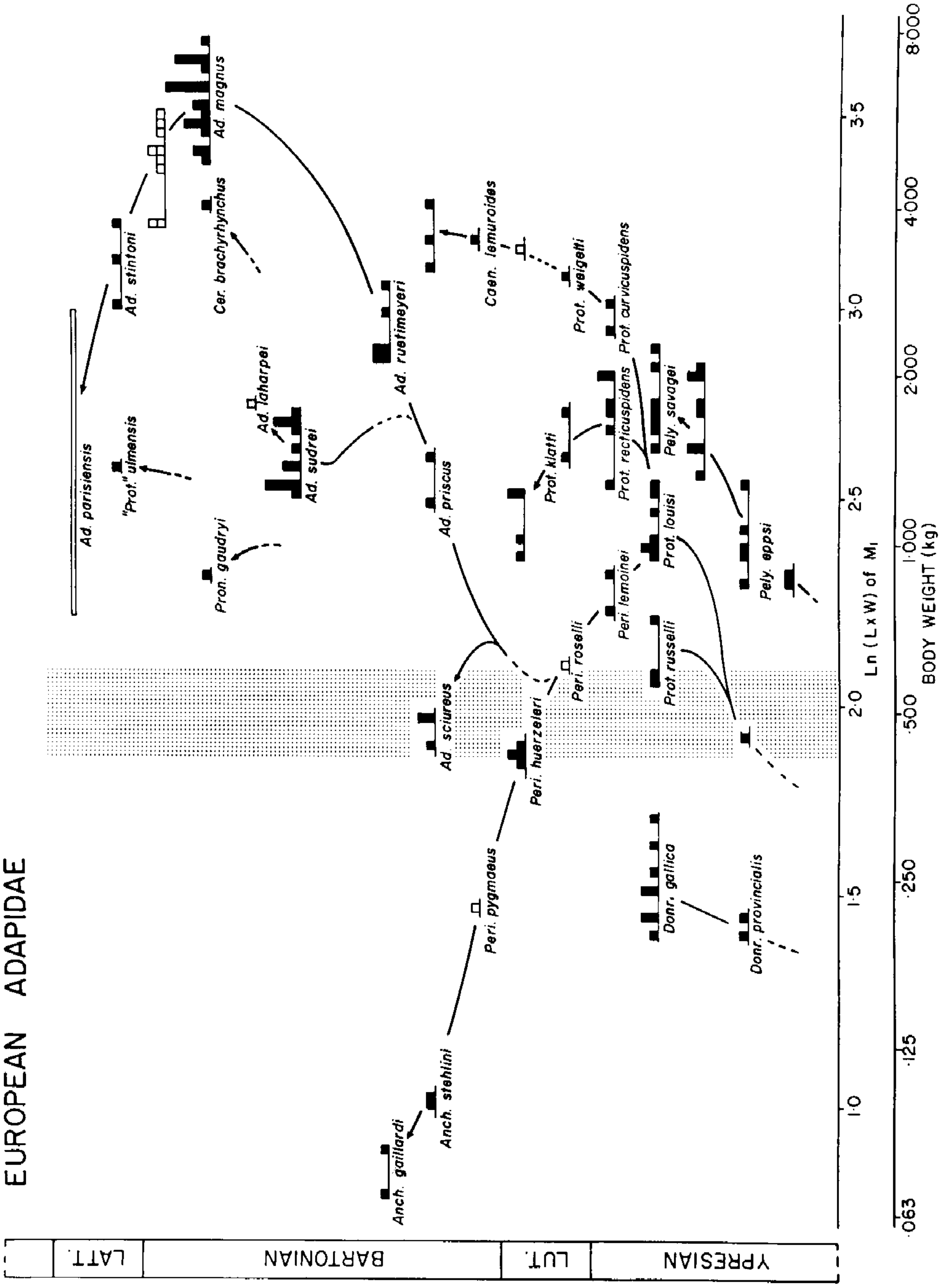
Fig. 1. Radiation of Eocene Adapidae in Europe. Histograms represent distribution of size of first lower molar (M_1) in samples from successive stratigraphic intervals. Abscissa is tooth size, and by inference body size (see text). Ordinate is time, based on biostratigraphic analysis of rodents and perissodactyls (see GINGERICH, 1977, and GODINOT, 1978, for documentation). Stippling shows KAY's 500 g threshold separating insectivorous from folivorous primates. Note radiation of Adapidae is largely on folivorous side of threshold.


EUROPEAN ADAPIDAE
LATT.
BARTONIAN
LUT.
YPRESIAN
Ad. parisiensis
"Prot." ulmensis
Pron. gaudryi
Ad. stintoni
Cer. brachyrhynchus
Ad. magnus
Ad. laharpei
Ad. sudrei
Ad. ruetimeyeri
Ad. priscus
Ad. sciureus
Caen. lemuroides
Prot. weigelti
Prot. curvicuspidens
Prot. klatti
Prot. recticuspidens
Pely. savagei
Prot. louisi
Peri. lemoinei
Peri. roselli
Peri. huerzeleri
Prot. russelli
Pely. eppsi
Peri. pygmaeus
Donr. gallica
Donr. provincialis
Anch. stehlini
Anch. gaillardi
1·0
1·5
2·0
2·5
3·0
3·5
Ln (L x W) of M1
·063
·125
·250
·500
1·000
2·000
4·000
8·000
BODY WEIGHT (kg)

while others, such as *Adapis,* have more sharply crested teeth indicating that they fed predominantly on leaves. Only one adapid lineage is known to have crossed the adaptive threshold and become insectivorous: the lineage from *Periconodon* to *Anchomomys.* The known North American radiation took place exclusively in the folivorous-frugivorous adaptive zone. By contrast with adapids, Eocene tarsiiform primates *(Omomyidae)* radiated primarily in the insectivorous-frugivorous adaptive zone. FLEAGLE (1977) has previously discussed this important dichotomy in body size adaptation within Eocene primates.

Cranium

Brain size and arterial circulation

Several genera and species of Adapidae are known from well preserved skulls. Best among these are the European *Adapis parisiensis* and North American *Smilodectes gracilis.* Comparing skulls of *Adapis* or *Smilodectes* with those of living lemurs or anthropoids, one of the most striking differences is in brain size. The fossil species have much smaller brains than those of living primates. The difference can be quantified using JERISON's (1973) encephalization quotient (EQ) as a measure of relative brain size corrected for differences in body weight. The endocranial volume of *Adapis parisiensis* can be estimated from two skulls, and these average about 8.8 cm^3 (= 8.8 g). Using this brain size, and a body weight estimate of 2.3 kg, the relative brain size of *Adapis parisiensis* is estimated at EQ = .42 (GINGERICH & MARTIN, 1980). A similar calculation for *Smilodectes,* using a brain weight of 9.3 g (JERISON, 1973; RADINSKY, 1977) and a body weight of 2 kg (estimated from M_1 size), yields an encephalization quotient EQ = .49, which is slightly larger than the estimate for *Adapis.* These EQ values are below those of any primate living today, although they are relatively high for the Eocene. Among living primates these estimates are closest to the relative brain size of *Lepilemur,* which has an EQ = .60 (JERISON, 1973).

The blood supply to the brain in Adapidae was in part by way of the internal carotid artery passing through the middle ear. This artery includes two branches, the promontory and the stapedial. In *Adapis parisiensis* the bony canal for the stapedial branch is about four times the cross-sectional area of the canal for the promontory branch. In the one specimen of *Notharctus* where these diameters have been compared, the pomontory branch was slightly more than twice the cross-sectional area of the stapedial branch (GINGERICH, 1973). Thus there appears to be significant variation in the relative size of different arterial branches supplying the brains of different Adapidae. The adaptive significance of these differences is discussed by CONROY (this symposium).

Dentition and diet

The dentition of *Adapis parisiensis* is illustrated in Fig. 2. The upper and lower incisors are vertically implanted and have spatulate crowns very much

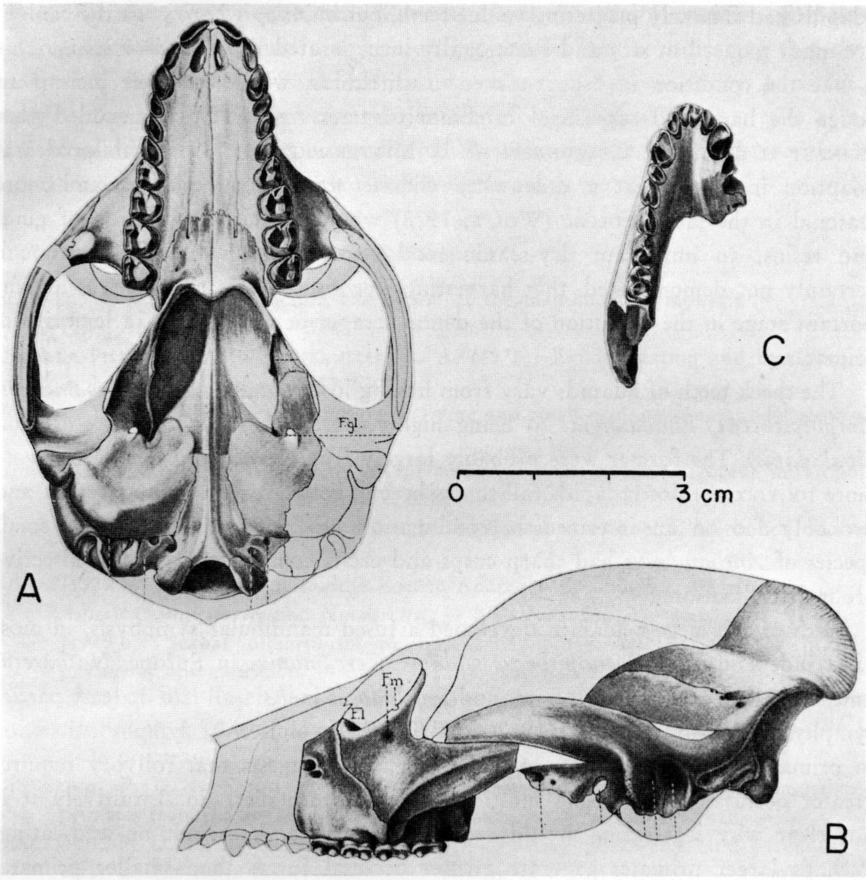


Fig. 2. Cranial anatomy of *Adapis parisiensis.* Judging from robust canines, large sagittal crest, and heavy flaring zygomatic arches, these specimens represent male individuals. A, cranium in palatal view. B, cranium in lateral view. C, anterior part of lower jaw in occlusal view. Short lower canines in this species functioned as a unit with the incisors, as in "short-tusked" callitrichids, possibly indicating an initial stage in the evolution of the dental scraper (tooth comb) characteristic of Lorisoidea and Lemuroidea. Figures from STEHLIN (1912).

like those of the living squirrel monkey *Saimiri.* The relative sizes of the incisors can be compared to those of living anthropoid primates using HYLANDER's (1975) regression of maxillary incisor width on body weight. Both *Adapis parisiensis* and *Adapis magnus* fall with the frugivorous primates on HYLANDER's figure, being about as far above his regression line as is *Saimiri.* Thus *Adapis* was not as highly specialized a folivore as, for example, modern colobines, even though cheek teeth of *Adapis* do suggest a folivorous diet.

The canine teeth of *Adapis magnus* are large, projecting, interlocking teeth, with the back of the upper canine honed by the front of lower P_1 and P_2. Most adapids had similarly projecting canine teeth, but in *Adapis parisiensis* the canines are much reduced in size and functionally incorporated in the incisor series. This is like the condition in "short-tusked" callitrichids, which use their incisors to gouge the bark and superficial cambium of trees to harvest the exuded gum (KINZEY et al., 1975; COIMBRA-FILHO & MITTERMEIER, 1976). A similar dental adaption in *Adapis*, at a time when climate was becoming dryer and more seasonal in the latest Eocene (WOLFE, 1978) would permit exploitation of gums and resins, an important dry-season food resource. It is plausible, although certainly not demonstrated, that harvesting tree gum in this manner was an important stage in the evolution of the dental scraper or tooth comb in lemuriform primates.

The cheek teeth of adapids vary from having low rounded cusps *(Cercamonius, Amphipithecus, Pondaungia)* to being highly crested *(Adapis, Notharctus,* and *Sivaladapis)*. The former were probably largely frugivorous while the latter were more folivorous. Most adapids fall somewhere in between these two extremes, and probably fed on an intermediate combination of fruit and leaves. The small species of *Anchomomys* had sharp cusps and crests consistent with their insectivorous specialization.

Each of the largest adapids developed a fused mandibular symphysis, in most cases independently. *Caenopithecus, Adapis, Cercamonius* in Europe, *Notharctus* and *Mahgarita* in North America, and *Sivaladapis* in Asia all had at least partial symphyseal fusion. BEECHER (1977) explains the evolution of symphyseal fusion in primates as an adaptation to leaf-eating, and suggests that folivory requires greater occlusal force during mastication than other diets do. Intuitively it is not clear why leaf-eating would require more force than fruit or seed-eating. Perhaps larger primates generate greater occlusal forces than smaller primates for allometric reasons. In this case symphyseal fusion in primates could simply be a reflection of increased size and not necessarily an indication of increased folivory.

Sexual dimorphism

Adapis magnus and *Adapis parisiensis* both have dimorphic crania, with the putative males having larger skulls, relatively enlarged saggital and nuchal crests, and robust flaring zygomatic arches (GINGERICH, 1979, 1980). *Adapis magnus* has dimorphic canine teeth, and the same may have been true for *Adapis parisiensis*, although the relatively reduced canines in the latter mask this relationship. Other genera have not yet been studied quantitatively, but *Notharctus* has been suggested to be dimorphic (GREGORY, 1920). Fig. 2 shows the cranial characteristics of a putative male specimen of *Adapis parisiensis*.

Orbital diameter

The relative size of the eyes and bony orbits surrounding them sometimes gives an indication of whether an animal was nocturnal or diurnal. This is true for living Malagasy Lemuroidea (WALKER, 1967). Diurnal lemuroids fall below the regression of log orbital diameter on log cranial length, indicating that they have relatively smaller eyes than their noctural counterparts. *Adapis parisiensis, Adapis magnus,* and *Smilodectes gracilis* all fall well below this regression line, indicating that they were probably diurnal. By contrast, the omomyid *Necrolemur* falls above the line, suggesting that it was nocturnal.

References

BEECHER, R. M. (1977): Function and fusion at the mandibular symphysis. — Amer. J. Phys. Anthrop. **47,** 325—336.

COIMBRA-FILHO, A. F. & MITTERMEIER, R. A. (1976): Exudate-eating and tree-gouging in marmosets. — Nature **262,** 630.

FLEAGLE, J. G. (1978): Size distribution of living and fossil primate faunas. — Paleobiol. **4,** 67—76.

GINGERICH, P. D. (1973): Anatomy of the temporal bone in the Oligocene anthropoid *Apidium* and the origin of Anthropoidea. — Folia Primatol. **19,** 329—337.

— (1977): Radiation of Eocene Adapidae in Europe. — Géobios, Mém. Spéc (Lyon) **1,** 165—182.

— (1979 a): Phylogeny of middle Eocene Adapidae (Mammalia, Primates) in North America: *Smilodectes* and *Notharctus.* — J. Paleont. **53,** 153—163.

— (1979 b): Sexual dimorphism in Eocene Adapidae: implications for primate phylogeny and evolution. — Amer. J. Phys. Anthrop. **50,** 442 [Abstract].

— (1980): Sexual dimorphism in the Eocene primate *Adapis.* — In preparation.

GINGERICH, P. D. & MARTIN, R. D. (1980): The Cambridge skull of *Adapis parisiensis.* — In preparation.

GINGERICH, P. D. & SAHNI, A. (1979): *Indraloris* and *Sivaladapis:* Miocene adapid primates from the Siwaliks of India and Pakistan. — Nature **279,** 415—416.

GINGERICH, P. D. & SIMONS, E. L. (1977): Systematics, phylogeny, and evolution of early Eocene Adapidae (Mammalia, Primates) in North America. — Contrib. Mus. Paleont. Univ. Mich. (Ann Arbor) **24,** 245—279.

GODINOT, M. (1978): Un novel adapidé (primate) de l'Eocène inférieur de Provence. — C. R. Acad. Sc. Paris **286,** 1869—1872.

GREGORY, W. K. (1920): On the structure and relations of *Notharctus,* an American Eocene primate. — Amer. Mus. Nat. Hist. Memoirs **3,** 49—243.

HARVEY, P. H., KAVANAGH, M. & CLUTTON-BROCK, T. H. (1978): Sexual dimorphism in primate teeth. — J. Zool. (Lond.) **186,** 475—485.

HYLANDER, W. L. (1975): Incisor size in anthropoids with special reference to Cercopithecidae. — Science **189,** 1095—1098.

JERISON, H. J. (1973): Evolution of the brain and intelligence. — Academic Press, New York.

KAY, R. F. (1975): The functional adaptations of primate molar teeth. — Amer. J. Phys. Anthrop. **43,** 195—216.

KAY, R. F. & HYLANDER, W. L. (1978): The dental structure of mammalian folivores with special reference to Primates and Phalangeroidea. — In: Ecology of Arboreal Folivores (G. G. MONTGOMERY, ed.), 173—191. Smithsonian Press, Washington.

KINZEY, W. G., ROSENBERGER, A. L. & RAMIREZ, M. (1975): Vertical clinging and leaping in a neotropical anthropoid. — Nature **255,** 327—328.

RADINSKY, L. (1977): Early primate brains: facts and fiction. — J. Human Evol. **6,** 79—86.

STEHLIN, H. G. (1912): Die Säugetiere des schweizerischen Eocaens -- *Adapis*. — Abh. Schweiz. Paläont. Ges. **38**, 1165—1298.

SWINDLER, D. R. (1976): Dentition of living primates. — Academic Press, New York.

WALKER, A. (1967): Patterns of extinction among the subfossil Madagascan lemuroids. — In: Pleistocene Extinctions (P. S. MARTIN & H. E. WRIGHT, eds.), 425—432. Yale Univ. Press, New Haven.

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