

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 evoluerter anatomischer Merkmale. Besonders im postcranialen Skelett weisen sie zum einen einige Spezialisierungen der Lemuriformes auf, zum anderen evoluierte 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 Totenkopffaffe 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.

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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:

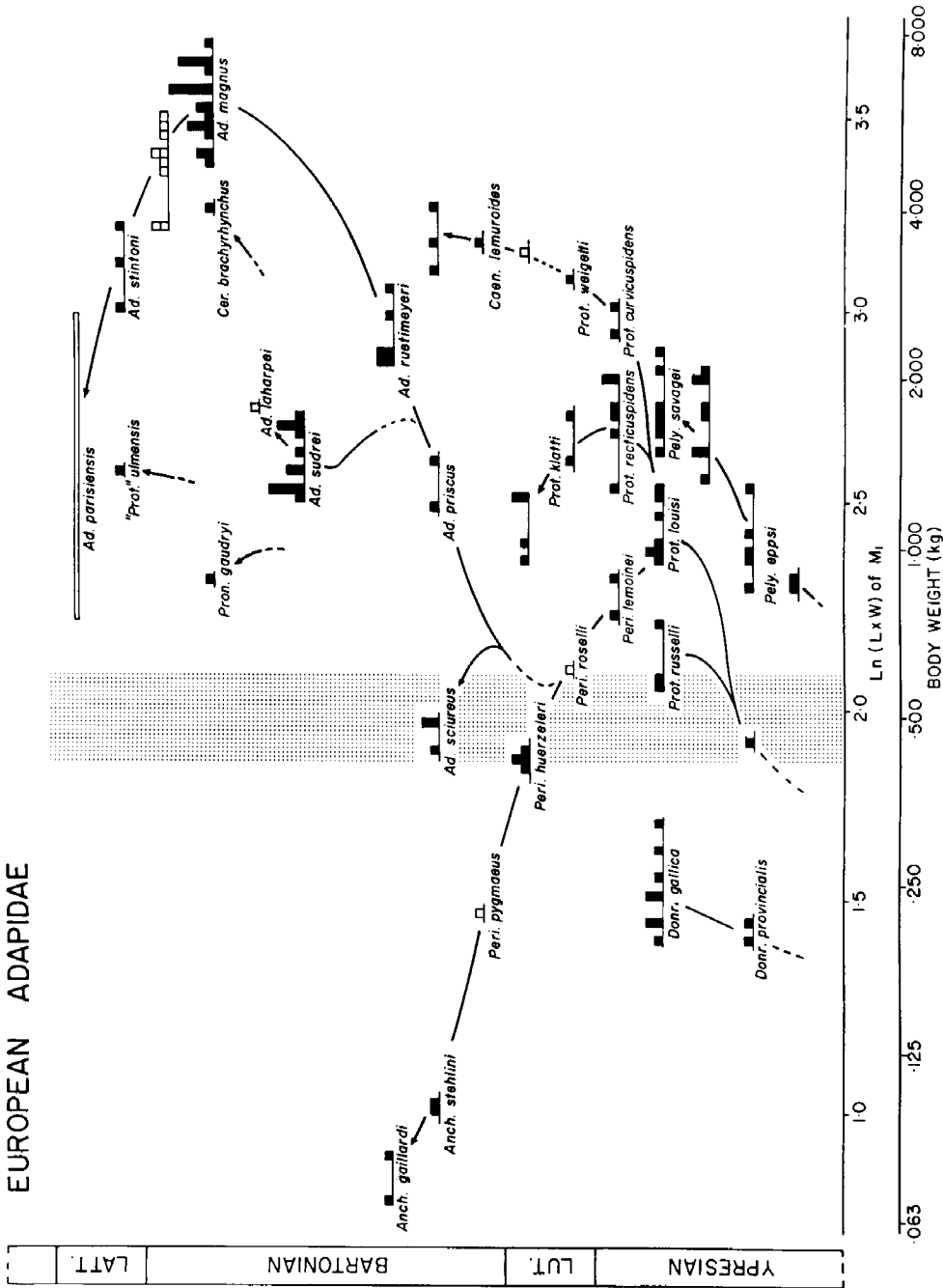
$$\text{Body weight} = \frac{[L \times W]^{1.62}}{48.4}$$

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,

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.

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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 cm³ (= 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 M₁ 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 stapedia. In *Adapis parisiensis* the bony canal for the stapedia 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 promontory branch was slightly more than twice the cross-sectional area of the stapedia 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

