

PLESIADAPIS AND DELINEATION OF THE ORDER PRIMATES

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INTRODUCTION

Biologists sometimes speak or write as if life in the past was pretty much like it is today, there just wasn't as much of it! Living species are most familiar to all of us. The false impression that species living in the past were little different from those living today may result from palaeontologists' constant comparison of extinct plants and animals with living models, or it may simply reflect poor communication between palaeontologists and neontologists. Fossils provide the only direct evidence of life in the past, and the fossil record indicates that enormous change has taken place since living organisms became abundant and diverse. Phanerozoic time, the past 600 million years, is conventionally divided into three eras, Palaeozoic, Mesozoic, and Cainozoic, based on the evolutionary grade of plants and animals living during each era. Mammals are known only from the last one-third of the Phanerozoic, and primates are known from the last one-third of this one-third. It is not surprising that primates should come on the scene so late - the major diversification of placental mammals has taken place only within the past 65 million years, that is, within the Cainozoic era.

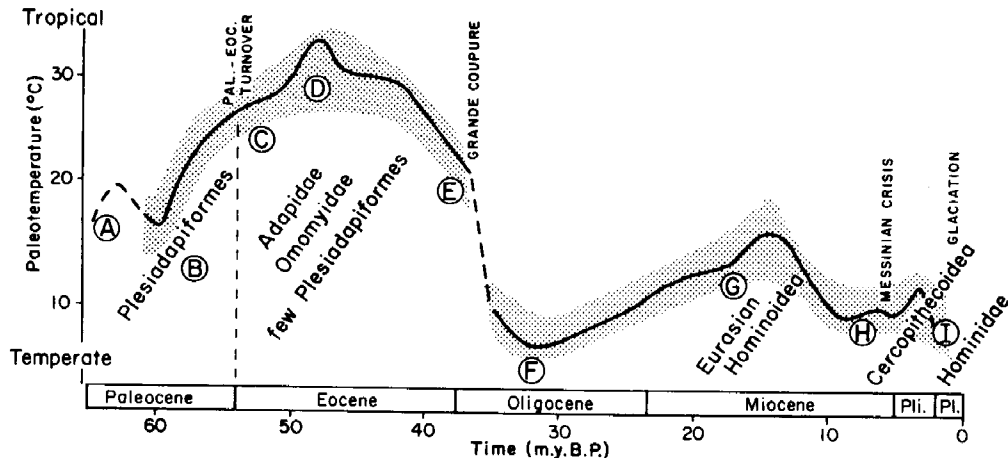
Cainozoic time can be subdivided into two periods, Tertiary and Quaternary (or alternatively Palaeogene and Neogene), and these in turn can be subdivided into six epochs (Figure 1). Each of these epochs contains distinctive mammalian faunas, but for our purposes here it is useful to recognize four intervals of primate history comprising the Palaeocene, the Eocene, the Oligo-Miocene, and the Plio-Pleistocene. Each of these intervals, comprising an episode of climatic warming and cooling, contains a progressively more advanced radiation of primates. Members of the first radiation, in the Palaeocene, are so primitive relative to later primates that they may not be primates at all. Members of the second radiation, the first "euprimates" in the Eocene, are so primitive relative to later primates that they may not be primates either. Members of the third radiation, "eu-euprimates" in the Oligo-Miocene, are so primitive relative to later primates that they too may not be primates at all. Members of the fourth radiation, "eu-eu-euprimates" (Hominidae) in the Plio-Pleistocene, are the only primates sufficiently advanced in ways we all deem important to rank unequivocally as members of our own esteemed mammalian order.

The order Primates could reasonably be restricted to Hominidae, and it could as well be restricted to Hominoidea, to Anthroipoidea, to Prosimii

+ Anthropoidea, or to Plesiadapiformes (Praesimii) + Prosimii + Anthro-
poidea. What one includes in an order or any other taxonomic category
matters far less than what one sees in examining the evolutionary history
of a particular group. Here I shall claim that the question of whether
Plesiadapis is a primate or not can only be answered arbitrarily, and
hence it is not a question of real interest or importance. I would hope
that this perspective might temper our natural enthusiasm for boundary
arguments. The more important questions concern what Plesiadapis and its
allies tell us about primate evolutionary history.

Figure 1. Overview of primate evolution in the northern hemisphere viewed in context of changing climates affecting their biogeographic distribution (climatic curve from Buchardt, 1978). A, appearance of Purgatorius following terminal Cretaceous cooling. B, radiation of plesiadapiform primates during cool phase of middle and late Palaeocene. C, appearance of primates of modern aspect in Europe and North America during phase of climatic warming (primates of modern aspect probably evolved in more equatorial areas, possibly in Africa), followed by final opening of North Atlantic. D, acme of primate diversity in Europe and North America, coinciding with warmest climates. E, decline and extinction of Eocene primate lineages in Europe and North America, coinciding with climatic cooling; Mahgarita apparently migrated to North America in the latest Eocene or early Oligocene. F, nadir of primate diversity in northern continents; known primate faunas are all in more equatorial areas (Bolivia, Egypt). G, appearance of Hominoidea in Europe and Asia during climatic warming of middle Miocene. H, disappearance of Hominoidea in northern continental faunas coinciding with cooler, dryer climates during Messinian crisis; major diversification of savanna- and woodland-adapted Cercopithecoidea; emergence of Hominidae. I, rapid evolution and dispersal of humans during Pleistocene climatic fluctuations.

PRIMATES IN THE NORTHERN HEMISPHERE

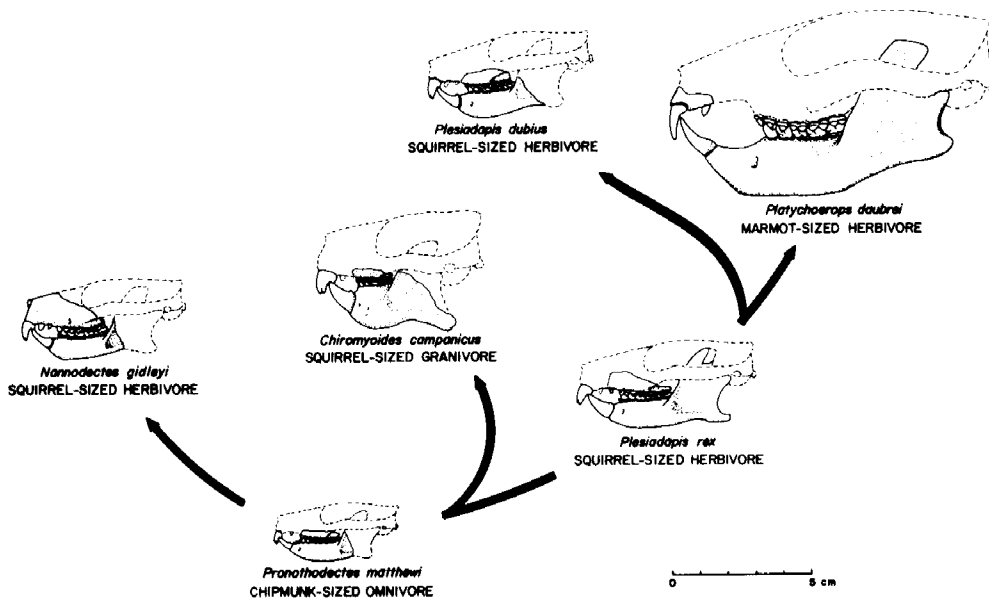


SYSTEMATIC POSITION OF PLESIADAPIS

Plesiadapis has always been problematical. Etymologically Plesiadapis means "near-adapis", clear reference to the common Eocene lemuriform Adapis. The first specimens of Plesiadapis were collected by the French physician Victor Lemoine of Reims. When Paul Gervais named and described Plesiadapis, he considered it to be "un petit mammifere de classification encore douteuse" (Gervais, 1877). Gervais was himself an authority on Adapis, and it is difficult to imagine what resemblance he saw to Adapis in the very limited fragments of Plesiadapis available in 1877. It seems likely that Gervais had other specimens in mind when he compared Plesiadapis to Adapis. These other specimens were described by Lemoine the following year as Plesiadapis, but later placed in Protoadapis. Adapis was (and is) widely recognized as lemuriform in grade, if not in class. Thus it is natural that Plesiadapis, given a name compounded from Adapis, should be compared with lemurs.

Many genera closely related to Plesiadapis are now known from Europe and North America. These are conventionally classified in five (or six) families: the microsyopoid Microsyopidae (and possibly Apatemyidae), and the plesiadapoid Paromomyidae, Picrodontidae, Carpolestidae, and Plesiadapidae. For reference, the evolutionary diversification of Plesiadapidae is shown in outline in Figure 2. Pronothodectes and Nannodectes are known only from

Figure 2. Outline of evolutionary diversification of European and North American Plesiadapidae, all drawn to same scale. Plesiadapidae range in age from middle Paleocene through early Eocene. Reproduced from Gingerich (1976).



North America, and Platychoerops is known only from Europe. Chiromyoides and Plesiadapis are known from both Europe and North America.

Lemoine (1887) clearly recognized that Plesiadapis was not in fact a lemur, and he expressed this in attributing to Plesiadapis "des caractères lémuriens avec un facies marsupial." Plesiadapis is not a marsupial either, but comparison with marsupials serves to highlight the great number of primitively generalized and also divergently specialized morphological characteristics of Plesiadapis. Stehlin (1916) regarded Plesiadapis and its allies as primates, in part because of their enlarged superficially Daubentonia-like ("Chiromys"-like) central incisors, and in part because of similarity in the structure of their molars to those of Eocene primates. Matthew (1917) was more cautious, reserving judgement until cranial and skeletal characteristics of plesiadapids could be more fully studied. Gidley (1923:16-17) discussed at length the dental evidence for primate affinities of Plesiadapis and its allies, writing:-

"I know of no species, certainly not primate, in which is found the peculiar combination of modifications described...as characteristic of Paromomys, and which is observed also in the Notharctidae [now a subfamily of Adapidae] and in some at least of the Eocene Tarsiidae [Omomyidae]. These modifications include for the lower molars a broad basined heel and narrower, more or less forwardly sloping trigonid in which the paraconid is progressively diminishing, or absent, its function being taken over by the anterior cingulum ridge continuing with the anterior flank of the protoconid to form a trigonid basin similar to but smaller and more elevated in position than the talonid depression; while the correlated modifications of the upper molars are a shallow anterior basin external to the protocone, which basin and cone function with the talonid portion of the corresponding lower molar, and a posterior basin, somewhat higher in position, formed by the posterior cingulum ridge continuing with the backwardly expanded border of the protocone to the summit of that cusp. The latter basin and ridge function with the trigonid of the lower molar next behind. This peculiar structure of the upper molars at least, while apparently distinctively primate, is, however, not observed in all groups of the order. But the stage just described, which in the Notharctidae is followed by the budding off of a hypocone from the posterior flank of the protocone, seems to have been an important basis of modification in all the anthropoids, including man, and in some but not all groups of Lemurs. The molar pattern of modern anthropoids seems to have been built on this model."

Simpson (1935) concluded his study of the dentition, limited cranial remains, and partial postcranial skeleton of Plesiadapis by ranking Plesiadapidae within the superfamily Lemuroidea. In discussing the dentition of Plesiadapis, Simpson wrote (1935:26):-

"As regards molar pattern, Plesiadapis resembles the primitive Notharctinae more closely than any other group. The resemblance to the Adapinae is more distant, but still striking in many respects. There is also considerable resemblance to Necrolemur, a later tarsioid, and to Paromomys, a middle Paleocene genus of doubtful position, perhaps tarsioid. Resemblance to the other main groups of early primates is more distant.

The resemblance to Pelycodus [Cantius], most primitive known notharctine, is really amazing and extends to the apparently most insignificant details. The upper molars are of almost identical structure throughout, differing only in details of the cingula and proportions such as may characterize species of one genus. In the lower molars, Pelycodus [Cantius] has the paraconids slightly more distinct, but the resemblance is equally striking and includes even such features as the minute grooving of the trigonid face of the metaconid and the exact structure of the complex grooving of the talonid face of the hypoconid and of the whole heel of M3. Matthew and others have noted this resemblance, although hardly recognizing its very complete character, but have tended to distrust or even reject it because of the well-known fact that early tuberculosectorial dentitions are all more or less alike and that erroneous allocations have frequently resulted from comparisons of molar teeth alone. This is, of course, true, but it is also true, as Gidley pointed out, that such complete convergence in a really complicated pattern as occurs between Plesiadapis and Pelycodus Cantius has rarely or never been found in mammals not truly related, and that the characteristic structure of Plesiadapis molars is encountered in no order other than the primates. The evidence of molar pattern is decidedly in favor of rather close relationship to the Notharctinae. As this happens to be correlated with other resemblances to that subfamily or, more broadly, to the general division of primates which it represents, there is every reason to accept this evidence as valid."

It is important to note, in evaluating Simpson's (1935) appraisal of the postcranial remains of Plesiadapis, that he accepted tree shrews as primates on the experience and authority of W.E. Le Gros Clark. Simpson wrote (p.25): "If the tupaioids are primates, then the plesiadapids are necessarily primates also." The converse would not

necessarily follow, that is, inclusion of plesiadapids in Primates would not require that tupaioids be classified here as well.

The first reasonably complete skull of Plesiadapis was described by Russell (1959), who reported that the auditory bullae were completely ossified and "dérivent seulement de l'os pétreux." He also noted the presence of an ossified tubular ectotympanic in Plesiadapis. Russell later (1964:105) concluded from the cranial anatomy of Plesiadapis:-

"Comme on l'a montré, les Adapidés qui ont vécu de l'Éocène moyen à l'Éocène tardif, présentaient, en commun avec Plesiadapis, un certain nombre de caractères craniens fondamentaux; le ressemblance va presque aussi loin avec les Notharctidés de l'Éocène ancien et moyen. Ces faits suggèrent que les trois groupes étaient apparentés de très près au début du Paléocène, mais que les Notharctidés se sont développés plus ou moins isolément en Amérique du Nord. Les Adapidés d'Europe, plus conservateurs, ont gardé des traces plus nettes de leur héritage commun, comme en témoignent certains traits du Plesiadapis paléocène. Toutefois les spécialisations présentées par celui-ci montrent que les trois lignes évolutives étaient déjà séparées dès le milieu ou peut-être même dès le début des temps paléocènes. Même en admettant que les faunes paléocènes d'Europe soient moins bien connues que les faunes contemporaines d'Amérique du Nord, il est vraisemblable que ce dernier pays fut le centre évolutif des Plesiadapidés."

Russell (1964) reported little on the postcranial skeleton of Plesiadapis, but he did describe several features of the clawed ungual phalanges present in newly collected material, noting that these were strongly curved, laterally compressed, and fissured dorsally over the distal one-third of their length, with a large basal tuberosity for insertion of a strong flexor tendon. Russell's postcranial material of Plesiadapis was described by Szalay et al. (1975), who argued forcefully that the mode of articulation of the radius and humerus, and a complex of characteristics of the tarsus of Plesiadapis, are evolutionarily advanced and shared only with primates.

My own research on Plesiadapis has been concerned primarily with evolutionary patterns and systematic relationships within Plesiadapidae, and to some extent with the systematic relationships of Plesiadapidae to other families within Plesiadapiformes. My comparisons of the abundant dental remains of Palaeocene Plesiadapis with those of later Eocene primates led me to conclude, as Gidley (1923) and Simpson (1935) had before, that Plesiadapis shares detailed resemblances of upper and lower molar morphology with Cantius of similar size. As noted by Gidley (1923), molars of smaller plesiadapiform genera, e.g. Elphidotarsius, resemble those of smaller tarsioids like Tetonius or Tarsius itself. Thus it seemed to me that molar resemblances might link Plesiadapis and its allies phyletically to all later primates and not just to lemuroids as Simpson (1935) had concluded.

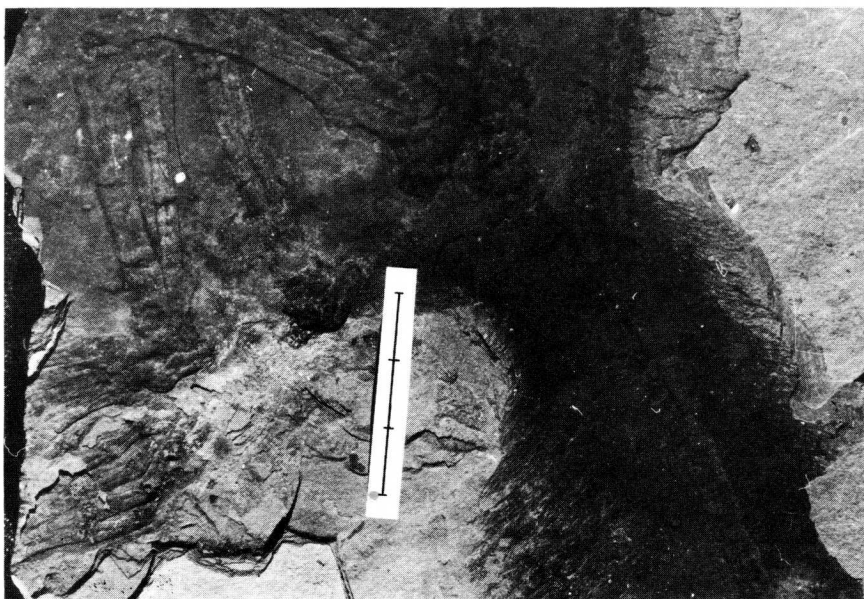
Other dental and cranial features suggested special affinity with tarsioids. These included enlarged, pointed central incisors, an ossified auditory bulla continuous with (if not actually comprised of) the petrosal, an ectotympanic anulus anchored to the auditory bulla by ossified Necrolemur-type struts, and an ossified tubular extrabullar extension continuous with (if not actually comprised of) the ectotympanic (Gingerich, 1975, 1976). Hence I proposed (1976) that primates be divided into two principal clades, Plesitarsiiformes, uniting Plesiadapiformes and Tarsiiformes, and Simiolemuriformes, uniting Anthropoidea (Simiiformes) and Lemuriformes. I still think this arrangement has as much cladistic merit as the popular actualistic alternative which groups tarsiers with anthropoids as Haplorhini, retains lemuroids and lorisoids in the primitive Strepsirhini, and removes Plesiadapis from Primates entirely.

Plesiadapis, and other plesiadapiform genera known from the Palaeocene, are clearly more primitive than any Eocene primates of modern aspect. All plesiadapiform genera lack a postorbital bar. Plesiadapis not only retained pedal grooming claws, as tarsioids, lemuroids, and lorisoids do today, but evidently retained claws on all phalanges. Parts of two lower limbs of a late Palaeocene specimen from Menat, preserved in articulation, are illustrated in Figure 3. The posterior part of the left foot is preserved in articulation with the tibia and fibula. Immediately below this, one can see the anterior part of a right foot that has become disarticulated and rotated through 180 degrees. The hallux of the rotated right foot now lies just below and parallel to metatarsals of the left foot. Judging from the preserved impression, the hallux (digit I) bears a sharply pointed claw. Pedal digits II through V are longer than digit I, and these too bear claws. The pollex is not preserved in the counterpart of this specimen, but digits II through V of the hand all bear claws (Gingerich, 1976, Pl.12).

Primitive mammalian characteristics retained by Plesiadapis and its allies, combined with many distinctive specializations, render any attempt to link Plesiadapiformes definitively with Tarsiiformes or Lemuriformes difficult. Plesiadapis is older geologically than any known tarsiiform or lemuriform primate, and it represents an evolutionary grade more primitive than these primates of modern aspect. Detailed, stratigraphically documented, studies of mammalian evolution across the Palaeocene-Eocene boundary in western North America, carried out intensively for the past ten years, suggest that major faunal turnovers may take place rapidly (on a geological time scale). The stratigraphic record and fossil record are rarely complete enough to document such turnover events in detail, and major worldwide episodes of climatic change sometimes facilitate intercontinental faunal dispersal in any case. Consequently, one might predict a priori that it is unlikely that such important faunal transitions will be preserved in the fossil record as a continuous series of intermediate genera and species linking early ancestors to later more advanced descendants. Our search for the origin of the tarsiiform Omomyidae and the lemuriform Adapidae in North America has permitted us to say that both groups appeared in the early part of the Wasatchian land-mammal age (early Eocene) as immigrants from elsewhere, with no likely ancestors evident in North America in older geological strata. Such negative evidence is never fully satisfying, but in this case the first appearance of Omomyidae and Adapidae coincides with the first

appearance of hyaenodontid creodonts and primitive equid perissodactyls likely to be African in origin. Hyaenodontids dominate Oligocene faunas of carnivorous mammals in Africa as nowhere else, and the dawn horse Hyracotherium resembles closely the hyracoid genus Microhyrax from the Eocene of Africa, a likely centre of origin for primates of modern aspect.

Fig. 3. Posterior part of skeleton of Plesiadapis insignis from French locality of Menat. Specimen is preserved as a negative (and thus reversed) impression in carbonaceous shale. Note preserved impression of fur on bushy tail, and impressions of nearly complete left and right posterior limbs. What appears here as a left foot remains articulated with the tibia and fibula. What appears here as a right foot has become disarticulated and rotated. Note clawed hallux (digit I) of right foot lying just below and parallel to metatarsals of left foot and clawed digits II-V as well. Scale in cm. Specimen is better illustrated with stereophotographs on Plate 12 in Gingerich (1976).



Intermediates linking primitive Plesiadapiformes to Tarsiiformes and/or Lemuriformes are unknown and unlikely to be discovered unless the African Palaeocene begins to yield a larger mammalian fauna. As a result of phylogenetic uncertainty regarding the origin of Tarsiiformes and Lemuriformes, any formal classification of Plesiadapiformes with one or another of these groups cannot readily be justified. A grade classification appears to express what we know (and do not know) about the phylogeny of early primates more accurately than a cladistic classification (Gingerich 1981, MacPhee et al., 1983).

PLESIADAPIS AND PRIMATE EVOLUTION

Plesiadapis is one of the most common mammals in late Palaeocene faunas of Europe and North America. This genus is represented by tens or hundreds of specimens in quarry samples representing the principal faunal zones of continental Thanetian (late Palaeocene) and Ypresian (early Eocene) ages in Europe, and continental Tiffanian (late Palaeocene) and Clarkfordian (transitional Palaeocene-Eocene) land-mammal ages in North America. Plesiadapis is important in providing a remarkably detailed record of mammalian evolution through an interval of 4-5 million years of geological time. The outline of changing tooth size and, by inference, body size shown in Figure 4 illustrates one of many evolutionary patterns recorded for this genus. The continuity of evolutionary change over time seen in Plesiadapis is evidence of the continuity of evolution as a general process (discontinuities too are common in the fossil record, as shown in the same figure by the absence of forms connecting Carpodaptes and Carpolestes). Figure 4 illustrates how phylogenetic hypotheses can be constructed on the basis of available stratigraphic and morphological information, and integrated phenetically without a priori assignment of primitiveness or derivedness to morphological characteristics to produce a temporally ordered minimum spanning tree. Figure 4 also illustrates how such a phylogenetic hypothesis can be tested when it serves as a target for future discoveries (closed circles and accompanying numerals represent new discoveries made after the phylogenetic pattern itself was drawn - these generally fall within the predicted target area).

The pattern linking successive species of Plesiadapidae together in Fig. 4 reflects a traditional approach to the study of evolutionary history that differs in several important ways from much current practice in systematic biology. For reasons that are not completely clear, systematics has become in recent years implicitly (and sometimes explicitly) actualistic. Available fossils are either ignored or they are treated as imperfect specimens coeval in time but secondary in importance to anatomically and biochemically complete living animals. The ages of fossils are often ignored lest such an independent perspective on time and evolutionary history bias an intuitive sense for how life in the past must have been, based on life in the present (hence the sentiment expressed in opening this essay - life in the past was "pretty much like today, there just wasn't as much of it."). The focus of systematic research today, as in Richard Owen's day, seems to be on archetypes rather than ancestors.

Figure 4 is explicitly about ancestors evidenced in the fossil record.

Given present knowledge of North American Plesiadapidae, Plesiadapis praecursor is the oldest known species of Plesiadapis, and it appears to be a plausible ancestor for all later North American species of Plesiadapis. P. praecursor is real, it is not a hypothetical archaetype. This is not to say that detailed study of morphological patterns in stratigraphic context will always identify plausible ancestors for all species under study. Carpolestes jepsoni stands out clearly as a species whose ancestry at the species level is unknown (although it is likely to have been derived from some species of Carpodaptes, perhaps even one of the known species).

PLESIADAPIS AND DELINEATION OF THE ORDER PRIMATES

The same approach to the study of evolutionary history illustrated by Plesiadapis can be applied on a broader scale to the study of all primate relationships (see Figure 5). In Figure 4 Plesiadapis dubius was linked to P. fodinatus, which was linked in turn to P. churchilli, P. rex, P. anceps, and P. praecursor, which was linked finally to Pronothodectes jepi. Each of these successive species is distinctive, and together they

Figure 4. Outline of the species-level phylogeny of North American Palaeocene Carpolestidae and Plesiadapidae, showing pattern of evolution in tooth size, and by inference body size, in stratigraphic column 1400 metres thick representing 4-5 million years on geological time. History of diversification of Plesiadapis might serve as a reasonable model for diversification of Plio-Pleistocene Hominidae. Reproduced with additions from Gingerich (1976, 1980).

