Cranial Anatomy and Evolution of Early Tertiary Plesiadapidae (Mammalia, Primates)

Philip D. Gingerich

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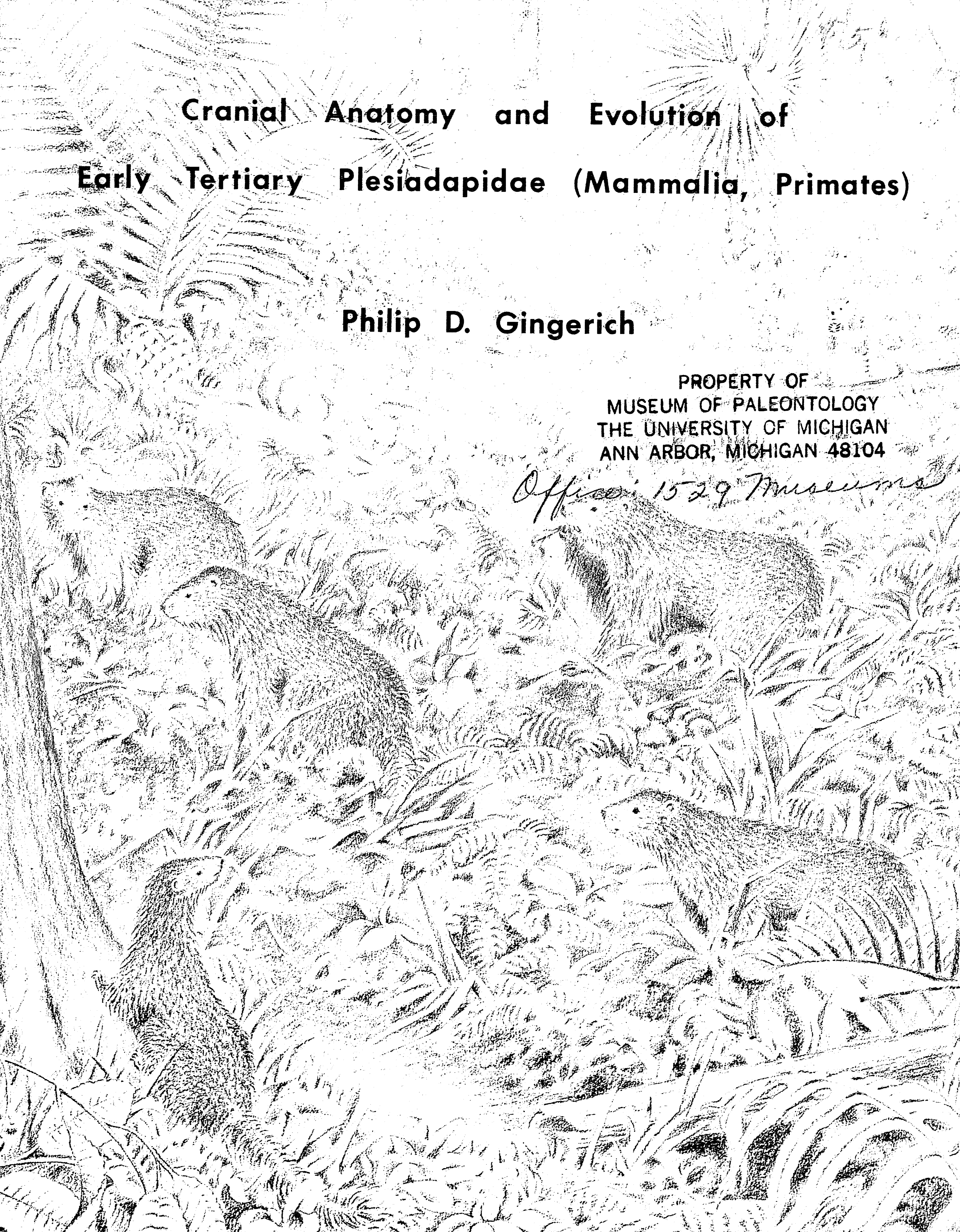

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CRANIAL ANATOMY AND EVOLUTION OF EARLY TERTIARY PLESIADAPIDAE (MAMMALIA, PRIMATES)

Reconstructed Clarkforkian landscape in northwestern Wyoming, with *Plesiadapis dubius* and several *Plesiadapis cookei* in the foreground, and *Chiromyoides major* in the background.

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CONTENTS

ABSTRACT

The Plesiadapidae are an important family of early fossil mammals presently known from middle Paleocene through lower Eocene strata in North America and Europe. Specimens of *Plesiadapis* are among the most common Paleocene fossil mammals, they are known from stratigraphic intervals spanning some 12 million years, and they changed and diversified greatly through this period of geological time. Thus the Plesiadapidae are an ideal group for detailed biostratigraphic and evolutionary study. Virtually all known specimens of Plesiadapidae were studied to: (1) determine the extent to which it is possible to study the evolution of a group of early Tertiary mammals *at the species level*, (2) improve the correlation of middle Paleocene through early Eocene continental sediments within and between North America and Europe, and (3) clarify the relationship of *Plesiadapis* to living and fossil primates.

A *stratophenetic* method of phylogeny reconstruction based on phenetic linking of fossils in adjacent stratigraphic intervals is proposed. Species in the fossil record are viewed as arbitrarily divided segments of biologically distinct evolutionary lineages that differ morphologically from other such segments, and a complete systematic revision is included. The family Plesiadapidae includes five valid genera and 26 species (one of which, *Plesiadapis russelli*, is newly described). Four distinct evolutionary lineages were present in North America during the late Paleocene. Three lineages were present in Europe, two of which paralleled very closely the evolution of their counterparts in North America. These pairs of North American and European lineages are so similar that they may have been parts of the same evolving pangeographic distribution, supporting the idea that there was a continuous or nearly continuous continental connection between North America and Europe during the late Paleocene.

The relatively complete stratigraphic record of Plesiadapidae in North America documents gradual phyletic evolution in both discrete and continuous morphological characters. Strong character divergence in tooth size (and by inference body size) is documented *following* the initiation of sympatry in recently separated sister lineages. Other morphological characters do not show this pattern of character divergence but undergo considerable parallel evolution presumed to indicate parallel adaptations. Similarly, adaptation is inferred to be the cause of two documented evolutionary reversals in the evolution of cusp patterns on incisors and premolars. Continued study of mammalian groups with detailed fossil records promises to considerably improve our understanding of speciation in natural populations, and of trends in the evolution of adaptations.

The Torrejonian, Tiffanian, and Clarkforkian in North America are subdivided into eight biostratigraphic range zones based on consecutive species in a single evolving lineage of *Pronothodectes* and *Plesiadapis*. Six biostratigraphic range zones are recognized in the evolution of *Plesiadapis* and *Platychoerops* during the Thanetian and Ypresian in Europe, but mammalian faunas from additional intermediate intervals remain to be sampled in Europe. The *Plesiadapis cookei* zone in North America is correlated with the Sparnacian *Plesiadapis russelli* zone in Europe on the basis of *Plesiadapis* and other contained mammalian faunas, and it is concluded that the Clarkforkian mammal age in North America is earliest Eocene, rather than latest Paleocene as it has conventionally been regarded.

The Plesiadapidae appear to have been herbivorous, basically terrestrial animals, most of which thrived at high population densities in warm temperate climates of the late Paleocene. Their closest living analogues in the mammalian faunas of North America and Europe today would appear to be rodents of the family Sciuridae (marmots, ground squirrels, etc.). It is possible that rodents evolved from a generalized early or middle Paleocene primate, but substantive fossil evidence is lacking. Rodents, like many other groups of modern mammals, appeared abruptly in the fossil record at the beginning of the Eocene when a subtropical climate again returned to Europe and North America, replacing the warm temperate climate of the late Paleocene. Being adapted to a temperate climatic regime, *Plesiadapis* became extinct in North America when it was replaced by new subtropical forms. In Europe *Plesiadapis* evolved rapidly into *Platychoerops*, which subsequently became extinct several million years later. The presence of a temperate climatic minimum during the late Paleocene in the areas of known fossil deposits helps to explain the gap in the fossil record between generalized primates of the subtropical early and middle Paleocene, and their abruptly appearing relatives of modern aspect in the subtropical early Eocene.

The dental and cranial morphology of primitive Plesiadapidae is similar to that of Eocene tarsiiform primates, and the two appear to be closely linked phylogenetically. Similarly, primitive lemuriform and anthropoid primates appear to be closely linked phylogenetically. A cladistic classification is employed uniting Plesiadapiformes with Tarsiiformes in one suborder, and Simiiformes with Lemuriformes in the other. It is recognized that a graded classification separating anthropoid primates from prosimians would also be consistent with the phylogeny proposed, and this graded classification might be preferable in some instances.

I

INTRODUCTION

NUMEROUS LOCALITIES yielding fossil mammals have been discovered in the Paleocene sediments of western North America during the past 50 years. Specimens of *Plesiadapis*, an extinct squirrel-sized mammal, are among the most common fossils in the collections made from these localities. As a result, there are now large samples of *Plesiadapis* from many North American localities of middle and late Paleocene age. Furthermore, European workers have described a number of large collections of *Plesiadapis* from the Paleocene strata of Europe. All of the described collections of *Plesiadapis*, together with a number of large new collections, have been studied in an attempt to reconstruct as accurately as possible the phylogenetic history of the family Plesiadapidae.

This new study of the Plesiadapidae has been undertaken for three principal reasons. The first reason for such a review was to see to what extent it is possible to reconstruct the history of a relatively well-known group of extinct early Tertiary mammals from the fossil record. The species is widely recognized as the basic unit of animal evolution, yet surprisingly, there has been almost no attempt to trace the evolution of *species* through the fossil record. The most often cited paleontological illustration of evolution through time, the evolution of the horse from *Hyracotherium* to *Equus*, is still understood only at the generic level. In this study, an attempt has been made to understand the evolution of *Plesiadapis* at the species level.

Eldredge and Gould (1972) recently proposed that the origin of new species or lineages involves very rapid evolution of a new morphotype in a peripheral isolate of a previously existing species. They believe that the intermediate forms linking new and old species are so rare and short lived that they have virtually no chance of appearing in the fossil record. According to their model, evolution proceeds with long periods of equilibrium interrupted ("punctuated") by the sudden appearance of a new derived species. Their punctuated-equilibrium model differs considerably from the more orthodox Darwinian model of gradual phyletic evolution. Both models can be defended theoretically, and it is only by detailed examination of well-preserved fossil sequences that the relative importance of phyletic gradualism and punctuated equilibrium can be determined. Thus it was anticipated that the fossil record and evolution of *Plesiadapis* might be of importance in evaluating the relative merits of these two models of speciation.

In another recent paper, three noted paleontologists have suggested that biostratigraphy, i.e., the stratigraphic distribution of fossils, is rarely relevant to understanding the relationships of fossil taxa (Schaffer, Hecht, and Eldredge, 1972). The results reported here are also of some importance in evaluating the usefulness of stratigraphic information in reconstructing phylogenies.

The second reason for reviewing the phylogeny of the Plesiadapidae is related to problems of paleogeography and correlation. Geophysical evidence collected in the past 10 years has demonstrated beyond doubt that prior to the opening of the North Atlantic Ocean, the European and North American continents were joined (see Fig. 1). Furthermore, it appears that the remarkable similarity (again, always discussed in terms of *genera*, not *species*) of the early Eocene mammal faunas of Europe and North America may be due to broad pangeographic distributions or transatlantic migration via Greenland before the two continents became completely separated (McKenna, 1972a). If such faunal interchange were possible in the early Eocene because of a transatlantic continental connection, one would expect it to have been possible in the Paleocene as well. Since *Plesiadapis* is a common fossil mammal in Paleocene deposits on both sides of the Atlantic, the closeness of relationship of its species in Europe to those in North America is a potential indicator of the amount of faunal interchange between the two continents in the Paleocene.

As was noted above, little attempt has been made to study the evolution of any Paleocene lineage at the species level. Perhaps the major reason for this is the absence of a detailed time framework for the continental

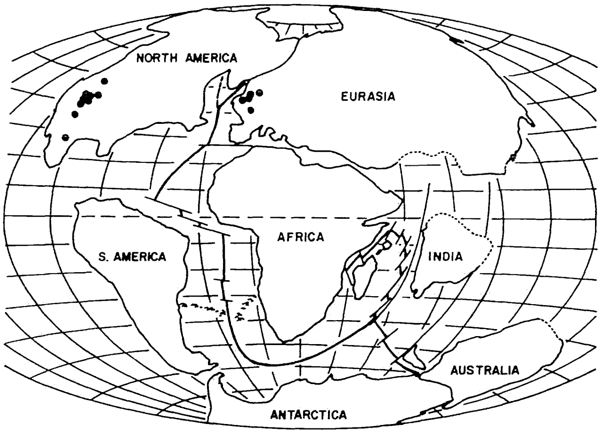

Figure 1. Configuration of continental masses at the beginning of Paleocene time. Filled circles show the location of major Paleocene and Eocene plesiadapid-bearing deposits. The precise configuration of continental margins and epicontinental seas is not shown. Base map from Dietz and Holden (1970).

Paleocene fossil localities and faunas of North America. A special effort has been made in this paper to develop a detailed stratigraphic correlation of the major deposits within North America based on the species of *Plesiadapis*. This correlation has then been extended to include the *Plesiadapis*-bearing deposits of Europe.

The third reason for reviewing the cranial anatomy and evolution of the Plesiadapidae concerns the prominent position usually given to *Plesiadapis* in the phylogeny of Primates. Virtually all general accounts of primate evolution (see Le Gros Clark, 1962, p. 85, for example) place this Paleocene genus near the base of the primate radiation. On the other hand, Martin (1972, p. 302), Hershkovitz (1974, p. 21), and others have questioned this placement. After a careful study of the cranial anatomy of *Plesiadapis* and all other relevant Paleocene and Eocene fossil primates, it is possible to state more clearly than has been done before the relationship of *Plesiadapis* to the early evolution of Primates.

In the remainder of this introductory chapter the geographic distribution of plesiadapid-bearing localities in North America and in Europe is described, and the terms and measurements used to describe the teeth of *Plesiadapis* are defined. In the second chapter, methods are outlined for studying populations and species of fossil mammals, their variation, and their relationships. This is followed by a systematic revision of the species of Plesiadapidae in Chapter 3. In Chapter 4 the stratigraphic sequence of fossil localities in the Tertiary basins of western North America is reviewed, localities containing the same species of *Plesiadapis* are correlated, and the phylogeny of the family in North America is interpreted within this stratigraphic framework. The correlation of North American and European plesiadapid-bearing deposits, a general Paleocene-early Eocene biochronology based on *Plesiadapis* evolution, and Palearctic-Nearctic mammalian faunal interchange in the Paleocene are discussed in Chapter 5. Dental function and the functional evolution of the incisors, premolars, and molars are described in Chapter 6. Important aspects of the cranial anatomy of *Plesiadapis* are discussed and compared in Chapter 7. Finally, a general discussion of the origin, early evolution, and classification of Primates follows in Chapters 8 and 9.

Geographic Distribution of Fossil Localities

Plesiadapids are at present known from early Tertiary sediments of only two continents: Europe and North America.[1] Reconstructions of the geographic relationship of Europe and North America in the Paleocene have been attempted by Sloan (1969), by Dietz and Holden (1970), and by Szalay and McKenna (1971). All three reconstructions agree in positioning North America and Europe much closer than they are today, and all of the authors seem to agree that some transatlantic crossing of the North Atlantic by terrestrial land mammals was probably possible at the beginning of the Tertiary. The approximate distribution of plesiadapid-bearing localities is plotted in Figure 1 on Dietz and Holden's (1970) reconstruction of continental positions at the beginning of the Paleocene. The latitudinal position of the plesiadapid-bearing deposits has apparently changed relatively little since that time.

A more detailed distribution map of the plesiadapid localities of North America is presented in Figure 2. These localities lie along a nearly north-south line following the trend of the eastern Rocky Mountains. Erickson's Landing, the most northern locality, is approximately 1800 miles (2800 km) from the most southern Black Peaks localities.

The distribution of the known plesiadapid-bearing localities in Europe is plotted in Figure 3. All of these localities lie within a triangular area bounded by Abbey Wood in the west, Walbeck in the east, and Menat in the south – the distance between each of these points being on the order of 500 miles or 800 kilometers.

Dental Terminology

Primitive plesiadapids have a total of nine teeth in each jaw. The most posterior three are undoubtedly homologous with the molars of the typical eutherian

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[1] Gaudry (1904;1906) regarded the Patagonian genus *Josepholeidya* as a synonym of *Plesiadapis*, but Simpson (1948b, p. 125) identifies it as a litoptern – plesiadapids are as yet known only from Europe and North America.

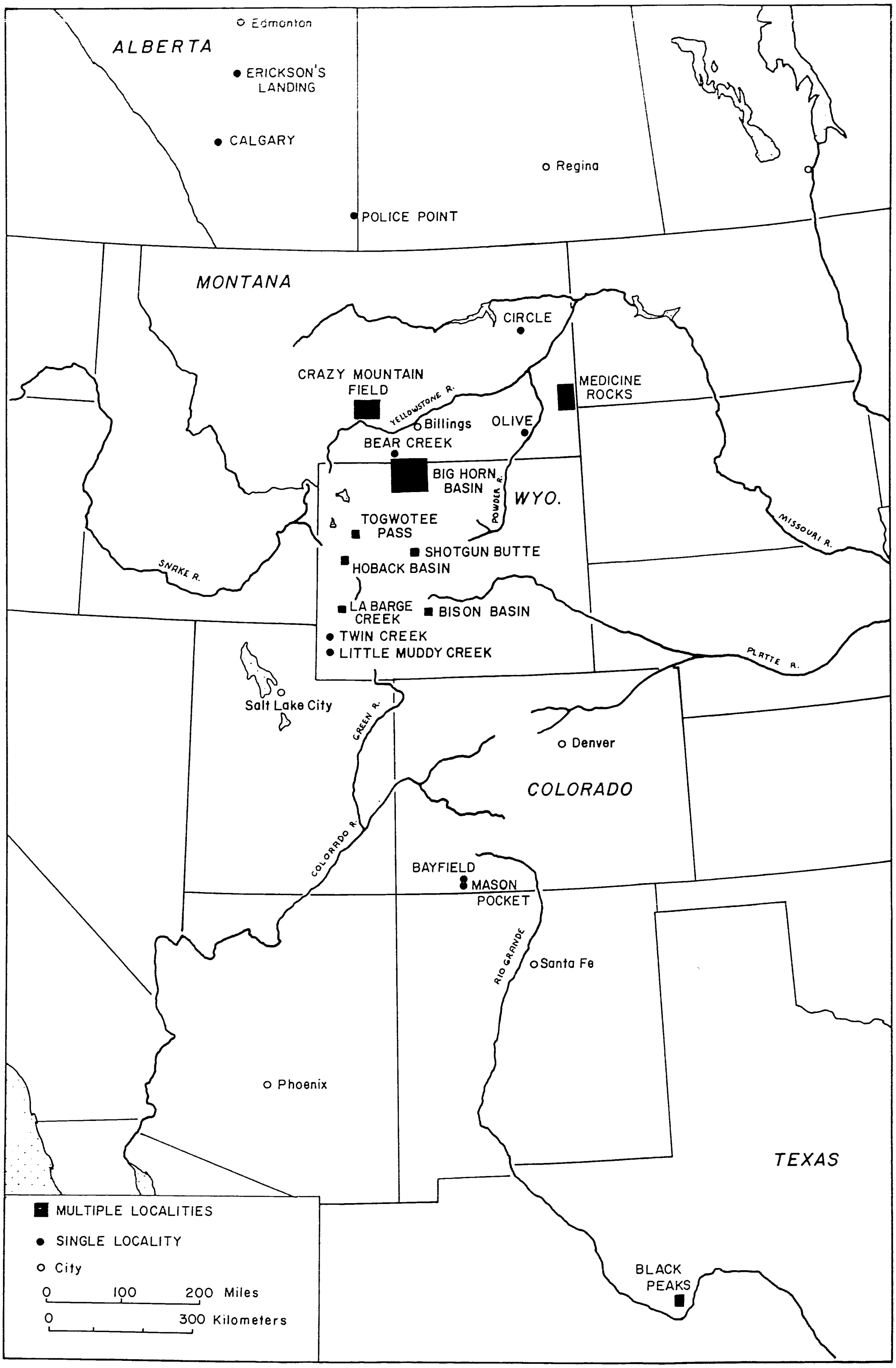

Figure 2. Major plesiadapid-bearing localities of western North America.

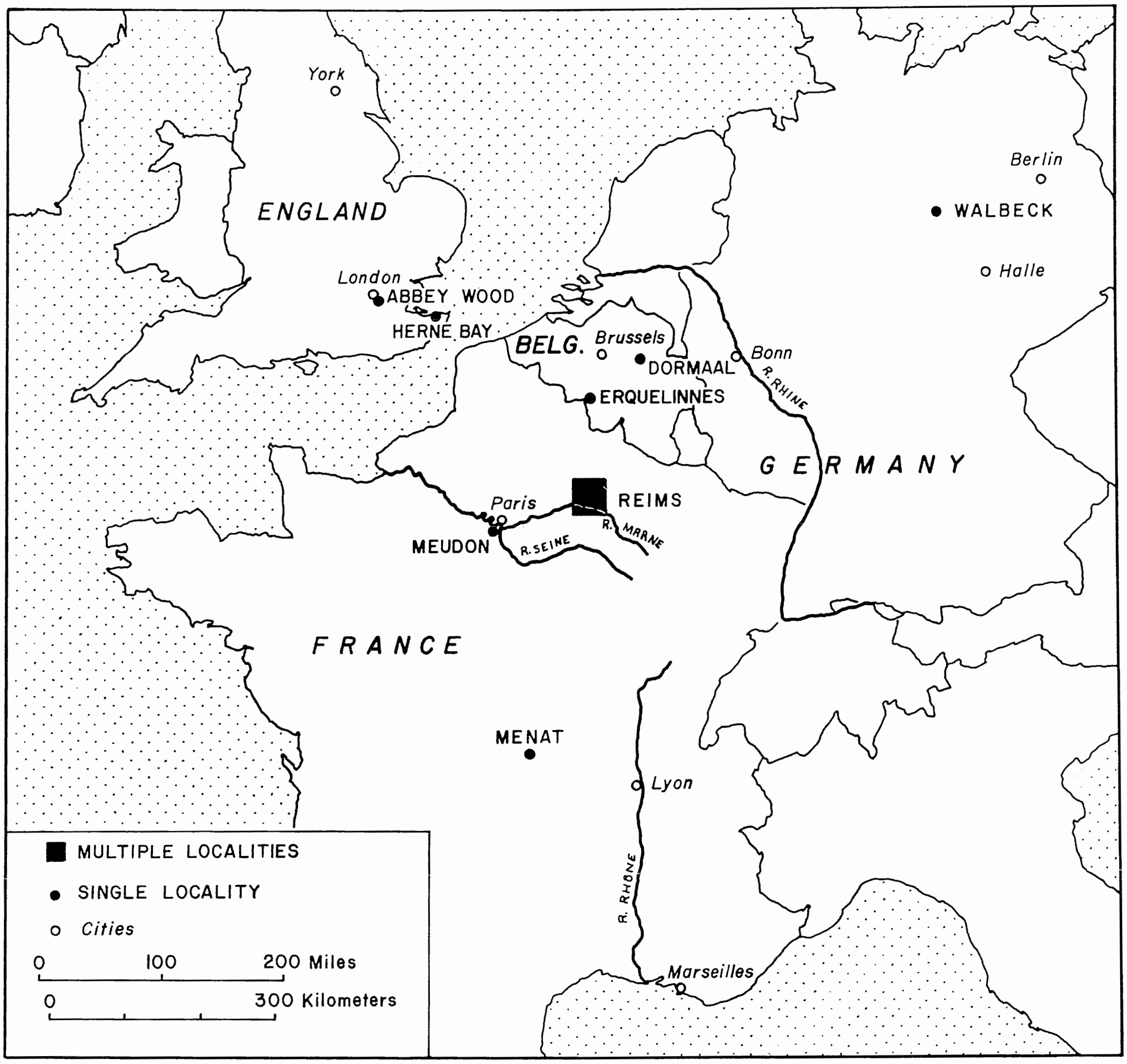

Figure 3. Major plesiadapid-bearing localities of western Europe.

dentition and will be referred to as M_1^1, M_2^2, and M_3^3. The most anterior tooth in the maxilla and the tooth occluding in front of it in the mandible are conventionally regarded as the canines (see discussion in Chapter 7). There is considerable functional justification for interpreting the reduction of incisors and premolars as happening next to the canines, i.e., when the typical eutherian formula of $\frac{3}{3}\ \frac{1}{1}\ \frac{4}{4}\ \frac{3}{3}$ was reduced to $\frac{2}{2}\ \frac{1}{1}\ \frac{3}{3}\ \frac{3}{3}$, I_3^3 and P_1^1 were the teeth lost rather than, for example, I_1^1 and P_4^4. The reason for this has to do with functional fields in the dentition of typical mammals: the incisors (left and right sides together) form one functional field used in ingestion; each individual canine is a specialized puncturing or shearing tooth; and the cheek tooth series on each side constitutes a single integrated puncturing, shearing, and grinding unit. Loss of I_1^1 or loss of P_4^4 would seriously disrupt incisor function or cheek tooth function, respectively, whereas the loss of I_3^3 or P_1^1 would not disrupt the functional integration of these units. For this reason, the teeth missing in the dental formula of primitive Plesiadapidae are thought to be I_3^3 and P_1^1, and the homologies of the teeth at the remaining nine positions are interpreted as I_{1-2}^{1-2}, C_1^1, P_{2-4}^{2-4}, M_{1-3}^{1-3}. This full complement of $\frac{2}{2}\ \frac{1}{1}\ \frac{3}{3}\ \frac{3}{3}$ in primitive plesiadapids was further reduced by the gradual loss of I2, C, and P2 in the more advanced species.

The terms used to describe details of the molar

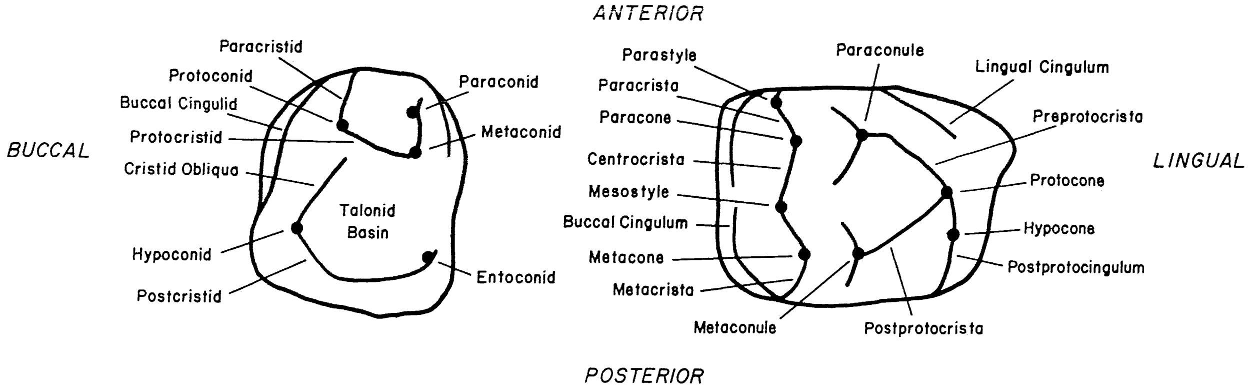

Figure 4. Cusp and crest nomenclature used to describe the molars of *Plesiadapis*. Lower molar at left, upper molar at right, both in occlusal view.

structure of *Plesiadapis* are given in Figure 4; all are in common use and require little discussion. It should be noted that the term postprotocingulum has been substituted in *Plesiadapis* for the "Nannopithex-fold" sometimes used by earlier writers (see Simpson, 1955, p. 435). The structure in *Plesiadapis* is, in fact, a strongly developed shelf connecting the protocone with the posterior cingulum of the upper molars. Although probably derived from a postprotocingulum, the Nannopithex-fold in *Nannopithex* is a much more delicate structure. The same molar terminology has been employed to describe the premolars of *Plesiadapis*, although the premolars of the earlier species obviously lack a number of the structures seen in the molar dentition.

The incisors of plesiadapids contribute much to our knowledge of the evolution of the family, and, to facilitate discussion, names have been given to each of the principal cusps of the upper and lower incisors. These new terms are illustrated in Figure 5. Each term describes the position of the named cone, conule, or crest on the incisor; the termination *id* has been used for names applied to lower incisors to distinguish them from the names of features of the upper incisors in accordance with this usage for lower molar terms.

The standard terms anterior, posterior, dorsal, ventral, medial, and lateral are employed throughout the paper to describe positions or aspects of the skull. In addition, buccal, lingual, and occlusal are used to describe positions and aspects of the teeth. The "mesial" and "distal" sides of incisors are referred to as medial and lateral, respectively, and of cheek teeth as anterior and posterior, respectively, since this is the more general usage in mammalian paleontology.

Dental Measurements

Some of the most important collections of *Plesiadapis* include large numbers of isolated teeth. It was thus necessary to employ a system of measurements that could be taken in exactly the same way on isolated teeth and on teeth in place in mandibles and maxillae. These measurements are illustrated in Figure 6. Note particularly that the length of a lower molar was measured from the front of the paracristid to the back of the postcristid, not to the back of the crown. This measurement is slightly shorter than the total crown length usually measured on lower molars but has the advantage of making measurements comparable, whether they were taken on isolated teeth or on teeth in mandibles.

All measurements were taken with a Helios vernier or dial calipers with specially sharpened wedge-shaped tips. Wedge-shaped tips proved much easier to use than sharply pointed tips when measuring the length and width of teeth. All measurements were made by positioning the tips of the calipers on the tooth to be measured under a low-powered binocular microscope. This assured accurate positioning of the tips, reduced to a minimum the chances of breaking specimens, and effectively removed any tendency to influence the measurements unconsciously, since it was impossible to read the dial while setting the tips. After the tips were set, the calipers were removed from under the microscope, the dial read, and the measurement recorded.

All measurements were recorded to the nearest tenth of a millimeter, since this seemed from a number of experiments to be the maximum level of reproducibility. Where two or more measurements are available for a sample from one locality, the mean and standard deviation are given to the nearest one-hundredth of a milli-

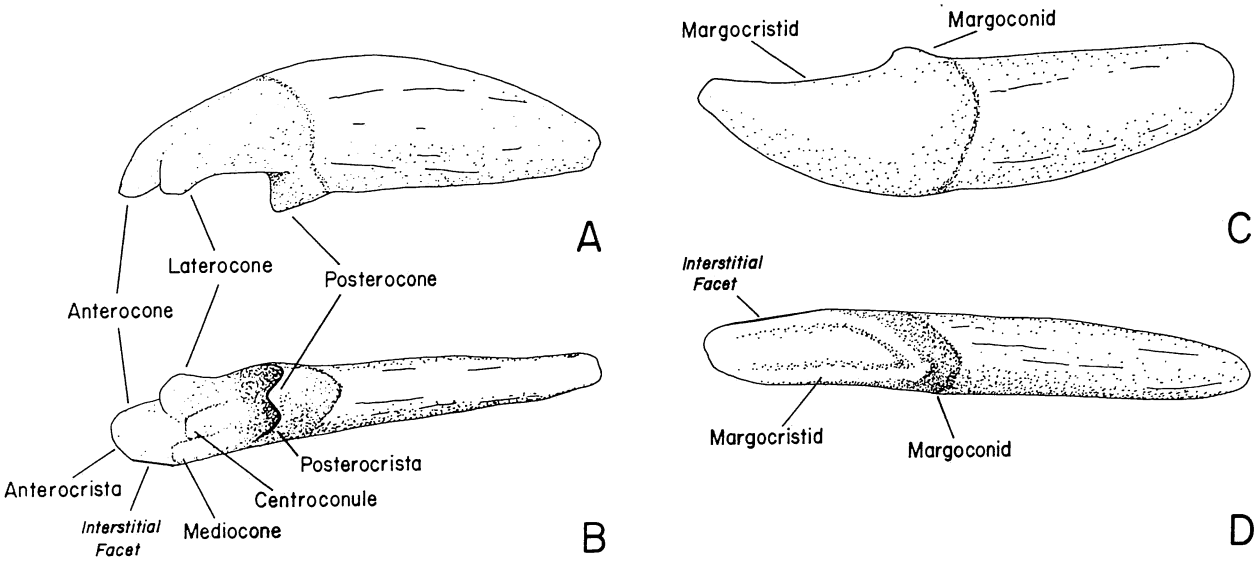

Figure 5. Cusp and crest nomenclature used to describe the incisors of *Plesiadapis*. Left upper incisor in lateral (A) and occlusal (B) view; left lower incisor in lateral (C) and occlusal (D) view.

meter. The statistics employed are defined and discussed in Simpson, Roe, and Lewontin (1960).

In the course of this study, sharp epoxy casts were made of almost all important specimens following the techniques of Russell, and of Waters and Savage (1972). These casts proved exceedingly valuable in making comparisons, particularly between European and North American specimens. Complete reference sets of these casts have been deposited in the collections of the Yale Peabody Museum and the University of Michigan Museum of Paleontology.

Institutional Abbreviations

Institutional names have been abbreviated as follows throughout this report:

AC	Pratt Museum of Geology, Amherst College
AMNH	American Museum of Natural History, New York
BMNH	British Museum of Natural History, London
CCM	Carter County Museum, Ekalaka (Montana)
CM	Carnegie Museum, Pittsburgh
FMNH	Field Museum of Natural History, Chicago
GH	Geiseltalmuseum, Halle (Germany)
IRSNM	Institut Royale des Sciences Naturelles de Belgique, Brussels (Belgium)
LGM	Laboratoire de Géologie, Faculté des Sciences de Marseille (France)
Louis	Private collection of Pierre Louis, Reims (France)
MCZ	Museum of Comparative Zoology, Cambridge (Mass.)
MNHN	Muséum National d'Historie Naturelle, Paris
NMB	Naturhistorisches Museum, Basle (Switzerland)
Pellouin	Private collection of M. Pellouin, Reims (France)
Poirier	Private collection of M. Poirier, Châlons-sur-Marne (France)
PU	Museum of Natural History, Princeton University, Princeton
TMM	Texas Memorial Museum, University of Texas, Austin
UCB	Université Claude Bernard, Lyon (France)
UCMP	University of California Museum of Paleontology, Berkeley
UM	Museum of Paleontology, University of Michigan, Ann Arbor
USNM	Smithsonian Institution, National Museum of Natural History, Washington
UW	University of Wyoming Geological Musuem, Laramie
YM	Yorkshire Museum, York (England)
YPM	Yale Peabody Museum, New Haven

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That this synthetic revision of the Plesiadapidae was possible is largely due to the field work and collecting efforts of Professor Jepsen of Princeton and Dr. D.E. Russell of the Muséum National d'Histoire Naturelle in Paris. Dr. Jepsen's large undescribed collection proved crucial in working out the phylogeny of plesiadapids, and I am greatly indebted to him for giving me unrestricted access to it. Drs. Russell and Sigogneau-Russell assisted in many ways during the total of some three months spent studying in Paris.

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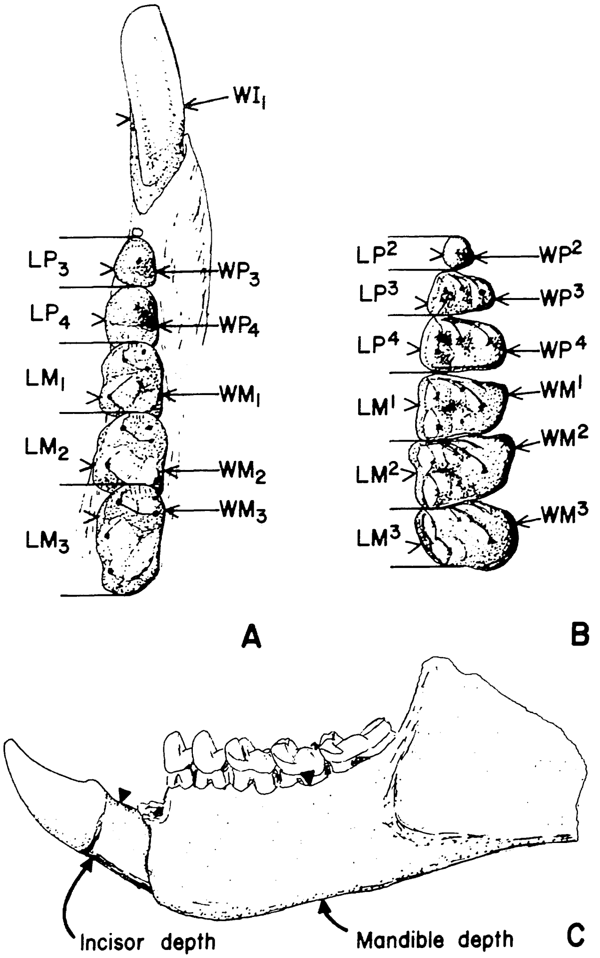

Figure 6. Measurements taken on teeth and mandible of plesiadapids. Lower (A) and upper (B) dentition in occlusal view, and mandible (C) in lateral view. L and W are length and width, respectively.

the Boyd Fund, Department of Geological and Geophysical Sciences, Princeton University; and a Shadle Fellowship of the American Society of Mammalogists made it possible to visit European museums and complete necessary field work in Wyoming, and facilitated early completion of the study. Final preparation of the manuscript for publication has been assisted by a Faculty Research Grant, Rackham School of Graduate Studies, University of Michigan.

II

VARIATION, SPECIES, AND PHYLOGENY RECONSTRUCTION

The fossil record demonstrates both increasing diversity and increasing specialization in the forms of life inhabiting the earth's surface over the course of geological time. The presence of distinctive but related faunas in successive geological periods leaves little doubt that animals have changed through time, and the presence of increasingly diverse faunas in successive periods indicates that diversification is an important aspect of evolution. The study of evolution thus seeks an explanation for observed changes within given "kinds" (species) of animals and for the general increase in the number of kinds inhabiting the earth. Change implies a time dimension, and significant evolutionary change in an animal species usually requires a relatively long period of time. For this reason, the fossil record alone has the potential to provide documentation of significant evolutionary change in natural animal populations.

One of the most important goals of studying the evolution of a group of related animals is to determine the sequence and timing of changes within the group. For such a study it is necessary to have some means of temporally ordering the specimens or species being studied. Specimens can be ordered into morphoclines, species can be ordered into *scala naturae*, and, given appropriate assumptions about the course of evolution, these morphoclines and scales can be given a time dimension. The problem here is that the "appropriate assumptions" about the course of evolution are *not* given – their discovery is one of the primary goals of any evolutionary study. Thus it is necessary to have a method of temporally ordering specimens and species that is independent of their morphology. Fortunately, stratigraphic sequences of sediments provide an independent means of temporal ordering for fossil specimens.

In this chapter a method of phylogeny reconstruction based on stratigraphic ordering of fossil samples is outlined. However, before discussing the reconstruction of evolutionary histories or phylogenies, it is necessary to understand several important characteristics of modern and fossil species of animals. Thus the concept of a species in the fossil record, variation in living and fossil populations, and the diagnosis of fossil species are reviewed first, followed by a discussion of phylogeny reconstruction.

BIOLOGICAL SPECIES IN THE FOSSIL RECORD

There are three basic concepts of a "species," each of which has some adherents in modern zoology and paleontology. A *typological* species concept unites specimens sharing the same or very similar morphology into "species." This practice is often unnatural, in that it sometimes separates all male animals into one species and females into another, or separates large animals from slightly smaller animals when in fact the two groups together show continuous, normal variation in all characters. Typology as a philosophy is discredited in modern evolutionary taxonomy, but discrediting it as a philosophy has not removed the practice of typology. There is a danger of artificial, typological separation of a single species into two or more whenever type specimens alone are used to represent a named species. There is a special danger of typological categorization in paleontology whenever a morphologically and temporally intermediate population of animals is discovered and compared with a named species from a lower stratigraphic level and one from a higher level. The intermediate population is then commonly divided, with the specimens resembling the species from the lower level being referred to that species, the specimens resembling the species from the upper level being referred to the species from the upper level. This gives the completely false impression that two species are present in the collection from the intermediate level, when in fact there is only one. There is also a danger of typological categorization whenever morphological characteristics alone are understood to *define* a species, rather than merely differentiate it from previously known species.

Recognition of the arbitrary and artificial nature of typological species led to the *biological* species concept.

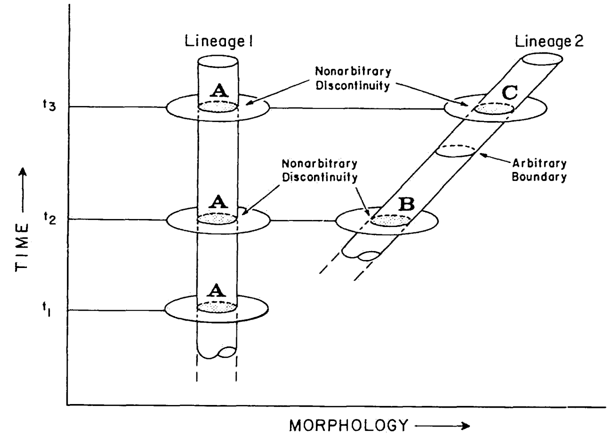

Figure 7. Diagram showing the relationship between biological species (e.g., A & B) sampled at any given time t, and generalized paleontological species viewed as units of evolutionary lineages (e.g., B & C). Species in the fossil record have both a biological dimension (where nonarbitrary morphological discontinuities are used to infer reproductive isolation on any given time plane), and a time dimension (where successive morphologically changing units of an evolving lineage must be separated at an arbitrary, time-parallel boundary). In some instances lineage branching points furnish natural, nonarbitrary boundaries between successive units of evolving lineages.

Biological species are defined by Mayr (1970, p. 12) as "groups of interbreeding natural populations that are reproductively isolated from other such groups." An attempt is made to include in one biological species all animals that share the same gene pool and (potentially, at least) are able to interbreed. Biological species are, in practice, usually recognized by their morphological characteristics, the inference being made that genetic cohesion underlies continuous morphological variation. Groups of animals exhibiting normally distributed, continuous variation in size or other morphological characteristics are grouped together into biological species. Discontinuities in morphological variation between groups are taken to indicate reproductive isolation of the groups. Reproduction, or potential reproduction, obviously requires that animals be living at the same time, and one can thus study the biological species living only at one given time. The biological species concept has no time dimension, and thus it has no meaning when animals separated by significant periods of geological time are considered.

The *paleontological* species concept is a generalization of the biological species obtained by adding a significant time dimension. A biologist attempts to identify the species living in a given place at a given time (usually the present). Similarly, a paleontologist must first identify the biological species living in a given place at a given time (in a given late Paleocene sedimentary stratum, for example), but a paleontologist must often also consider the relationships of his species to those in earlier or later strata. For example, referring to Figure 7, a paleontologist would conclude that there are two biological species present at time t_2. One biological species is present at time t_1, and two are present at time t_3. Since one of the species samples is virtually identical in all three levels, one would be justified in referring all to the same species, species A. The three successive samples of species A constitute a lineage, Lineage 1, which apparently changed little if at all through the time period sampled.

The presence of a second biological species (B) at time t_2 indicates that there is a second evolutionary lineage, Lineage 2, present as well. If this lineage changed significantly through time, the samples of the lineage at time t_3 might differ significantly from species B, and designation of a new species "C" would be justified. Paleontological species are thus units of evolutionary lineages with both a biological and a time dimension, i.e., the units are reproductively isolated from other contemporaneous evolutionary units, and they persist through a variable length of geological time depending on how rapidly they are evolving morphologically. It should be noted that contemporaneous biological species are separated from each other by real morphological and/or reproductive discontinuities, whereas successive species in an evolutionary lineage must be separated arbitrarily. Furthermore, the arbitrary boundary between any two successive paleontological species must lie in a time plane, or an artificial indication of two species would be given near this boundary when only one is ever present.

VARIATION IN FOSSIL POPULATIONS

Study of modern animal species demonstrates the near universal presence of morphological variation in living animals, and similarly, the study of fossils nearly always reveals variation in a given population. Morphological variation in a population can be a result of several factors. Animals change as they grow, and thus some variation may be ontogenetic. Males and females are significantly different in some species, and some variation may thus be due to sexual dimorphism. An additional component is simply due to individual variation. Individual variation has both an environmental and a genetic component (which includes both dominance and additive genetic variance). The existence of variation is important in providing the raw material on which natural selection acts, and it is the fraction of phenotypic variation due to additive genetic factors (heritability) that determines the susceptibility of a given trait to evolution

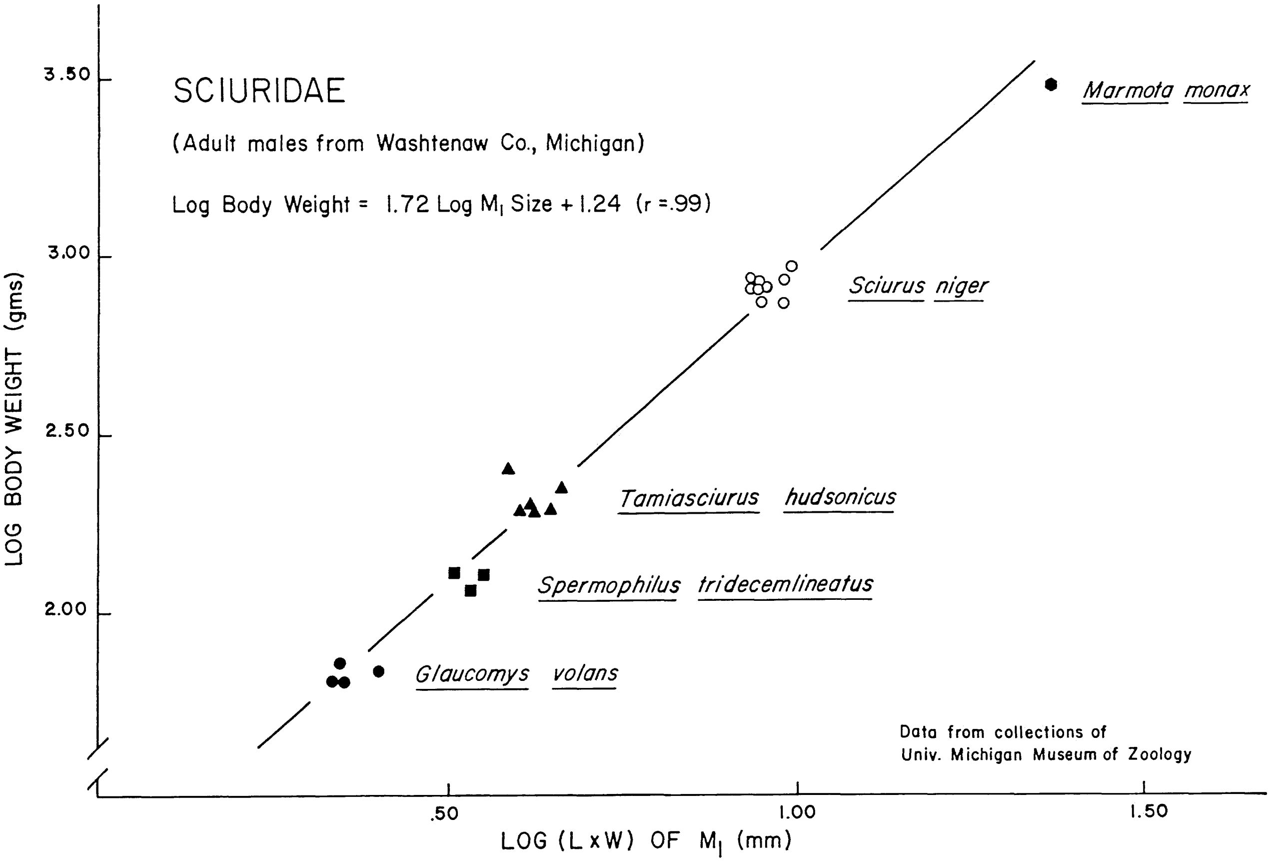

Figure 8. Correlation of body weight with tooth size in living squirrels of the family Sciuridae. Five species are shown, approximating the size range of the species of Plesiadapidae discussed in this paper. Within each species the correlation of body weight with tooth size is relatively low; however, within the range spanned by the entire family, the correlation of body weight and tooth size is very high (r=.99). Thus, within a group of related species spanning a significant size range, tooth size is probably a good general predictor of relative body size.

by natural selection.

Ideally, for an evolutionary study one should choose characteristics of an animal that are unaffected by ontogenetic development and sexual dimorphism, and that have a small environmental component of phenotypic variation with demonstrated high heritability. In practice, there is relatively little choice of characters possible in evolutionary studies of fossil mammals – usually teeth are the only remains preserved in sufficient quantities to permit detailed studies of variation and change in the fossil record. Fortunately, most mammalian teeth are nearly ideal for evolutionary study for the following reasons:

1. They are unaffected by ontogenetic growth – the crown forms before a tooth erupts, and once erupted, the crown of a mammalian tooth cannot continue to grow.
2. They are little affected by sexual dimorphism (especially the anterior molars, $M\frac{1}{1}$ and $M\frac{2}{2}$, see below).
3. They have demonstrated high heritability (see Bader, 1965; Alvesalo and Tigerstedt, 1974).

These characteristics, plus the existence of a relatively abundant and detailed stratigraphic record, make mammalian teeth ideal for documenting evolutionary changes through significant periods of geological time. Furthermore, since a mammal acquires food with its teeth, evolutionary changes in the dentition often imply significant functional changes in the animals ecological adaptations.

The size and form of its teeth obviously do not reveal everything about the adaptations of a given fossil species, but given the high level of correlation and integration of anatomical systems in a mammal, it seems reasonable to assume (in the absence of evidence to the contrary) that *closely related* fossil species that differed only slightly in dental morphology probably differed only slightly and in a correlated manner in other charac-

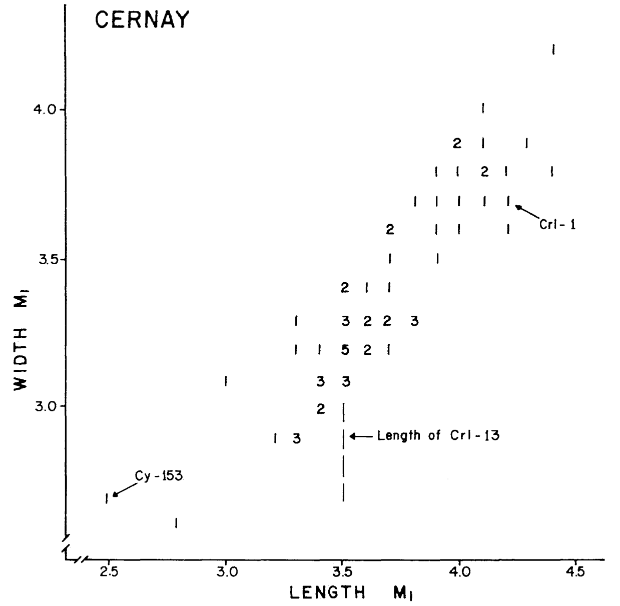

Figure 9. Scatter diagram of length versus width of M_1 for all plesiadapids at Cernay. Cy-153 is the type specimen of *Chiromyoides campanicus*. Crl-13 is type specimen of *Plesiadapis remensis*. Crl-1 is the type specimen of *Plesiadapis gervaisi*, a junior synonym of *Plesiadapis tricuspidens*.

teristics as well. Thus, for example, given a pattern of increasing tooth size in a lineage, the high level of correlation of tooth size and body size allows one to postulate that body size was increasing in the lineage as well. This is important in considering the significance of marked trends in the evolution of tooth size in *Plesiadapis* and other fossil mammals.

As background for interpreting tooth size in the Plesiadapidae, size variation was studied in the teeth of living mammals. The investigation showed that among the cheek teeth generally available for study in fossil mammals, the first molar, M_1, is usually the least variable tooth in the dental series (within a given population or species), and it is thus the best tooth on which to base diagnoses of closely related fossil species (Gingerich, 1974e). This does not mean that all species can be separated on the basis of tooth size alone, or even that the size of M_1 will always distinguish two sympatric congeneric species. Rather, if two or more congeneric species are found in a single fossil sample and they cannot be distinguished by differences in form, any size differences between species are most likely to appear in measurements of M_1. This is because distributions of characters with low variability are more peaked than distributions of highly variable characters, and the modes of the two or more species are thus more likely to be distinguishable using M_1 than, for example, P_4 or M_3. A specific example of this is discussed in the following section.

A second important aspect of tooth size is its correlation with body size within closely related groups of similarly adapted species of animals. Figure 8 shows the correlation of tooth size with body size in sympatric squirrels of the family Sciuridae in Michigan. Tooth size and body size are not necessarily very highly correlated within a species (r=.59 within *Sciurus niger* in Fig. 8, for example), but when related species spanning a significant size range are considered, there is a high correlation of tooth size with body size (r=.99). Body size is an important component of an animal's adaptation, and it is apparent that measurements of teeth (especially M_1) give a good measure of body size when related species are considered.

TOOTH SIZE AND SPECIES DIAGNOSIS

The dentitions of sympatric fossil (or living) mammalian species that share a relatively recent common ancestor often cannot be distinguished by their form alone. In such cases, size differences are important in diagnosing the species. The ability to distinguish closely related sympatric species is obviously fundamental to reconstructing the phylogenetic history of the Plesiadapidae, or any other group, from the fossil record, and the species of *Plesiadapis* at Cernay provide a good example of the importance of using measurements that have low variability when diagnosing closely related species. The Cernay example is discussed here at some length to justify the use of the log of the crown area of M_1 as the best available measure of overall size in comparing specimens and species of *Plesiadapis*.

The French fossil locality at Cernay, near Reims, is a classic Paleocene locality, having been discovered and worked by Lemoine some 30 years before the first comparable fauna was discovered in North America. *Plesiadapis* is one of the most common mammals in the Cernay deposits. Lemoine (1891) believed three species of *Plesiadapis* were present at Cernay, as did Schlosser (1921). Stehlin (1916) recognized two species of *Plesiadapis* and one species of the new, related genus *Chiromyoides*. Teilhard (1922) recognized only one species of *Plesiadapis* plus *Chiromyoides*. Simpson (1935b) believed that at least three species of *Plesiadapis*, possibly four, were present at Cernay. Russell (1964), studying a much larger number of specimens than were previously available, concluded that more than one species was indicated by the high coefficients of variation of the tooth measurements, but he was unable to find any consistent morphological characters on which to base diagnoses, and he therefore finally recognized only one species of *Plesiadapis* at Cernay.

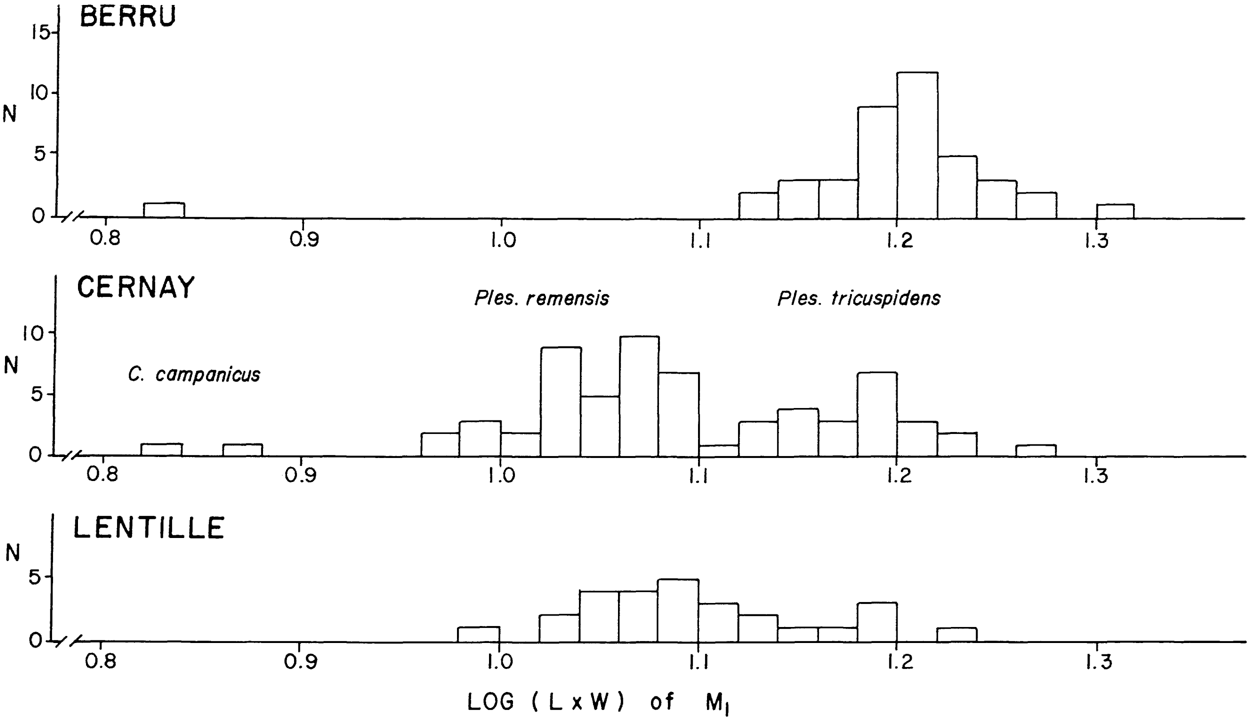

Figure 10. Comparison of $\log_{10}$ of the crown area of M_1 for plesiadapids from Berru, Cernay, and Lentille. These three samples are very nearly the same age but probably differ slightly, Lentille being slightly older than Cernay, and Berru being slightly younger.

In a new attempt to solve this problem, the teeth of virtually all of the specimens of *Plesiadapis* from Cernay were remeasured, with special care being taken to ensure comparability of measurements taken on isolated teeth with those taken on teeth still in mandibles. Only lower teeth were used in the following analysis, since upper first and second molars could not be distinguished with complete certainty.

Two measurements (length and width) were taken of each tooth, thus two "bits" of information are available for each. Most of the teeth are isolated, thus a multivariate approach considering the overall size of the specimens based on many measurements was impractical. Making univariate plots of the lengths and widths separately, as Russell (1964) did, ignores in turn one or the other bit of information available for each tooth. Making bivariate plots of length versus width takes into account all of the information available for each tooth.

Bivariate scatter plots of length versus width were made for each of the five lower cheek teeth. Of these five plots, only that for M_1 (Fig. 9) showed any tendency to cluster into distinct groups. This led to an analysis of the variability in tooth size of modern mammals (Gingerich, 1974e), with the results discussed in the preceding section of this chapter. Scanning the coefficients of variation of the lower cheek teeth of the plesiadapid species for which large samples are known (see Appendix) shows that plesiadapids conform to the general mammalian pattern, with M_1 generally having the smallest coefficients.

As illustrated in Figure 9, it is clear from the scatter plot that width and length are highly correlated (in fact, $r=.90$). In other words, most of the information about the length and width of plesiadapid cheek teeth will be contained in a single variate compounded from width and length measurements. There are a number of different ways to compound width and length into a single measure of size, all of which yield approximately the same results. The most direct method is simply to multiply length by width. The resulting variate is a measure of the crown area of the tooth. One of the most important functions of plesiadapid cheek teeth, grinding, is a function of their crown area; thus the crown area is probably one of the most important aspects of the teeth controlled by natural selection, and it is an appropriate variate to use in comparing the size of closely related plesiadapid species.

The Cernay specimens illustrated in Figure 9 were replotted (Figure 10) using the new crown area variate to express each specimen's size. Because the variance associated with a sample of large specimens is much greater than that of a sample of smaller specimens,

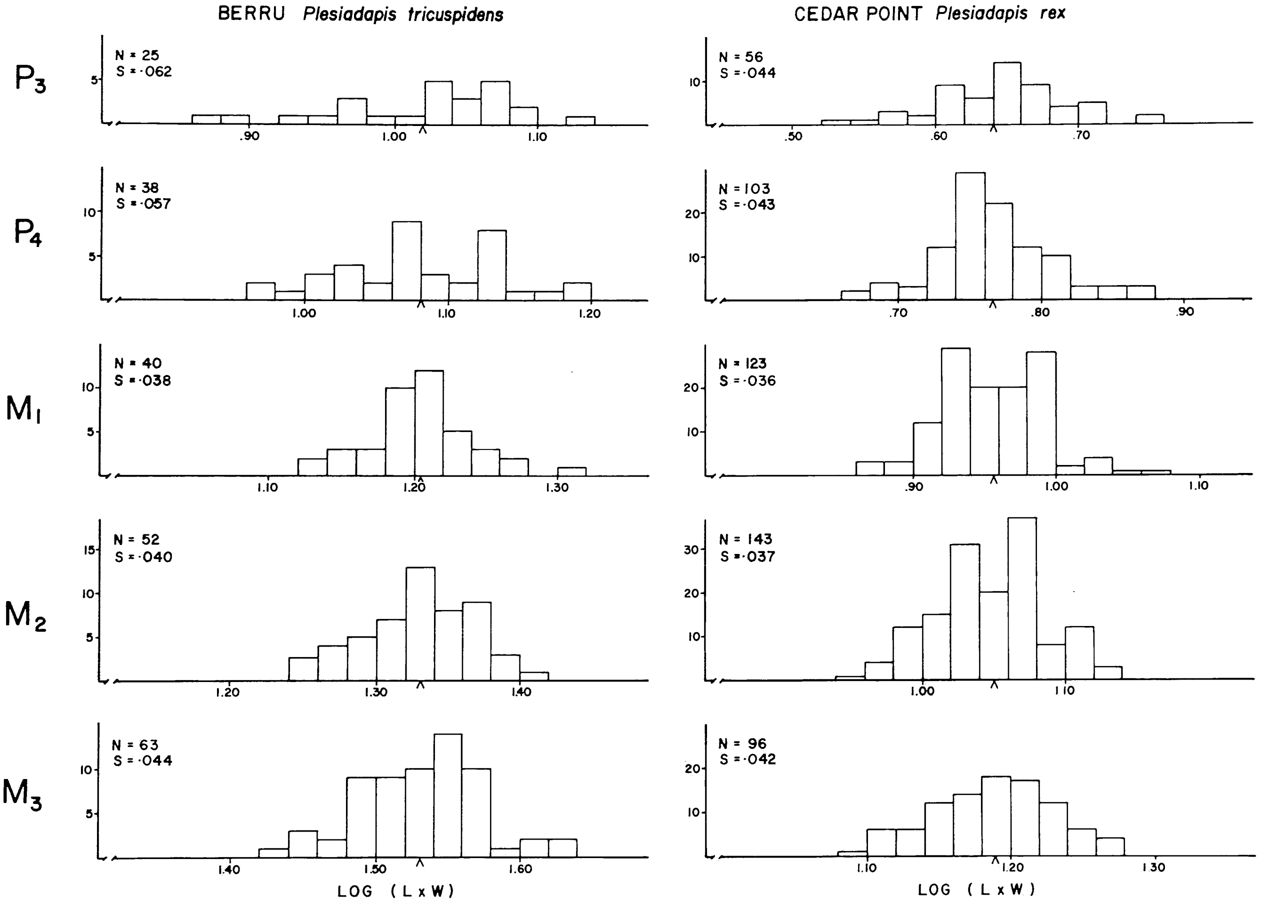

Figure 11. Comparison of size variability for each cheek tooth in *Plesiadapis tricuspidens* from Berru and *Plesiadapis rex* from Cedar Point. Standard deviation (S) of log of crown area is equivalent to coefficient of variation of crown area (Lewontin, 1966). Note correlation of low variability with central position in tooth row, and absence of consistent bimodality within species samples.

logarithms of the crown areas are plotted. The use of logarithms makes the variance of the measurements of a sample of large specimens comparable to that of a sample of small specimens. Figure 10 shows a pattern similar to that seen in Figure 9: there is a cluster of about 24 large specimens, a distinct cluster of some 38 medium-sized specimens, and a third cluster of two small specimens. The position of named type specimens in each of the clusters is illustrated in Figure 9, and the species names are given above the appropriate cluster in the Cernay plot of Figure 10.

Scatter diagrams are often used in comparing the samples of one or more related species from a series of localities, but the result is often confusing (see Szalay, 1969, figs. 9-15 as one of many possible examples). The advantage of using the log of crown area (or some other appropriate compound variate) for comparing samples from different localities is apparent in Figure 10, where samples from Berru, Cernay, and Lentille are compared. The relative sizes of the specimens and of the samples are clearly indicated, and the stratigraphic (or other) distinction between the samples is clearly maintained. As was described above, both *Ples. remensis* and *Ples. tricuspidens* are present at Cernay. At Berru the only *Plesiadapis* species represented by a lower dentition is *Ples. tricuspidens*, and the specimens appear to be significantly larger than those from Cernay. At Lentille both species of *Plesiadapis* are represented, though they are not so distinct in size as at Cernay. The presence of *Chiromyoides campanicus* at Cernay and Berru is also indicated.

Where a large number of samples are to be compared and it is not possible to illustrate each sample by a histogram, the range, mean, standard error and sample size can be illustrated compactly, as was done for 47 stratigraphically superposed samples of *Hyopsodus* (Gingerich, 1974a) and here in Chapter 6 for the North American Plesiadapidae (see Fig. 24).

Plotting size as a single variate also permits a simple visual examination of the variability of cheek teeth in different tooth positions (Fig. 11). As was stated above, in plesiadapids, as in most mammals, the size of M_1 is less variable than the size of the other lower cheek teeth. The fact that M_1 is the first permanent cheek tooth to erupt may partially explain its lower variability. On the other hand, the variability of tooth size at each position is correlated with position in the tooth row – with the central teeth being the least variable. The central tooth might be constrained to be the least variable either for some functional reason related to its central position in the morphogenetic and functional field controlling the cheek teeth, or because of the timing of its development.

The idea that early formation and eruption might explain the low variability of M_1 in a sample including both sexes is an outgrowth of research on the development of sexual dimorphism in primates. Pelvic dimorphism is the result of changes in the hormonal balance of females at puberty (Gingerich, 1972a). These hormonal changes might also affect the development of successively erupting teeth – the later erupting teeth being the most dimorphic. In *Plesiadapis*, the sequence of tooth eruption is M_1-M_2-M_3-P_3-P_4 (see Chapter 7). As Figure 11 shows, the standard deviations of log tooth area in the cheek teeth of *Ples. tricuspidens* and *Ples. rex* do increase in approximately this order. However, there is no apparent increase in bimodality correlated with the eruption sequence, and if species of *Plesiadapis* were sexually dimorphic, the teeth appear not to be sufficiently sensitive to demonstrate the dimorphism. Whatever the reason, M_1 is the least variable lower cheek tooth, and it is therefore the best tooth on which to base diagnoses of closely related fossil species that differ only in overall body size.

PHYLOGENY RECONSTRUCTION

At the beginning of this chapter, it was noted that one of the most important goals of any study of the evolution of a group of related animals is determining the sequence and timing of morphological changes within the group. In order to do this, specimens and species must be temporally ordered using information independent of their morphology. The temporal and genealogical relationships hypothesized for a group are usually summarized in a historical tree diagram, or "phylogeny" (i.e., a diagram showing both genealogical relationships and the temporal ordering of all known taxa). Paleontology is unique among the evolutionary sciences concerned with phylogeny reconstruction in having access to a source of temporal ordering of specimens that is independent of their morphology: relative stratigraphic position. Interpretation of the stratigraphic record and the role of stratigraphy, phenetics, and cladistics in reconstructing the phylogeny of a group of animals are outlined here. This will be illustrated at both the species level for Plesiadapidae, and at higher levels for the major groups of Primates in the following chapters.

Two principles are usually involved in establishing the temporal relationship of fossil specimens from their stratigraphic distribution. The first, Steno's Principle of Superposition, states that in a normal sequence of strata any given stratum is younger than those underlying it. Thus fossils found in this stratum will be younger than fossils found at lower stratigraphic levels. William Smith's Principle of Faunal Succession and Correlation notes that successive strata in a given sequence often contain distinctive faunas, and that these strata can be correlated with those in other sequences on the basis of close similarities in fossil content. Technically, if the taxa under study are the only ones available, this correlation is done using individual specimens or population samples and not species, since paleontological species can only be delimited once the phylogenetic relationships of the lineages involved are fairly well understood. In practice, it is sometimes possible to identify to species most or all of the available fossil samples, and one can thus work directly with the named species. This is, however, not possible when there is a very dense and continuous fossil record, as in the Eocene mammals *Hyopsodus*, *Haplomylus*, and *Pelycodus*, for example (Gingerich, 1976).

The first step in reconstructing the phylogeny of a group of fossil animals is *stratigraphic organization*. This is accomplished by studying the superpositional relationships of all specimens or species in each stratigraphic column, and then correlating stratigraphic intervals containing indistinguishable specimens or species. The result is a sequence of range zones or concurrent-range zones with the oldest zone at the bottom and the youngest at the top of the sequence. Specimens in any given biostratigraphic range zone will thus be younger than those in underlying zones.

Phenetic linking is the second step in phylogeny reconstruction. Each biological population or species in each of the biostratigraphic zones is compared to the populations or species in adjacent zones, and samples that are phenetically similar are linked together. In some cases, where there are gaps in the fossil record, it may be necessary for links to be carried across two or more zones before a similar form is found. The resulting pattern of linking is itself a phylogeny, with each series of links representing a separate evolutionary lineage. The minimum number of evolutionary lineages in each zone will be dictated by the maximum number of biological species or populations present in that stratigraphic interval, and the most parsimonious phylogeny will be the one requiring the minimum number of evolutionary lineages to link all of the observed populations in any zone to those in adjacent zones.

The third step in reconstructing the phylogeny of a group of animals is critical *testing*. The phylogenetic hypothesis derived from the above pattern of linking can be tested by asking the following questions:

1. Is the density and continuity of the fossil record sufficient to support the proposed pattern of linking? Obviously, the more fossil specimens there are available, the better the documentation for a given pattern, and the greater one's confidence in the pattern. Similarly, the greater the similarity between specimens in adjacent intervals, and the more they link together into continuous graded chains, the better the documentation for the pattern.
2. Does the proposed pattern make sense in terms of paleogeography? If all specimens come from one restricted geographic region, such as western North America, it is plausible that a sample in one zone evolved from a similar sample in a lower zone. On the other hand, it would be more difficult to derive a North American species from one on another continent, and a major migration would have to be postulated.
3. Does the evolution of individual morphological characters in the proposed phylogeny make sense in terms of the animals' adaptations? For example, is there a plausible functional reason for the independent acquisition of crenulated enamel on the teeth in several different lineages of early primates? Is there a plausible functional reason that will explain evolutionary reversals such as the acquisition of a centroconule on the upper incisors of *Plesiadapis* and its subsequent loss in later species?

Obviously, the real test of a proposed phylogeny is its stability – the extent to which new discoveries are predicted by it, and the degree to which new discoveries fit into the phylogeny.

The method of phylogeny reconstruction proposed here is based on stratigraphic organization and phenetic linking of fossils in adjacent stratigraphic intervals, and the method can thus be termed *stratophenetic* to distinguish it from the cladistic method and other methods of phylogeny reconstruction advocated by comparative anatomists. The stratophenetic method of phylogeny reconstruction requires a relatively dense and continuous fossil record – if this is not available, it is sometimes possible to draw useful phylogenetic inferences from cladistic analysis of morphological characters in the available specimens, but these inferences will necessarily be biased by assumptions about the evolution of characters inherent in the cladistic method. The only way to actually determine the morphology of the ancestral form of any group, and the only way to determine the importance of parallelism and evolutionary reversals in the phylogenetic history of the group is to have a dense and continuous historical record (i.e., a good fossil record).

In the following chapter, the fossil species included in the family Plesiadapidae are reviewed, and this is followed by a stratophenetic reconstruction of the phylogenetic history of the North American Plesiadapidae. A similar analysis of the major groups within the order Primates is outlined in the final chapter.

III

SYSTEMATIC REVISION

The family Plesiadapidae includes five genera and 26 species, of which one species is new. Systematic descriptions of each of the genera and species here regarded as valid are included in this chapter. The relationship of the family to other families of Primates and the classification of primates at the subordinal level are discussed in Chapter 9. In addition to the 26 species recognized here, two additional species (*Nannodectes* aff. *gidleyi*, and *Plesiadapis* aff. *remensis*) are probably distinct and worthy of recognition, but the specimens now known are inadequate for satisfactory diagnosis. The specimens discussed under *Platychoerops ?richardsonii* probably belong to *Plat. richardsonii* but cannot yet be adequately compared.

The species diagnoses presented here are entirely morphological. Knowing the stratigraphic position of a sample was sometimes of value in determining whether or not a formal species distinction was justified, in the species of *Chiromyoides* for example, but it was not necessary to include stratigraphic information as part of a diagnosis. As a result, given a sample of a few mandibles, maxillae, and upper and lower incisors, it is possible to identify with little question which species is represented. Species identification of a single specimen is usually possible if the specimen is sufficiently complete. The evolution of the incisors has in the past never been considered important, and these teeth are sometimes not seriously collected or curated – they are, however, among the most diagnostic elements of the plesiadapid dentition.

The term *diagnosis* has been strictly interpreted, and as a result only those features that serve to differentiate a given genus from another, or one species of a genus from another, are included in the diagnosis. Other details and comparisons of a given species are discussed in the sections on description. Specimens from the type locality of a species are listed under the heading *typodigm*, and it is the typodigm of the species which has been used to characterize and compare species in each case. The term *hypodigm* is retained to include all specimens referred to a given species: the typodigm is thus the most important subset of any given hypodigm.

The successive units recognized in each evolutionary lineage are regarded as species, rather than subspecies or "stages" (as applied for example by Maglio, 1971; 1973, p. 77). The concept of subspecies, and the use of trinomials, is probably best limited to discussions of geographic variation. Trinomials convey no more information than do binomials when stages of a lineage are being discussed, and relationships must be shown by a phylogenetic tree in either case. Thus taxa that have long been recognized as species have not been reduced in rank to subspecies to indicate their close phylogenetic relationship, nor have new taxa been described as subspecies because they are closely related to another species. Similarly, since relationships between genera are shown in phylogenetic trees, recognition of subgenera would contribute no additional information about relationships and would only serve to complicate taxonomic nomenclature.

An attempt has been made to include in the synonomies all studies based on original materials. A few important secondary sources are included, but most are omitted. It has proved useful in the genera *Plesiadapis* and *Chiromyoides* to discuss the North American and European species separately. Otherwise, the order in which the species are discussed corresponds to their temporal position in a given lineage, with the smallest lineages of each genus being discussed first.

The allocation of various specimens and species previously referred incorrectly to the Plesiadapidae are discussed in a final section of *nomina addenda.*

Class MAMMALIA

Order PRIMATES Linnaeus, 1758

Suborder PLESITARSIIFORMES Gingerich, 1975

Infraorder PLESIADAPIFORMES Simons, 1972

Family **Plesiadapidae** Trouessart, 1897

Platychoeropidae Lydekker, 1887, p. 3. Type genus: *Platychoerops* Charlesworth, 1855.

Plesiadapidae Trouessart, 1897, p. 75. Type genus: *Plesiadapis* Gervais, 1877.

Apatemyidae (in part), Matthew, 1915, p. 477.

Chiromyidae (in part), Teilhard, 1922, p. 24; 1927, p. 13.

"Tillarvernidae" Piton, 1940, p. 290. Type genus: *Menatotherium* Piton, 1940.

Included genera.— *Pronothodectes* Gidley, 1923; *Nannodectes* Gingerich, 1975; *Plesiadapis* Gervais, 1877; *Chiromyoides* Stehlin, 1916; and *Platychoerops* Charlesworth, 1855.

Known distribution.— Middle Paleocene through earliest Eocene (Torrejonian through Clarkforkian) in western North America. Late Paleocene and early Eocene (Thanetian through Cuisian) in western Europe.

Diagnosis.— Differ from Microsyopidae in having tricuspate upper incisors. Differ from Carpolestidae in being much larger and in lacking the enlarged, bladelike P$_4$ and correspondingly modified P$^{3\text{-}4}$ of carpolestids. Differ from Paromomyidae (incl. Saxonellinae) in having more robust lower incisors with distinct margoconids.

Comments.— Suppression of the *nomen oblitum* Platychoeropidae Lydekker, 1887, in favor of the junior but better known synonym Plesiadapidae Trouessart, 1897, has been proposed to the International Commission on Zoological Nomenclature (Gingerich, 1974d). Jepsen (1934) first diagnosed the two apparently unrelated families Apatemyidae and Plesiadapidae. Teilhard (1922, 1927) and others placed *Plesiadapis* in the Chiromyidae, but subsequent research has shown that *Plesiadapis* is unrelated to *Daubentonia (Chiromys).* Simpson (1948a) has noted that "Tillarvernidae" Piton, 1940 is invalid under the international rules of zoological nomenclature because it is improperly formed.

PRONOTHODECTES Gidley

Pronothodectes Gidley, 1923, p. 12. Type: *Pronothodectes matthewi* Gidley.

Included species.— *Pronothodectes matthewi* Gidley; *Pro. jepi* Gingerich.

Known distribution.— Middle Paleocene (Torrejonian) of Wyoming and Montana in North America only.

Diagnosis.— Species of *Pronothodectes* differ from those of other plesiadapid genera in being smaller and in retaining the primitive plesiadapid dental formula of 2.1.3.3/2.1.3.3.

Pronothodectes matthewi Gidley

(Plate 1 A, E, G)

Pronothodectes matthewi Gidley, 1923, p. 12; pl. 2: 1; pl. 3: 2, 11, 12; pl. 4: 3. Simpson, 1955, pl. 34: 3; pl. 35: 5.

Type.— USNM 9547, a right maxilla with P^{4}M$^{1\text{-}2}$ from Gidley Quarry (Sec. 25, T 5 N, R 15 E, Sweetgrass Co.), Crazy Mountain Field, Montana.

Diagnosis.— Similar to *Pro. jepi* but significantly smaller – mean length and width of M$_1$ are 2.13 and 2.03, respectively, versus 2.35 and 2.22 in *Pro. jepi* (see Tables A-1 and A-2).

Description.— *Pronothodectes matthewi* is represented by 10 mandibles, three maxillae, and two isolated upper incisors. The full lower dental formula can be determined in four specimens (AMNH 35462, USNM 9332, 9443, and 9531) and in every case there are alveoli for two incisors, the canine, three premolars, and three molars. One maxilla (AMNH 35470) preserves the alveoli for the upper canine, three premolars, and three molars. Since primitive species of *Plesiadapis* have two teeth I$^{1\text{-}2}$ in the premaxilla, we can assume that *Pro. matthewi* had these two premaxillary teeth also. Thus the full dental formula was $\frac{2}{2}\,\frac{1}{1}\,\frac{3}{3}\,\frac{3}{3}$ – no specimens are known to have had fewer teeth than this. At least one crown is known for each tooth in the dentition, except for the upper canine and the second incisors above and below; thus a rather complete description can be given of the teeth of this primitive species.

The lower central incisor, I$_1$, is an enlarged, procumbent, single-rooted tooth with the well-developed margoconid and margocristid typical of later species of *Plesiadapis*. It is somewhat narrower than is typical of *Plesiadapis*. I$_2$ is known only from its alveolus – it was a very small, slightly procumbent, single-rooted tooth closely appressed to I$_1$. USNM 9332 preserves the crowns of both the lower canine and P$_2$. The lower canine is very small, about the same size as I$_2$ must have been, with a single root, and a single, forwardly inclined cusp. P$_2$ is also single rooted, but it is a little larger than the canine and has a similar forwardly inclined cusp with a rudimentary heel on the posterior side of the cusp. P$_3$ and P$_4$ are both double rooted, with relatively high, wedge-shaped crowns and small but well-developed talonids. These talonids are not basined, nor are they sharply crested. The three lower molars all have relatively high trigonids compared to other plesiadapids. The entoconid of M_{1-2} in all specimens is a well-developed cusp, but this corner of the tooth is neither particularly rounded nor squared out. The cristid obliqua of M_1 runs up the posterior side of the metaconid, whereas it is aligned much more toward the protoconid in M_{2-3}. This characteristic, shared by all plesiadapids, enables isolated M_1 and M_2 to be easily distinguished from one another. The hypoconulid of M_3 tends to be rather broad, rounded, and unfissured. Buccal cingulids are variably developed on P_{3-4} and on M_{1-3}. The enamel of all of the teeth is smooth.

AMNH 35470, a left maxilla, preserves part of the alveolus for the upper canine and the crowns of P^{2-4} and M^{1-2}. The P^2 of this specimen has two roots and a small, triangular, and heavily worn crown. P^3 is much larger than P^2 and has a well-developed paraconule, with a small metacone on the posterior side of the paracone. P^4 is present in four specimens – all have well-developed, distinct paraconules and metacones. The upper molars all have well-developed paraconules and metaconules, distinct postprotocingula, strong buccal cingula, no lingual cingula, and no mesostyles. The enamel on all upper teeth is smooth.

One upper incisor (USNM 10005) has a well-preserved crown, a specimen figured by Gidley. The three apical cusps, anterocone, laterocone, and a small mediocone, as well as the posterocone are all well developed. The mediocone and laterocone are both at the same distance behind the anterocone, as is typical of most *Plesiadapis* incisors. The crown of I^1 is relatively narrow for a plesiadapid, as is the crown of the lower central incisors. There is no trace of a centroconule. USNM 10044, another upper central incisor figured by Gidley, has a still smaller mediocone, which extends forward to form a well-developed midline shelf along the medial side of the anterocone.

Summary statistics for the upper and lower teeth of the type sample of *Pronothodectes matthewi* are listed in Table A-1.

No additional cranial or postcranial material is known of this species.

Typodigm.– Fortunately a number of important new specimens have been collected since Simpson (1937b) last reviewed this species. The type sample from the Gidley Quarry is as follows: ANMH 35462–35470; and USNM 9332, 9443, 9531, 9547 (type), 9847, 10005, 10044.

In addition, two specimens from Site 1 in the Medicine Rocks area of Montana (PU 16590 and 21582) are provisionally referred to this species on the basis of their small size. More specimens are needed before a definitive identification can be given.

Pronothodectes jepi Gingerich

(Plate 1 B, C, E, F, H)

Pronothodectes jepi Gingerich, 1975b, p. 138, pl. 1:1, 3.

Type.– PU 14782, a left mandible with alveoli for I_{1-2}, C, P_2, and the crowns of $P_{3-4}M_{1-3}$ intact; from Rock Bench Quarry (Sec. 26, T 57 N, R 99 W, Park Co.), Big Horn Basin, Wyoming.

Diagnosis.– Significantly larger species than *Pro. matthewi* – the mean length and width of M_1 in *Pro. jepi* are 2.35 and 2.22, respectively, compared to 2.13 and 2.03 in *Pro. matthewi* (see Tables A-1 and A-2).

Description.– Thirteen mandibles, four maxillae, and several isolated incisors are presently known from the type locality. This species is virtually identical to *Pro. matthewi* described above except for being significantly larger. The entire alveolus of the upper canine is preserved in the maxilla PU 17500 – this tooth had a single root, which was anteroposteriorly elongated, as was the upper canine in the skull of *Palaechthon nacimienti* recently described by Wilson and Szalay (1972). The complete lower dental formula can be determined in five mandibles – all five had a dental formula of 2.1.3.3 as in *Pro. matthewi.* Tooth measurements are summarized in Table A-2.

Typodigm.– The type sample, all from the Rock Bench quarry, includes the following specimens: PU 14303, 14782, 14783, 17435, 17436, 17454, 17458, 17500, 17484, 17493, 17577, 18482-18485, 18660, 19795, 21579-21581.

Two additional mandibles (PU 17930-17931) collected by E.L. Simons from 5 mi SE of Belfry, Montana (Sec. 28, T 8 S, R 23 E) in the Big Horn Basin probably also represent *Pro. jepi*, but the material is too fragmentary for an unequivocal determination.

NANNODECTES Gingerich

Nothodectes (in part), Matthew, 1917, p. 832.
Plesiadapis (in part), Simpson, 1935a, p. 1.
Pronothodectes (in part), Gazin, 1956a, p. 20; 1971, p. 16.
Nannodectes Gingerich, 1975b, p. 138. Type: *Nannodectes gazini* Gingerich.

Included species.– Nannodectes intermedius (Gazin); *N. gazini* Gingerich; *N. simpsoni* (Gazin); and *N. gidleyi* (Matthew).

Known distribution.– Late Paleocene (Tiffanian) from Wyoming to Texas in North America only.

Diagnosis.– A small lineage evolving in parallel with *Plesiadapis* but distinctly smaller than the contemporaneous species of the latter genus. *Nannodectes* differs

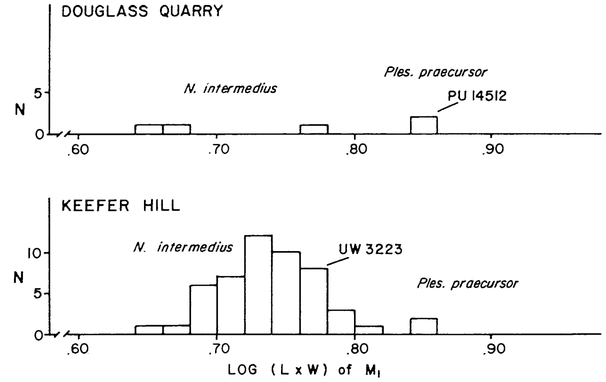

Figure 12. Histograms comparing the crown area of M_1 of *Nannodectes intermedius* and *Plesiadapis praecursor* from the Douglass Quarry and from the Keefer Hill locality. UW 3223 is the type specimen of *N. intermedius*, and PU 14512 is the type specimen of *Ples. praecursor*.

from *Pronothodectes* in consistently lacking I_2, and in the later species lacks the lower canine as well. Differs from contemporaneous species of *Plesiadapis* in being smaller, retaining the lower canine and P_2 for a longer time, having much narrower central incisors and cheek teeth (especially noticeable in the lower premolars), having a more triangular P^3 (usually lacking a paraconule), and in never developing a centroconule on I^1.

Discussion.– As must be expected when two evolving lineages are sampled shortly after their separation from a common ancestor, *Nannodectes* and *Plesiadapis* share many morphological characteristics, and as they both became larger, they evolved a number of characteristics in parallel (for example, a mesostyle on the upper molars, an incipient cristid obliqua on the lower premolars, and loss of the lower canine). The species included here in the genus *Nannodectes* cannot be accomodated in *Pronothodectes* without considerably extending the concept of that primitive genus, nor can they be included in *Plesiadapis*, which they closely resemble, without including *Pronothodectes* in *Plesiadapis*, or making the latter biphyletic. In consequence, the best solution seems to be placement in a separate genus.

The earlier species of *Nannodectes* occur together with primitive species of *Plesiadapis*; *Nannodectes gidleyi* is known only from Colorado and Texas in the southern United States, while *Plesiadapis* is known only from the more northern states and Canada. This appears to be additional evidence suggesting that the Paleocene faunas of southern North America differed from those at higher latitudes (Sloan, 1969, p. 444). Significantly, it is the more southern genus, *Nannodectes*, which seems not to have reached the European continent.

Nannodectes intermedius (Gazin)

(Plate 2 A, E, I)

Pronothodectes intermedius Gazin, 1971, p. 16, fig. 1.

Type.– UW 3223, a left mandible with P_4M_{1-3}, from the Shotgun Member of the Fort Union Formation (Secs. 30-31, T 6 N, R 3 E, Fremont Co.), in the Wind River Basin, Wyoming.[1]

Diagnosis.– Differs from earlier species of *Pronothodectes* in lacking I_2, and from *Nannodectes gazini* and *Plesiadapis praecursor* in retaining the lower canine. *Nannodectes intermedius* is slightly but significantly larger than *N. gazini*, and it is smaller and has narrower teeth than the contemporary and sympatric species *Ples. praecursor.*

Description.– The type sample of *Nannodectes intermedius* consists of a dozen partial mandibles, four maxillary fragments, and a large number of isolated teeth, including upper incisors. The lower dental formula can be determined with certainty only in the type specimen, UW 3223. Gazin (1971) interpreted another mandible (USNM 26339) as having a dental formula of 1.1.3.3 also, but this specimen is broken and the presence of a lower canine cannot be confirmed or denied.

The upper incisors of *N. intermedius* are of approximately the same crown length as those of *Ples. praecursor* from the same deposit (all of the plesiadapid incisors from Keefer Hill are catalogued as UW 5499), but they are significantly narrower. If the width of the upper incisor is measured half way between the mediocone and posterocone, the seven incisors of *N. intermedius* have a mean width of 1.90 mm with a standard deviation of .17 mm. Two incisors of *N. intermedius* from the Douglass Quarry (PU 21578) measure 1.7 and 2.0 mm in width, respectively. By comparison, the four incisors of *Ples. praecursor* from Keefer Hill have a mean width of 2.40 mm with a standard deviation of about .16 mm. The upper incisors of *N. intermedius* are very similar to those of the species of *Pronothodectes* but differ slightly in having a relatively smaller midline cingulum.

A fragmentary maxilla (UW 5498) preserves part of the alveolus for the upper canine, alveoli for the two-rooted P^2, and the crown of P^3. $P^{3\text{-}4}$, known from UW 5498, MCZ 18742, and numerous isolated teeth, have well-developed paraconules, and at least a vestige of a metacone is retained on the upper premolars.

The lower incisor of this species is not represented, but it was probably relatively narrow like the upper

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[1] This is one of the small localities hereafter referred to as the Keefer Hill locality (using McIntyre's, 1966, term for the only geographic feature in the area), all of which appear to be contemporaneous (C.B. Wood, pers. comm.).

incisors. The crowns of the lower canine and P_2 are also not represented in the collections at hand. The most striking characteristic of the premolars and molars of *N. intermedius*, when compared with the sympatric *Ples. praecursor* and other early species of *Plesiadapis*, is their narrowness. As a result, the lateral walls of the buccal cusps of the lower molars are inclined more steeply than is seen in the early species of *Plesiadapis*. Gazin (1956a) first noted that this difference in the slope of the outer walls distinguishes the species here referred to *Nannodectes gidleyi* from *Plesiadapis anceps*. Russell (1964) also recognized the importance of this difference and erected the subgenus *Ancepsoides* for those species having less steeply sloping outer walls (which are the primitive species of *Plesiadapis*).

Several other characteristics of the lower cheek teeth of *N. intermedius* should be noted. The premolar trigonids consist only of a large, wedge-shaped protoconid; a paraconid or metaconid is never present. The premolars have no trace of a cristid obliqua on the talonid or on the back of the protoconid. M_{1-2} have talonids with the entoconid corner moderately squared and cusped. The hypoconulid or third lobe of M_3 varies from narrow to broad, and it is always rounded and unfissured. The enamel on all of the teeth is smooth.

Measurements of the lower dentition of *N. intermedius* from Keefer Hill are summarized in Table A-3. The size of M_1 of *N. intermedius* from Keefer Hill and the Douglass Quarry is compared with that of *Ples. praecursor* from the same localities in Figure 12.

Typodigm.– The type sample includes numerous specimens in the UW, USNM, MCZ, CM, and AMNH. The most important of these are UW 3223 (type), 3224-3227, 5498, 5499, and additional uncatalogued jaws and teeth; USNM 26339-26341; MCZ 18742; CM 17795; and AMNH 88308.

In addition, four mandibles (PU 14623-14625, 14628) and two upper incisors (PU 21578) are known from the Douglass Quarry in the Crazy Mountain Field.

Nannodectes gazini Gingerich

(Plate 2 B, F, J)

Pronothodectes cf. *matthewi*, Gazin, 1956a, p. 20; pl. 2: 1, 2.
Pronothodectes cf. *simpsoni*, Gazin, 1956a, p. 21; pl. 3: 2.
Cf. *Pronothodectes matthewi*, Gazin, 1969, p. 7; pl. 2: 9.
Nannodectes gazini Gingerich, 1975b, p. 138; pl. 1: 2, 4.

Type.– AMNH 92008, a right mandible with alveoli for I_1, C, and P_2, and the crowns of P_{3-4} and M_1 intact; from the Saddle Locality (Sec. 28, T 27 N, R 95 W, Fremont Co.) in the Bison Basin of Wyoming.

Table 1. Measurements of M^2 of *Nannodectes gazini* from Little Muddy Creek.

	Length	Width
USNM 25725	2.4	3.5
USNM 25726	2.6	3.7

Diagnosis.– The smallest species of *Nannodectes* – mean length and width of M_1 are 2.35 and 2.09 for *N. gazini*, compared with 2.42 and 2.24 mm for *N. intermedius*, and 2.69 and 2.58 mm for *N. simpsoni*. Dividing the width of M_1 by its length gives a ratio of .89 for *N. gazini*, compared with .93 for *N. intermedius* and .96 for *N. simpsoni*. Thus, this species apparently had on average narrower cheek teeth than either of those species. *Nannodectes gazini* differs from *N. intermedius* in having a less well-developed paraconule on P^3 (it is entirely absent in one specimen of *N. gazini*, CM 20956).

Description.– A much larger sample of this species is now available than was known when Gazin (1956a) first described the "*Pronothodectes*" from the Bison Basin Saddle locality. The lower dentition is represented by 20 mandibles and some additional isolated teeth including lower incisors. The lower dental formula can be determined with certainty in seven mandibles – in all seven it is 1.1.3.3. The upper dentition is represented by 10 maxillae and several isolated teeth. Unfortunately the upper incisors are not yet known.

The lower incisors of *N. gazini* have well-developed margoconids and margocristids but, as is typical of *Nannodectes*, have very narrow crowns. The lower canine and P_2 are both of moderate size and single rooted. As was mentioned in the diagnosis, all the cheek teeth are very narrow – even narrower than in the other species of *Nannodectes*.

The crowns of the lower premolars have a high, wedge-shaped protoconid, with no paraconid or metaconid. The posterior slope of the protoconid and the small heel show no trace of a cristid obliqua. The entoconid corner of M_{1-2} tends to be squared out, with a distinct entoconid cusp, but in one specimen (CM 18750) this corner is rounded. The heel of M_3 tends to be narrow, and it is always rounded. Only one specimen has an M_3 with a partially fissured heel (UW 1064).

Four specimens are known of both P^3 and P^4. A paraconule is always present on P^4; only one P^3 has this cuspule well developed, and it is entirely lacking in another specimen (CM 20956). Development of a metacone on P^{3-4} is variable. The upper molars of *N. gazini* are nearly square, a condition that generally differentiates *Nannodectes* from *Plesiadapis*. The enamel on all upper molars of *N. gazini* is smooth.

Measurements of the type sample of *N. gazini* are summarized in Table A-4.

Discussion.– There has been considerable confusion regarding the identification of specimens and their localities in the Bison Basin. Therefore all of the known specimens of *N. gazini* are listed in the typodigm.

The two teeth described by Gazin (1969, p. 7) as Cf. *Pronothodectes matthewi* from the Little Muddy Creek locality are too large to belong to that species. Dimensions of these teeth are listed in Table 1. From the table it is apparent that the teeth are longer and narrower than the known sample of *Pronothodectes jepi* but agree very well in size and shape with *N. gazini*. The teeth have the plain, relatively square morphology characteristic of upper molars of *N. gazini*, and there seems to be little doubt that they represent this species. The fragmentary lower molar trigonid mentioned by Gazin from the Little Muddy Creek locality is not a plesiadapid but appears to be a worn fragment of the species "Cf. *Torrejonia wilsoni*" described by Gazin (1969, p. 6) from this locality.

Typodigm.– The specimens from the Bison Basin Saddle locality are as follows: AM 86696-86698, 88116, 88389, 92008 (type), 92014, 92026, 92029, 92063, 92092, 92119, 92130, 92143; CM 18746-18751, 18753, 18767, 20954, 20956, 20972; MCZ 7379-7382, 18628, 18658, 18667, 18674, 18675, 18684, 18686, 18689, 18691, 18694, 18701, 18703; USNM 20758, 20764, 20766-20768, 20772, 20782, 26338, 186791; UW 1052, 1054, 1057, 1062, 1064, 1066, 1099, 1691, 1692, 1696, 1699, 1700, 1709, 1713, 5433.

In addition, two specimens are known from Little Muddy Creek: USNM 25725, 25726.

Nannodectes simpsoni (Gazin)

(Plate 2 C, G, K)

Pronothodectes simpsoni Gazin, 1956a, p. 20; pl. 3: 1,3.
Plesiadapis jepseni (in part), Gazin, 1956a, p. 23; pl. 4: 2.

Type.– USNM 20754, a right mandible with alveoli for I_1, C, P_{2-3}, and the crowns of P_4 and M_{1-3} intact; from the Ledge locality (Sec. 28, T 27 N, R 95 W, Fremont Co.), in the Bison Basin, Wyoming.

Diagnosis.– Differs from *Nannodectes intermedius* and *N. gazini* in being significantly larger – mean length and width of M_1 are 2.69 and 2.58, respectively, for *N. simpsoni*, compared with 2.42 and 2.24 for *N. intermedius*, and 2.35 and 2.09 mm for *N. gazini*. Differs from *N. gidleyi* in retaining the lower canine and in being significantly smaller – mean length and width of M_1 in *N. gidleyi* are, respectively, 2.88 and 2.70 mm.

Description.– Thirteen mandibles and four maxillae of *N. simpsoni* are known. Unfortunately neither the upper nor the lower incisors have yet been collected. The lower dental formula can be determined with certainty in four specimens, in each of those it is 1.1.3.3. The mandible USNM 20775 appears also to have retained the canine, while it was possibly lost in USNM 20757. The dental formula of these two specimens, however, cannot be determined with certainty.

The crowns of the lower canine and P_2 are unknown. P_3 is known in only one specimen (USNM 20775). It has a very narrow crown with a single large cusp, the protoconid. The P_4 is represented in six specimens, none of which show any development of a paraconid or metaconid. One of these specimens (USNM 20576) has a distinct hypoconid on P_4, with a small cristid obliqua on the talonid. A cristid obliqua is weakly developed on the heel of three other fourth lower premolars. The entoconid corners of M_{1-2} tend to be squared and always have a distinct cusp. The heel of M_3 tends to be narrow, and it is always rounded and unfissured. Two specimens show some crenulation of the enamel on M_3. One of these (USNM 20755) closely resembles *N. gidleyi* in having a relatively broad, rounded, and crenulated hypoconulid lobe on M_3.

In the upper dentition, P^3 is known from two specimens, both of which lack a paraconule and have a triangular outline. One of these (USNM 20780) has a distinct metacone, while the other (USNM 20781) has no trace of a metacone. The P^4 is known in three specimens and always has both a paraconule and a metacone. The upper molars of *N. simpsoni* closely resemble those of *N. gazini*, with the exception that one M^2 (in maxilla CM 18771) has a small mesostyle, the earliest manifestation of this character in the *Nannodectes* lineage.

Measurements of the teeth of *Nannodectes simpsoni* are summarized in Table A-5.

Typodigm.– The following specimens of *N. simpsoni* are known from the type locality, the Bison Basin Ledge locality: AMNH 92185; CM 18770-18773; USNM 20754 (type), 20755-20757, 20765, 20769-20771, 20774, 20775, 20780, 20781, 186792.

In addition, two mandibles (both UW 1708) were described by Gazin (1956a, p. 3) as "*Ples. jepseni*" from the Bison Basin Saddle locality, but possibly 50 ft higher stratigraphically. Similarly, an ACM mandible (field no. 68-34) comes from 25-30 ft higher stratigraphically than the main Saddle locality concentration. This higher level at the Saddle locality is hereafter referred to as the Saddle Annex locality. The three mandibles from the Saddle Annex locality clearly represent a species of *Nannodectes*, not *Plesiadapis*. They have teeth too large to represent *N. gazini* but well within the range of *N. simpsoni*, which is the species they almost certainly represent. One mandible of *N. simpsoni* (AMNH 86682) is known from the Bison Basin

West End locality.

Nannodectes gidleyi (Matthew)

(Plate 2 D, H, L)

Nothodectes gidleyi Matthew, 1917, p. 832; pl. 99-102.
Plesiadapis tricuspidens (in part), Teilhard, 1922, p. 24. Abel, 1931, p. 264.
Plesiadapis gidleyi, Simpson, 1928, p. 7. Simpson, 1935a, p. 2; fig. 1-11. Also, numerous subsequent papers by Simpson and others.

Type.– AMNH 17170, nearly complete upper and lower dentition of a single individual; from the Mason Pocket (Sec. 20, T 33 N, R 6 W, La Plata Co.), in the San Juan Basin in southern Colorado.

Diagnosis.– *Nannodectes gidleyi* differs from the other species of *Nannodectes* in being significantly larger, never retaining the lower canine, having a cristid obliqua on the lower premolars, crenulated enamel on the talonid of M_3, and mesostyles on the upper molars.

Description.– *Nannodectes gidleyi* is anatomically one of the best known plesiadapid species. Specimens in the American Museum of Natural History include many details of the anatomy of the skull of this species, including the deciduous dentition. Postcranial remains are also known and were described by Simpson (1935a). Only those dental elements of the skull of importance to plesiadapid systematics will be discussed in this section. A more complete description of the cranial elements will be found in the chapter on cranial anatomy.

The upper dental formula of *N. gidleyi* is consistently the primitive plesiadapid 2.1.3.3. I^2 or its alveolus is preserved in three specimens, and the upper canine or its alveolus is preserved in five specimens. The lower dental formula of *N. gidleyi* is consistently 1.0.3.3 in all specimens in which it can be determined. The lower canine is definitely missing in four specimens, and seven specimens preserve P_2 or its alveolus.

The lower incisor of *N. gidleyi* tends to be somewhat broader, as are the other teeth in this species, than is characteristic of earlier species of *Nannodectes*, although two specimens do retain a relatively narrow incisor crown. The crown of P_2 is preserved in the type specimen – it is very small and oval shaped, with a maximum diameter of .8 mm. The crown of P_2 is positioned just in front of the base of P_3, and it must have just projected through the gum in the living animal. P_{3-4} have a high, wedge-shaped protoconid, as in earlier species of *Nannodectes*, and lack any development of a paraconid or metaconid. There is, however, a slight development of a cristid obliqua on the back of the protoconid and on the heel of P_3 in some specimens, and this crest is more strongly developed on P_4. The entoconid corners of M_{1-2} tend to be squared, and they always have a distinct entoconid cusp. The heels of M_3 in *N. gidleyi* are consistently broad, rounded, unfissured, and have crenulated enamel on the occlusal surface.

The upper incisors consistently have a large anterocone, laterocone, and posterocone, with a small mediocone and no centroconule. I^2 is a relatively large tooth, with a single root and a simple pointed crown (maximum diameter 2.1 mm). The upper canine is only half the size of I^2 but resembles it in having a single oval root and a simple pointed crown (maximum diameter 1.6 mm). P^2 is consistently two rooted with a crown about the size of that of the upper canine, but the crown of P^2 is generally more triangular than that of the canine. P^3 is preserved in five specimens. In one it has a well-developed paraconule, in one it lacks any trace of a paraconule, and in the other three a paraconule is weakly developed. All have a small but distinct metacone. A paraconule and metacone are present on P^4 of all seven specimens preserving this tooth. Of nine specimens preserving M^1, six have a small mesostyle. A small mesostyle is present on all five specimens preserving M^{2-3}, and these teeth tend to have crenulated enamel on the occlusal surfaces.

Measurements of the upper and lower teeth of the type sample of *N. gidleyi* are summarized in Table A-6.

Discussion.– In addition to the type collection, several other samples have been ascribed in the literature to *N. gidleyi*. Simpson (1927) identified several isolated teeth from the Erickson's Landing locality in Alberta as "*Nothodectes* cf. *gidleyi*." These teeth were later described by Russell (1964) as a new species "*Plesiadapis paskapooensis*." In fact, they represent the previously poorly known *Ples. rex*. Dorr (1958) identified a number of jaw fragments and isolated teeth from the Hoback Basin Battle Mountain locality as "*Ples. gidleyi*," but these too represent *Ples. rex*. More recently, Schiebout (1974, p. 17) has identified specimens from two localities in the Black Peaks Formation of southern Texas as "*Ples. gidleyi*." A mandible and two isolated teeth included in this sample by Schiebout undoubtedly belong to species of *Chiromyoides*, but the remainder of the specimens appear to be related to *N. gidleyi*, and they are discussed below under *N.* aff. *gidleyi*.

Typodigm.– The type sample of *N. gidleyi* from the Mason Pocket includes AMNH 17170 (type), 17171-17174, 17200, 17365, 17366, 17372, 17386-17389, 17396, 17404, 17506, 56275, 56276, 56296, and several uncatalogued specimens; also UCMP 36518-36520.

Nannodectes aff. gidleyi

Plesiadapis gidleyi (in part), Schiebout, 1974, p. 17, fig. 16b-c, e-h, j, k, 17.

Diagnosis.– Specimens of *Nannodectes* aff. *gidleyi* are about the same size as those of *N. gidleyi* but differ from that species in having a more squared hypoconulid lobe on M_3, relatively larger premolars, more crenulated enamel, and possibly in lacking P_2.

Description.– Only one mandible (TMM 41366-77) and about two dozen teeth are known from "Joe's Bonebed" in the Black Peaks area of Texas. A description of the material and illustrations are presented in Schiebout (1974, figs. 16, 17). No complete upper or lower incisors are known. No specimen of P^3 is known, but two specimens of P^4 both have distinct metacones. One has a distinct paraconule, the other lacks it. The upper molars consistently have strong mesostyles. Three specimens of P_4 are known, each with a small distinct hypoconid and a distinct cristid obliqua. M_{1-2} have squared, cusped entoconid corners as in *N. gidleyi*. The hypoconulid lobe of M_3 is represented by five specimens, which vary from rounded (TMM 41365-194) to distinctly squared (TMM 41365-541). The hypoconulid lobes all have highly crenulated enamel but unfissured borders.

There is no trace of P_2 in the one known mandible, but the diastema region in front of P_3 is damaged slightly, and it is possible that P_2 was originally present.

Discussion.– The relatively large premolars, strong mesostyles, squared heels on M_3, possible absence of P_2, and highly crenulated enamel on the occlusal surfaces are all characters more advanced than those in *N. gidleyi*; but until a larger sample, including complete incisors, is available, it will not be possible to adequately diagnose the form represented. The name *N.* aff. *gidleyi* is employed to show that it is related to *N. gidleyi* but probably distinct from it.

Hypodigm.– The entire sample of this form is from the Black Peaks Joe's Bonebed and includes TMM 41366-77 (a mandible), and about two dozen isolated teeth catalogued under TMM 41365.

PLESIADAPIS Gervais

Plesiadapis Gervais, 1877, p. 76. Type: *Plesiadapis tricuspidens* Gervais.
(Tricuspidens) Lemoine, 1887, p. 192; 1891, p. 280. Type: *Plesiadapis (T.) gervaisi* Lemoine.
Sciurus (in part), Launay, 1908, p. 393.
Nothodectes Matthew, 1915, p. 482. Type: *Nothodectes dubius* Matthew.
Tetonius (in part), Gidley, 1923, p. 11.
Sciuroides (in part), Piton, 1940, p. 289.
Menatotherium Piton, 1940, p. 290. Type: *Menatotherium insigne* Piton.
(Ancepsoides) Russell, 1964, p. 115. Type: *Plesiadapis (A.) anceps* Simpson.

Included species.– *Ples. praecursor* Gingerich; *Ples. anceps* Simpson; *Ples. rex* (Gidley); *Ples. churchilli* Gingerich; *Ples. fodinatus* Jepsen; *Ples. dubius* (Matthew); *Ples. simonsi* Gingerich; *Ples. cookei* Jepsen; *Ples. insignis* (Piton); *Ples. walbeckensis* Russell; *Ples. remensis* Lemoine; *Ples. tricuspidens* Gervais; *Ples. russelli*, nov.

Known distribution.– Late Paleocene to early Eocene in western North America (Tiffanian and Clarkforkian) and western Europe (Thanetian and early Sparnacian).

Diagnosis.– *Plesiadapis* differs from *Pronothodectes* and most species of *Nannodectes* in lacking the lower canine. Differs from advanced species of *Nannodectes* in generally having centroconules on the upper incisors, broader cheek teeth, and more squared, fissured heels on M_3. Differs from *Chiromyoides* in having a relatively shallow mandible and in having less robust incisors. Differs from *Platychoerops* in having a tricuspid upper central incisor, with a distinct anterocone, laterocone, and posterocone.

Discussion.– This diagnosis of *Plesiadapis* is less definite, for a number of reasons, than one might wish. The early species of *Nannodectes* and *Plesiadapis* were sympatric. As long as they remained sympatric, they differed significantly in size and morphology. However, after the *Nannodectes* lineage became (apparently) largely confined to southern latitudes (or possibly became extinct – we have no further record of it) a lineage of small *Plesiadapis* convergently evolved several characters (relatively small size and narrow cheek teeth) characteristic of *Nannodectes*. The species of *Platychoerops* are the final segment of one evolutionary lineage of *Plesiadapis*, and a diagnosis of the two genera is necessarily arbitrary. The absence of a laterocone on the upper incisors has been made the criterion of membership in *Platychoerops* because this is the distinction most generally used since Lemoine's diagnosis of "*Tricuspidens*" and "*Subunicuspidens*" in 1887.

As discussed in the introduction to this chapter, recognition of subgenera has not been found to be particularly useful in understanding the phylogeny or classification of *Plesiadapis*, and the subgenera *Tricuspidens* Lemoine and *Ancepsoides* Russell are synonymized with *Plesiadapis*. *Tricuspidens*, it should be noted, is certainly a junior synonym of *Plesiadapis* (had proper taxonomic procedures been followed by Lemoine, it would be a junior objective synonym).

Russell (1967a) recently recognized the plesiadapid affinity of Piton's enigmatic *Menatotherium insigne*. The type specimen is the impression of a nearly complete skull and skeleton – all crushed flat on a slab of bituminous shale. By reversing stereo photographs, Russell was able to obtain a positive image of the specimen, which is as he concluded undoubtedly a plesiadapid. With a dental formula of $\frac{2}{1}\ \frac{1}{0}\ \frac{3}{3}\ \frac{3}{3}$, "*Menatotherium*" could be either an advanced species of *Nannodectes* or an early *Plesiadapis*. The length of the lower tooth row (P_3-M_3) is 14 mm. This compares closely with *N. gidleyi* and is also similar to *Ples. praecursor* and *Ples. anceps*. The crown of P_2 of "*Menatotherium*" is approximately 1.5 mm long. Such a large P_2 is known in early *Plesiadapis* (see for example PU 18738) but not in *Nannodectes*. The closest affinities of *Ples. insignis* appear to be with the North American *Ples. praecursor* or *Ples. anceps*.

Because of their geographic separation, the North American and European species of *Plesiadapis* are listed and discussed separately.

North American Species

Plesiadapis praecursor Gingerich

(Plates 3 A; 4 A)

Plesiadapis sp., Gazin, 1971, p. 22.

Plesiadapis praecursor Gingerich, 1975b, p. 141, pl. 2: 1, 5.

Type.– PU 14512, a left mandible with alveoli for I_1, P_{2-3}, M_3, and with the crowns of P_4, M_{1-2} intact; from the Douglass Quarry (Locality 63 of Simpson, 1937b; Sec. 18, T 5 N, R 15 E, Sweetgrass Co.), Crazy Mountain Field, Montana.

Diagnosis.– Smallest species of *Plesiadapis* that still retains P_2. The average length and width of M_1 in *Ples. praecursor* are 2.63 and 2.57 mm, respectively, compared with 2.87 and 2.84 mm for *Ples. anceps* and 3.07 and 2.95 mm for *Ples. rex*. Differs from later species of *Plesiadapis* in consistently retaining P_2. Differs from species of *Pronothodectes* in being larger and in lacking I_2 and the lower canine. Differs from contemporaneous *Nannodectes intermedius* in being larger (see Figure 12) and in lacking the lower canine.

Description.– Two mandibles of *Ples. praecursor*, a maxillary fragment, and several isolated teeth are known from the Douglass Quarry, where it is found together with the smaller species *Nannodectes intermedius* (see Fig. 12). *Ples. praecursor* is also represented by several isolated teeth mentioned by Gazin (1971) from the Keefer Hill locality in the Shotgun Butte area. The upper dental formula cannot be determined from any specimens yet known, but it was almost certainly 2.1.3.3, as in *Pronothodectes* and later species of *Plesiadapis*. The lower dental formula is known from two mandibles (the type and PU 21576) to be 1.0.3.3.

The upper central incisors of *Ples. praecursor* have prominent anterocones, laterocones, and posterocones, a small mediocone, and no centroconule. The only upper incisor from the type locality (Douglass Quarry) has a width of 2.3 mm; as was noted in discussing the incisors of *N. intermedius*, the upper incisors of *Ples. praecursor* from Keefer Hill have a mean width of 2.4 mm with a standard deviation of .16 mm. Alveoli in the only maxillary fragment yet known of this species (PU 14626) show P^2 to have been double rooted. P^{3-4} in this species have small metacones and well-developed paraconules. M^1 is damaged, and the only feature to be noted is the absence of a mesostyle.

Table 2. Measurements of cheek teeth of *Plesiadapis praecursor* from Douglass Quarry (D) and Keefer Hill (K). All measurements in millimeters.

	Specimen	Length	Width
P_3	PU 21576 (D)	2.1	1.8
	PU 21577 (D)	2.2	1.7
P_4	PU 14512 (type, D)	2.1	2.3
M_1	PU 14512 (type, D)	2.6	2.6
	PU 21576 (D)	2.7	2.6
	PU 21577 (D)	2.6	2.5*
	UW 5498 (K)	2.7	2.5
	UW 5498 (K)	2.6	2.7
M_2	PU 14512 (type, D)	2.9	2.9
	UW 5498 (K)	2.9	3.0
	UW 5498 (K)	3.1	3.1
M_3	PU 21577 (D)	3.8	2.5
P^3	PU 14626 (D)	2.2	3.0*
P^4	PU14626 (D)	2.2	3.7*
M^1	PU 14626 (D)	2.7	4.4*

*Estimated

The two mandibles (PU 14512 and 21576) both have an alveolus for I_1, followed by an alveolus for P_2. In PU 21576 this P_2 alveolus is relatively large, approximately the size of the alveolus for the root of P_3. In PU 14512 the alveolus for P_2 is distinctly smaller. The crowns of P_{3-4} each have a single wedge-shaped protoconid followed by a short heel lacking crests. M_{1-2} are relatively broad molars, with the less steeply sloping outer walls characteristic of the early species of *Plesiadapis*. The entoconid corner is squared and cusped in all specimens. Only one M_3 (PU 21577) of *Ples. praecursor* is known. It too is broad with a relatively large buccal cingulid and a less steeply sloping protoconid than in *Nannodectes*. The heel of M_3 is broad, rounded, and unfissured, with smooth enamel on the occlusal surface.

I have been unable to locate several of the teeth of *Plesiadapis* from the Keefer Hill locality mentioned by Gazin (1971), but his description of these missing teeth fits that to be expected in *Ples. praecursor*, and there is little doubt that they belong to this species.

Measurements of the teeth of *Ples. praecursor* from the Douglass Quarry and from the Keefer Hill locality are given in Table 2.

Typodigm.– The specimens of *Plesiadapis praecursor* from the type locality (Douglass Quarry) are all in the Princeton collection: PU 14512 (type), 14626, 21576, 21577.

The specimens mentioned here from the Keefer Hill locality are all in the University of Wyoming collection: UW 5498, 5499.

Plesiadapis anceps Simpson

(Plates 3 B; 4 B)

Plesiadapis anceps Simpson, 1936, p. 19, fig. 8-9; 1937a, p. 5.

Plesiadapis jepseni Gazin, 1956a, p. 23, pl. 4: 1, 3 [Type: USNM 20760, from Bison Basin Saddle locality]

Type.– AMNH 33822, a ?congenitally malformed, crushed left mandible with I_1, $M_{1\text{-}3}$, associated P_4 and maxillae with P^4 $M^{1\text{-}2}$; from the Scarritt Quarry (Sec. 13, T 5 N, R 14 E, Sweetgrass Co.), Crazy Mountain Field of Montana.

Diagnosis.– *Plesiadapis anceps* differs from most later species of the genus in retaining P_2. Differs from *Ples. praecursor* in being larger, and from *Ples. rex* in being smaller, lacking upper molar mesostyles, lacking centroconules on I^1, and in having a more rounded heel on M_3. Average length and width of M_1 in the type sample of *Ples. anceps* (n=3) are 3.00 and 3.03 mm, respectively, compared to 2.63 and 2.57 mm in the type sample of *Ples. praecursor* (n=3), and 3.30 and 3.10 mm in the type sample of *Ples. rex* (n=2).

Description.– The upper dentition of *Ples. anceps* is poorly known. Only one specimen (AMNH 92048) shows the canine-premolar region – the upper dental formula is 2.1.3.3. The lower dental formula in 11 of the 12 specimens complete enough to permit a determination is 1.0.3.3. One specimen (USNM 20585) lacks any trace of P_2, an anomalous condition. Since P_2 is consistently present in species leading to and derived from this species, it seems likely that the absence of a P_2 in one specimen is accidental.

Two upper central incisors of *Ples. anceps* are known from the Saddle locality. They are larger than the incisors of *Ples. praecursor*, with widths of 2.6 mm and 2.8 mm, respectively. The anterocone, laterocone, and posterocone are large, a small mediocone is present, and there is no trace of a centroconule. I^2 is not represented in the collections. The upper canine is known only from its alveolus. A tooth with a broken crown in place in the maxilla AMNH 92048 shows that P^2 had two roots. P^3 is also preserved in this specimen, and has a small but distinct metacone, and a distinct paraconule (which is absent in the type specimen). A single P^4 is known, in the type specimen, and it has a distinct metacone and paraconule. Of seven upper molars, only one (MCZ 18687) shows a faint trace of a mesostyle.

The lower incisor of *Ples. anceps* is known in only one specimen (apart from the apparently malformed type specimen). This specimen (PU 18783, from the Medicine Rocks area) has a stout but narrow incisor (height 4.8 mm, width 2.2 mm). It has an average-sized margoconid and a distinct margocristid. The P_2 in this specimen and in the type specimen appear to have been larger than average, with a root diameter of slightly more than 1 mm. The crown of P_2 is not represented in any collection. The unworn crowns of $P_{3\text{-}4}$ have a high, wedge-shaped protoconid, which, when worn (as in the type of *Ples. "jepseni"*), resembles the slightly more inflated protoconid of *Ples. rex*. The entoconid corner on M_1 and M_2 tends to be squared, with a distinct entoconid cusp. The third lobe of M_3 is almost always of moderate width, varying from rounded to square, and with about half of the specimens showing a small fissure dividing the nearly flat hypoconulid into medial and lateral halves. The occlusal surface of M_3 has smooth, uncrenulated enamel.

Measurements of the lower dentition of *Ples. anceps* from the Bison Basin Saddle locality are summarized in Table A-7.

Discussion.– The type specimen of *Ples. anceps* is, as sometimes happens, rather atypical of the species it represents. The mandibular ramus of the type specimen is very shallow and rather bloated, somewhat like the normal condition in juvenile mandibles, although this specimen does not represent a juvenile. The lower incisor of the type mandible apparently lacked a margoconid, and P_4 and the lower molars have an inflated appearance uncharacteristic of any plesiadapid species, an appearance that is further exaggerated by the absence of buccal cingulids. The upper cheek teeth also have an inflated appearance, and this inflation may account for the complete absence of a paraconule on P^3 in the type specimen.

Fortunately, the year after Simpson (1936) first described *Ples. anceps*, he was able to report the find of a second mandible of *Plesiadapis* from the same small quarry as the type specimen (Simpson, 1937a, p. 5). This new mandible he included without question in *Ples. anceps* in spite of some morphological differences. The teeth of the new mandible (AMNH 33978) are almost identical in size to those of the type specimen but have the morphology of typical early *Plesiadapis*. While the type specimen serves to identify *Ples. anceps* as the Scarritt Quarry *Plesiadapis* species of moderate size with no mesostyles and a dental formula of 1.0.3.3, the second mandible of *Plesiadapis* found there probably more adequately represents the species for comparative purposes.

Similarly, the specimen chosen by Gazin as the type of *Ples. "jepseni"* has a broad heel on M_3, and it is worn in such a way that it appears somewhat different from *Ples. anceps*. Several other specimens in the collection of *Ples. "jepseni"* from the Saddle locality have teeth virtually identical to those in the second mandible of *Ples. anceps* from the Scarritt Quarry (compare especially USNM 20586, figured in Gazin, 1956a, pl. 4, fig. 1), and there is little doubt that the two populations belong to the same species.

It should be noted that Gazin's statement (Gazin, 1956a, p. 23) that the type of *Ples. "jepseni"* comes from the Ledge locality is in error – the type and all other specimens of this species come from the Saddle locality (Gazin, *in litt.*, has rechecked and confirmed this). The maxilla figured by Gazin (1956a, pl. 4, fig. 2) does come from the Ledge locality, but it is a specimen of *Nannodectes simpsoni*, not *Ples. "jepseni."*

Finally, the incisor from the Scarritt Quarry figured by Simpson (1936, fig. 10; AMNH 33824) is possibly an upper incisor of a species of *Nannodectes*, presumably *N. gazini.*

Typodigm.– The following specimens are known from the type locality, the Scarritt Quarry: AMNH 33822 (type), 33823, ?33824, 33825, ?33976, 33977, 33978.

Of specimens included in the hypodigm of the species, the largest sample comes from the Bison Basin Saddle locality: AMNH 88108, 92019, 92028, 92048, 92103, and several uncatalogued isolated teeth; CM 20952; MCZ 18687; USNM 20585-20587, 20589, 20760, 20773, 20779, 186785, 186786; and an unnumbered M_2 in the UW collection. In addition, one mandible (PU 17816) comes from the type section of the Polecat Bench Formation in the Big Horn Basin, the most complete mandible of the species (PU 18738) comes from the Medicine Rocks Highway Blowout locality in Montana. Three isolated incisors (PU 21583, CCM 7310) from the White Site, and a partial cranium (PU 19642) from Seven-up Butte, both in the Medicine Rocks area of Montana, probably belong to this species as well.

Plesiadapis rex (Gidley)

(Plates 3 C, D; 4 D, H)

Tetonius rex Gidley, 1923, p. 11; pl. 3: 4.
Nothodectes cf. *gidleyi*, Simpson, 1927, p. 4, fig. 4.
Plesiadapis rex, Simpson, 1937b, p. 167.
Plesiadapis jepseni (in part), Gazin, 1956a, p. 23.
Plesiadapis cf. *fodinatus* (in part), Gazin, 1956a, p. 22; pl. 2: 3.
Plesiadapis cf. *fodinatus*, Gazin, 1956b, p. 708.
Plesiadapis gidleyi, Dorr, 1958, p. 1222.
Plesiadapis rubeyi (in part), Gazin (in Oriel), 1962, p. 2167.
Plesiadapis paskapooensis Russell, 1964, p. 117; pl. 7: 3-5.
Plesiadapis sp., McKenna (in Love), 1973, p. 45.

Type.– USNM 9828, a left M_2; from Locality 13 (Sec. 22, T 5 N, R 14 E, Sweetgrass Co.), Crazy Mountain Field, Montana. Earlier confusion about the type locality of *Ples. rex* was resolved by Simpson (1937b, p. 168).

Diagnosis.– *Plesiadapis rex* differs from *Ples. praecursor* and *Ples. anceps* in being larger, in consistently having a distinct centroconule on I^1, and in generally having a squared, fissured heel on M_3 and mesostyles on M^{2-3}. *Plesiadapis rex* differs from *Ples. churchilli* and other later species of the genus in consistently retaining P_2 and in lacking a significant mandibular diastema. Average length and width of M_1 in the type sample of *Ples. rex* are 3.30 and 3.10 mm (n=2), compared with 3.00 and 3.03 mm in the typodigm of *Ples. anceps* (n=3), and 3.47 and 3.27 mm in the typodigm of *Ples. churchilli* (n=4).

Description.– The type sample of *Plesiadapis rex* from Locality 13 in the Crazy Mountain Field consists of a number of isolated and broken teeth, which show that this species is identical to the one from the Cedar Point quarry in the Big Horn Basin. The description that follows is based largely on the Cedar Point sample of over 160 mandibles, 15 maxillae, and hundreds of isolated teeth, including upper incisors.

The upper dental formula, in all specimens in which it can be determined, is 2.1.3.3. Three specimens preserve the alveolus for the upper canine (PU 21263, 21300, 21432). The lower dental formula can be determined in 80 specimens – in all 80 it is 1.0.3.3.

The upper central incisors of *Ples. rex* have a prominent anterocone, laterocone, and posterocone, with a small mediocone, and a distinct centroconule between and slightly behind the laterocone and mediocone. Crowns of I^2 and the upper canine are unknown. $P^{3\text{-}4}$ have strong paraconules and generally small metacones. The mesostyle on the upper molars is usually weak or absent on M^1, but a small mesostyle is usually present on M^2 and on M^3. The enamel on the occlusal surfaces tends to be crenulated on M^2 and M^3, but this characteristic is not so strongly developed in *Ples. rex* as it is in later species.

The lower incisor has a distinct margoconid and usually a strong margocristid. The alveolus for P_2 is consistently very small, but the crown of the tooth itself is not preserved in any specimen. $P_{3\text{-}4}$ resemble those teeth in *Ples. anceps* in having a single protoconid cusp and a small heel, but the protoconid tends to be slightly more inflated, making it less wedge shaped than it is in *Ples. praecursor* and *Ples. anceps.* M_{1-2} have squared entoconid corners, with distinct entoconid cusps. The third lobe of the heel of M_3 tends to be broad and squared, with a small fissure dividing the hypoconulid into medial and lateral parts. The enamel on the occlusal surfaces of M_3 is usually moderately crenulated.

One mandible (PU 21246) is almost complete and very little distorted. It shows that the mandibular condyle was slightly above the level of the tooth row, that the coronoid process of the mandible was well developed, and that the angle of the mandible extended backwards as a rather pointed process.

Measurements of the teeth of the Cedar Point sample of *Ples. rex* are summarized in Table A-8.

Discussion.– The type sample of *Plesiadapis rex* consists of the crowns of six molars, several nearly complete incisors, and a number of tooth fragments in the PU and USNM collections. These teeth show the consistent development of a centroconule on I^1 but do not adequately document the other diagnostic features of this species. As with *Ples. anceps*, the type specimen of *Ples. rex* identifies the species, but it is not adequate for comparisons. Lacking adequate comparative material of *Ples. rex*, it is not surprising that no writer subsequent to Gidley (1923) referred specimens to this species. Only with the large Cedar Point sample of the species, almost all of which was collected between 1967 and 1972, has *Ples. rex* become adequately known. This has in turn permitted a number of other previously described collections to be recognized as *Plesiadapis rex.*

Typodigm.– The type sample of *Plesiadapis rex* consists of the following specimens from Crazy Mountain Field Locality 13: USNM 9827, 9828 (type), 16865, 16866; PU 14535, 14629.

The sample of *Ples. rex* from the Big Horn Basin Cedar Point locality includes about 200 catalogued specimens in the PU collection, the most complete being the mandibles PU 20058, 21246, and maxillae PU 21300, 21347, and 21448. Some 40 additional mandibles and maxillae were collected from Cedar Point in 1974 and 1975 and these are now in the Yale Peabody Museum and University of Michigan Museum of Paleontology.

In addition, the following specimens are known from the Big Horn Basin Jepsen Quarry: PU 17789, 17790. From Erickson's Landing: AMNH 15543d-i. From the Hoback Basin Battle Mountain locality: UM 34766-34773; CM 8806, 8807, 8823, 8828, 8830. From the Bison Basin Ledge locality: USNM 20762, 20763, 20776, 20777, 20783; CM 18768; AMNH 92178, 92180; MCZ 18640. From the Bison Basin West End locality: USNM 20778, 20784, 186784, 186788; AMNH 86681-86683, 88384. From the Twin Creek locality: USNM 20788 and numerous isolated teeth (USNM 208975). From the Togwotee Pass Love Quarry: AMNH 86773, 86779, 86780, 88190, 88218, 88248, 89693, 89697, 89699-89702, 89705. From La Barge Section 17 (Chappo-17): USNM 186790 mandible fragment with M_{1-2}, and three isolated teeth in USNM.

Plesiadapis churchilli Gingerich

(Plates 3 F, G; 4 E)

Plesiadapis churchilli Gingerich, 1975b, p. 142; pl. 2:2, 6.)

Plesiadapis farisi, Krishtalka, et al., 1975, p. 202.

Type.– PU 21234, a left mandible with I_1, P_{3-4}, M_{1-3}; from the Long Draw quarry (Sec. 24, T 9 S, R 23 E, Carbon Co.), Big Horn Basin, Montana.

Diagnosis.– Differs from *Ples. rex* and earlier species in being larger and in having P_2 variably present, a significant diastema between I_1 and P_3, and well-developed mesostyles on all upper molars. Differs from *Ples. fodinatus* and *Ples. dubius* in being larger, lacking highly crenulated enamel, and having a more squared entoconid corner on M_{1-2}. Differs from *Ples. simonsi* and *Ples. cookei* in being smaller. (See Tables 3, 4, A8-A13, for comparative measurements.)

Description.– Eleven mandibles of *Ples. churchilli* are known, coming from six localities. The lower dental formula can be determined in six of these: three retained P_2, two definitely did not (the type and PU 17753), and the sixth (PU 14964) has a very small foramen in front of P_3, apparently for a minute, vestigial P_2. Three maxillae of *Ples. churchilli* are known. One (PU 20845) preserves alveoli for all the maxillary teeth, including a small canine. The dental formula for *Ples. churchilli* is thus $\frac{2}{1}\ \frac{1}{0}\ \frac{3}{2-3}\ \frac{3}{3}$, with P_2 being retained in 50-60% of the specimens.

Plesiadapis churchilli is the earliest species of *Plesiadapis* to show a significant diastema between the lower incisor and P_3. This is a result of the incisor being relatively smaller compared to the cheek teeth in later species, as well as to its more forward position and the loss of P_2. The lower incisor retains a well-developed margoconid and margocristid. The crown of P_2 is not preserved in any specimens, but it was always small judging from the size of the preserved alveoli for P_2. P_3 tends to be a more anteroposteriorly elongated tooth in *Ples. churchilli* than in the earlier species, but P_4 is normally proportioned. Both have large, slightly inflated protoconids with no accessory cusps, and small simple talonids. A cristid obliqua is weakly developed on the posterior slope of the protocone and on the heel in several specimens (PU 20846, for example). M_{1-2} generally have squared entoconid corners with distinct entoconid cusps, but several specimens (M_2 of PU 19019, for example) show the more rounded, crested pattern characteristic of later species of *Plesiadapis*. The hypoconulid or third lobe of M_3 is broad, squared, fissured, and has relatively smooth enamel on the occlusal surfaces.

The upper incisors of *Ples. churchilli* are virtually identical to those of *Ples. rex* but appear to be slightly smaller relative to the size of the cheek teeth. A distinct centroconule is present on all specimens, and a small accessory lateroconule and medioconule are present behind their respective cones in some specimens. P^3 is an almost triangular tooth with a small but distinct paraconule and metacone. P^4 is a relatively broad tooth with a large paraconule and a small but distinct metacone. Mesostyles are strongly developed on M^{2-3} and almost always present on M^1 as well. The enamel on the occlusal surfaces is generally somewhat crenulated but not to the extent as in later species.

Measurements of the type sample of *Ples. churchilli* from the Long Draw quarry are summarized in Table A-9.

Typodigm.— The type sample of *Ples. churchilli* from the Big Horn Basin Long Draw locality includes: PU 20845, 20846, 20858, 20859, 21234 (type), and a dozen isolated teeth.

Several other Big Horn Basin localities have produced *Ples. churchilli*, including from the Croc Tooth quarry: PU 14964, 17744, 21584, 21585; from the Divide quarry: PU 17752-17754; from the lower Sand Draw area: PU 17762, 17787, and a dozen isolated teeth; from the Airport locality: PU 13217, 19158; from the area west of Polecat Bench: PU 19019.

An additional collection from the Badwater area "Malcolm's locality" includes two jaw fragments: CM 12471, 16194, and about 70 isolated teeth (Krishtalka et al., 1975, p. 202). Average length and width of M_1 for the Badwater collection, measured as described in the introduction, are 3.26 and 2.97 mm, respectively (n=7).

Plesiadapis fodinatus Jepsen

(Plates 3 H; 4 F, I)

Plesiadapis fodinatus Jepsen, 1930, p. 515; pl. 5:3-6.
Plesiadapis rubeyi Gazin, 1942, p. 217, fig. 1; 1956c, p. 4, pl. 1:10.
Plesiadapis farisi Dorr, 1952, p. 79, fig. 4; pl. 6: 1,2. Dorr, 1958, p. 1227.
Plesiadapis cf. *fodinatus* (in part), Gazin, 1956a, p. 22.
Plesiadapis cf. *jepseni*, Gazin, 1956a, pp. 6, 23.

Type.— PU 13278, a right mandible with I_1, P_3, M_{1-2} intact; from the Princeton Quarry (Sec. 21, T 57 N, R 100 W, Park Co.), Big Horn Basin, Wyoming.

Diagnosis.— *Plesiadapis fodinatus* differs from *Ples. rex*, earlier species of *Plesiadapis*, and *Nannodectes gidleyi* in consistently retaining P_2, in having curved and crested entoconids, and in having strong mesostyles on all upper molars. Further differs from *N. gidleyi* in having squared and fissured heels on M_3 and in usually having a small centroconule on I^1. Differs from *Ples. churchilli* in lacking squared entoconids on M_{1-2}, in having basined heels with a distinct cristid obliqua and often a distinct entoconid on P_{3-4}, and in having more crenulated enamel. Differs from *Ples. dubius* in being larger, and in sometimes retaining P_2. Differs from *Ples. simonsi* and *Ples. cookei* in being smaller. (See Tables 3, 4, A9-A13, for comparative measurements.)

Description.— Virtually the entire upper and lower dentition of *Ples. fodinatus* is represented in the collection from the type locality or the nearby Schaff Quarry, and a crushed partial skull (in a concretion) is known from the Fossil Hollow locality in the Big Horn Basin. Several specimens (PU 13393, 17614, 19499) show that the upper dental formula is 2.1.3.3. The lower formula can be determined in numerous specimens. It is 1.0.2-3.3, with P_2 being retained in 9 of 24 determinable specimens from the Princeton Quarry and in 7 of 19 specimens from the Schaff Quarry (which is 37% in both).

The upper central incisors consistently have a strong anterocone, laterocone, and posterocone, and a small mediocone. A crested centroconule is present in about half of the specimens. I^2 is a relatively small (maximum diameter about 2.1 mm), slightly curved caniniform tooth. The upper canine has the same form as I^2, but it is much smaller (only 1.4 mm in maximum diameter). Short diastemata separate each of the anterior teeth. P^2 is a small, narrow tooth with a small posteromedial cingulum. In one specimen (PU 14002) P^2 is triangular in outline and a small, distinct protocone is present on the medial corner of the crown. P^3 usually lacks a paraconule, but it is present in several specimens and strongly developed in one (PU 14002). The metacone on P^3 varies, being absent, weak, or distinctly developed in about equal proportions. A paraconule is usually present on P^4, but this too varies, and a paraconule is completely lacking in several specimens. A distinct metacone appears always to be present on P^4. The upper molars of *Ples. fodinatus* always have a relatively strong mesostyle. Rudimentary but distinct hypocones are present on the postprotocingula of M^1 in about 10% of the specimens and on M^2 in about 25% of the specimens. The enamel on the occlusal surfaces of the upper molars tends to be highly crenulated, especially on M^3.

The lower incisor of *Ples. fodinatus* has a distinct margoconid and margocristid. When present, the root of P_2 is only about .5 mm in diameter; the crown is not preserved in any of the specimens. Some examples of P_3

and P_4 resemble those teeth in *Ples. churchilli* or *Ples. rex* in that they lack a cristid obliqua and have a domed heel. In most, however, the heel is distinctly basined, with both the cristid obliqua and a distinct entoconid present. A distinct paraconid and very incipient metaconid are rarely present on P_4. M_{1-2} consistently show a curved, crested entoconid, as opposed to the distinct cusp and squared corner in *Ples. rex, Nannodectes gidleyi*, and earlier species. This curved entoconid crest (described by Dorr, 1958, p. 1227, as a "long entoconid slope") is seen in some specimens of *Ples. churchilli* and is characteristic of all later species of *Plesiadapis* in both North America and Europe. M_3 consistently has a broad, squared, fissured heel with highly crenulated enamel on the occlusal surface and lacks a posterior cingulid.

Measurements of the teeth of *Ples. fodinatus* from the Princeton Quarry type locality are summarized in Table A-10, and those from the Schaff Quarry are summarized in Table A-11.

Discussion.– Gazin (1956c, p. 5) expressed the possibility that *Plesiadapis "rubeyi"* might not be specifically distinct from *Ples. fodinatus* but nevertheless continued to use the former name for the La Barge specimen. With *Ples. fodinatus* now adequately known, it is clear that the characters Gazin cited do not distinguish the two populations. An M_1 length of 3.0 mm (see Gazin, 1942) in *Ples. "rubeyi"* is well within the size range of *Ples. fodinatus*. PU 13940, for example, from the Princeton Quarry has both the short trigonid summit and incipient metaconid on P_4 seen in the type and only good specimen of *Ples. "rubeyi."*

Similarly, Dorr (1958, p. 1227) recognized that *Ples. farisi* might be conspecific with *Ples. fodinatus* but continued to use the former name for the Hoback Basin form, believing his sample to differ from *Ples. fodinatus* in having a less distinct paracone and metacone and a stronger and more distinct paraconule ("protoconule") on P^{3-4}, in having P^3 relatively wider and more rectangular in outline, in having P^{3-4} and M^2 distinctly wider in relation to M^1, and in having a paraconule on P^3 (Dorr, 1952, p. 80-81). The type specimen of *Ples. farisi* (UM 27230) appears to be unique only in having a small paraconule on P^3 and a very small metacone on P^4 – no single maxilla of *Ples. fodinatus* is known with both of these characters, although either one by itself is sometimes present in *Ples. fodinatus*. However, this small difference is certainly not sufficient to warrant recognition of a distinct species, especially in view of the number of diagnostic characters of *Ples. fodinatus* (size; strong mesostyles on M^{1-3}; broad, squared, fissured, and highly crenulated hypoconulid lobe of M_3) in the small sample of *Ples. "farisi."*

Typodigm.– About 40 mandibles and 30 maxillae of *Ples. fodinatus* are known from the type locality, the Princeton Quarry in the Big Horn Basin. All of these specimens are in the PU collection, except for one mandible (BMNH M16679). The most complete and important specimens are: PU 13278 (type), 13393, 13930, 13955, 14405.

Other Big Horn Basin localities yielding *Ples. fodinatus* are the Schaff Quarry: about 35 mandibles and 17 maxillae, all in the PU collection, except MCZ 19433, 19434; the Fossil Hollow locality: PU 18352, 20621, and several uncatalogued fragmentary specimens; and numerous isolated specimens from west of Polecat Bench, all in the PU collection. From the La Barge Creek area, Section 1 (Chappo-1): USNM 16696. From the Hoback Basin Dell Creek locality: UM 27230, 27512-27519; CM 8873, 8881, 8884, 8889. From the Bison Basin *Titanoides* locality: USNM 20761; UW 1081, 1082, 1084, 1085.

Plesiadapis dubius (Matthew)

(Plates 3 I; 4 G)

Nothodectes dubius Matthew, 1915, p. 482, fig. 52.
?Plesiadapis sp. undet., Simpson, 1928, p. 7, fig. 4.
Plesiadapis cf. *fodinatus*, Van Houten, 1945, p. 450.
Plesiadapis? pearcei Gazin, 1956c, p. 6; pl. 1: 9.

Type.– AMNH 16073, a right mandible with P_4, M_{1-3}; from "Clark Fork beds at base of bluff [Polecat Bench, Big Horn Basin] northeast of Ralston, Clark Fork basin, Wyoming" (Matthew, 1915).

Diagnosis.– *Plesiadapis dubius* is very similar to *Ples. fodinatus* but differs from it in being smaller, consistently lacking P_2, and in having slightly more angular cusps and crests on the upper and lower molars. Differs from earlier species of *Plesiadapis* in lacking P_2 and in having highly crenulated enamel. Differs from *Ples. simonsi* and *Ples. cookei* in being much smaller. (See Tables 3, 4, A9-A13, for comparative measurements.)

Description.– The number of maxillary teeth in *Ples. dubius* can be determined in one specimen (UW 6118), which has alveoli for both the upper canine and P^2. No premaxilla of *Ples. dubius* is known, but considering the strong I^2 present in *Ples. fodinatus*, it is almost certain that this species retained a full upper dental complement of 2.1.3.3. The diastema in front of P_3 is preserved in the type specimen and in two other specimens (PU 19892, 21151). None retained P_2, making the lower dental formula of *Ples. dubius* 1.0.2.3.

The only known upper incisor of *Ples. dubius* (PU 17890) has a distinct anterocone, laterocone, and posterocone, with two very small medioconules. It has no trace of a centroconule. The crowns of I^2, C, and P^2 are unknown. P^3 in one specimen has a distinct protocone, paracone, and metacone, but no paraconule. P^4 in two specimens has a distinct metacone, but the typical *Plesiadapis*-type paraconule is much reduced in one and absent in the other. This paraconule is replaced by a small cuspule on the preprotocrista, which is a strong crest on P^4 in *Ples. dubius* connecting the protocone with the parastyle as it does in the molars. The paraconule on the preprotocrista of *Ples. dubius* is serially homologous to the paraconule on the molars, and it is different from the paraconule of earlier plesiadapids. A paraconule of molar type is present on P^4 in some specimens of *Ples. fodinatus* (it occurs together with a typical plesiadapid-type paraconule in PU 14120). The stronger preprotocrista and incipient paraconule of molar type in *Ples. dubius* parallel developments in *Ples. russelli* and early *Platychoerops* and are related to the molarization of P^4. This will be discussed at greater length in a later section on functional evolution of the plesiadapid dentition. The upper molars are smaller but otherwise resemble closely those of *Ples. fodinatus* in having relatively large mesostyles, crenulated enamel, and sometimes a rudimentary hypocone on the postprotocingulum of M^{1-2}.

A small but distinct margoconid and a well-developed margocristid are present on the lower incisor, which is separated from the anterior premolar by a diastema. P_{3-4} have a high, pointed protoconid followed by a short heel with a distinct entoconid, and a hypoconid forming part of a weak cristid obliqua. P_4 in the type specimen has a small, distinct paraconid and an incipient metaconid, again suggesting a tendency to molarize the fourth premolar. The other examples of P_4 do not show these accessory trigonid cusps. M_{1-2} differ slightly from their counterparts in *Ples. fodinatus* in having a posterior basal cingulid continuous with the buccal extension of the entoconid crest. The result, when slightly worn, is a rectangular molar closely resembling the lower molars of *Platychoerops daubrei*. This distinctive appearance of M_{1-2} is undoubtedly what prompted Gazin (1956c, p. 7) to suggest that possibly his "*Plesiadapis? pearcei*" represented a new mammalian genus. M_3 in *Ples. dubius* is generally smaller but otherwise very similar to that tooth in *Ples. fodinatus*, having a broad, squared, fissured hypoconulid lobe, and highly crenulated enamel in the talonid basin.

Measurements of the largest known sample of *Ples. dubius*, that from the Big Horn Basin Paint Creek locality, are given in Table A-12. Since neither the type specimen of *Ples. dubius* nor that of *Ples. "pearcei"* come from the Paint Creek locality, their measurements are listed in Table 3 for comparison.

Discussion.– Gazin (1956c) correctly noted that the trigonids of the two specimens (right and left mandibles possibly belonging to the same individual animal) of "*Plesiadapis? pearcei*" are relatively narrower than in the type specimen of *Ples. dubius*. No new specimens of *Ples. dubius* have been found with such narrow trigonids, but specimens in the large Princeton Quarry sample of *Ples. fodinatus* show the same variation (compare especially PU 13955 with PU 13930). This characteristic and the characters of the trigonid cusps cited by Gazin are hardly sufficient to warrant recognition of a separate species name for the La Barge form, especially in view of the fact that it is of almost exactly the same size and shares the distinctive *Platychoerops*-like structure of the heel of M_{1-2} with the type specimen of *Ples. dubius*.

Table 3. Tooth size of *Plesiadapis dubius* and *Plesiadapis "pearcei"*. (L, length; W, width)

		Ples. dubius AMNH 16073 (type)	*Ples. "pearcei"* USNM 20786	*Ples. "pearcei"* USNM 20787 (type)
P_3	L	2.4	–	–
	W	1.8	–	–
P_4	L	2.4	–	–
	W	2.0	–	–
M_1	L	3.0	2.9	2.9
	W	2.5	2.5	2.5
M_2	L	3.2	–	3.1
	W	2.8	–	2.8

An isolated M_3 (AMNH 22154) from the Bear Creek fauna was originally described by Simpson (1928) as "?*Plesiadapis* sp. undet." Van Valen has since restudied this tooth and concluded that it belonged not to *Plesiadapis* but to *Paromomys* or *Phenacolemur* (see Van Valen and Sloan, 1966, p. 273). The tooth has a length/width ratio of 1.65, which is very close to the 1.60 typical of *Ples. fodinatus* and *Ples. dubius* and considerably smaller than the ratio of 1.85-1.90 characteristic of *Paromomys* and *Phenacolemur*. In spite of some moderate wear, details of the trigonid and talonid of the tooth identify it unquestionably as *Plesiadapis*. Furthermore, the small size of the tooth (L=5.1 mm, W=3.1 mm) together with its broad, squared, fissured heel, indicate that it almost certainly represents *Ples. dubius*.

Finally, it has been reported (Van Houten, 1945, p. 450; R. Wood, 1967, p. 26) that specimens of *Plesiadapis fodinatus* have been found in the Gray Bull beds of the Willwood Formation in the Big Horn Basin. The museum numbers of the specimens in question were not cited, but the record is presumably based on several Princeton specimens from the Paint Creek locality in the Willwood Formation which are labelled "*Plesiadapis* cf. *fodinatus*." Their identification as such is a result of a typological approach to species identification. If the Paint Creek and Princeton Quarry samples are each studied as a unit, it is clear that only one small plesiadapid species is present at

Table 4. Measurements of mandibular dentition of *Plesiadapis simonsi*.

		PU 17814 (type)	PU 20091
P_4	L	–	4.2*
	W	–	–
M_1	L	4.0*	3.9*
	W	3.9	–
M_2	L	4.4	4.8*
	W	4.2	–
M_3	L	–	8.0*
	W	–	–
Mandibular depth		9.9	11.4

*Estimated

each locality. Furthermore, the specimens from Paint Creek are on the average significantly smaller than those from the Princeton Quarry. Although there is some overlap in size, when a collection of several mandibles or maxillae is available, the two can be easily distinguished. *Plesiadapis fodinatus* and *Ples. dubius* are closely related, but they are not, as R. Wood (1967, p. 26) suggests, synonyms. The type specimen of *Ples. dubius* is of the same small size as the Paint Creek specimens, and this is the proper name for all of the small *Plesiadapis* from Paint Creek. As will be discussed in more detail in a later chapter, *Ples. fodinatus* is not found in the Gray Bull beds.

Several specimens of *Plesiadapis dubius* were collected by Professor B. Patterson from Plateau Valley localities in Colorado. These specimens (in the FMNH) further confirm the Clarkforkian age of the Plateau Valley fauna.

Hypodigm.– *Plesiadapis dubius* is known from several localities in the Big Horn Basin, including: south side of Polecat Bench, AMNH 16073 (type, exact locality unknown); Paint Creek locality, PU 17890, 17892, 17942, 17943, 21151, YPM 24616, 24617; Coon Creek area, PU 17890, UW 6118. From Bear Creek: AMNH 22154. From La Barge section 12 (Chappo-12): USNM 20786, 20787. From the Togwotee Pass localities: Red Creek I, UCMP 113570; Low locality, AMNH 86729, 89723; New Taeniodont locality, AMNH 86863, 86892, 88199. From Plateau Valley localities: FMNH P26061, P26068, P26084, P26112.

Plesiadapis simonsi Gingerich

(Plate 5 E, F)

Plesiadapis simonsi Gingerich, 1975b, p. 142, pl. 2:3, 4.

Type.– PU 17814, a right mandible with M_{1-2}; from the middle level of the Sand Draw area (Sec. 24, T 55 N, R 97 W, Big Horn Co.), Big Horn Basin, Wyoming.

Diagnosis.– Differs from all other North American species of *Plesiadapis*, except *Ples. cookei*, in being significantly larger. Resembles *Ples. cookei* in known details but significantly smaller than that species. Length and width of M_1 in type specimen of *Ples. simonsi* are 4.0 and 3.9 mm, respectively, compared to 3.47 and 3.27 mm in the typodigm of *Ples. churchilli*, and 5.41 and 5.10 mm in the type sample of *Ples. cookei.*

Description.– The type specimen of *Ples. simonsi* consists of a portion of the right mandibular ramus, with a slightly damaged M_1 and intact M_2, followed by the alveoli for M_3. The cancellous bone and shallow mandibular ramus indicate that the specimen belonged to a relatively young individual, although M_3 was fully erupted. The structure of the two preserved molars is very similar to that in *Ples. cookei, Ples. fodinatus*, and some *Ples. churchilli*, with the distinctive curved entoconid crests distinguishing these later species of *Plesiadapis* from earlier species.

A second mandible of *Ples. simonsi* (PU 20091) preserves the ramus almost intact from the front of P_4 to the back of M_3. The roots of these teeth are still in the specimen, but the crowns are all broken off. It is possible to estimate the lengths of the molars and these estimates are given in Table 4, together with measurements of the teeth of the type specimen.

Discussion.– *Plesiadapis simonsi* is unfortunately represented by only two fragmentary specimens. However, both specimens indicate a species significantly larger than *Ples. churchilli* and smaller than *Ples. cookei*. Their importance lies in demonstrating for the first time the relationship of *Ples. cookei* to the other species of *Plesiadapis* and in demonstrating that the large *Ples. cookei* probably evolved in North America and is not an immigrant.

Plesiadapis simonsi is of additional significance in that its molar structure bears a closer resemblance to the European species of *Plesiadapis* from Cernay than any other North American species of *Plesiadapis. Plesiadapis simonsi* is of about the same size as *Ples. tricuspidens* from Cernay and could eventually prove to be conspecific with it, the two possibly being regarded as geographic subspecies of the same species. M_2 in *Ples. simonsi* appears to be relatively wider than the corresponding tooth in most *Ples. tricuspidens*, and the mandibular ramus of *Ples. simonsi* is significantly less deep than that of *Ples. tricuspidens*. Considering these differences, the geographic distance separating the two localities, and the small sample of *Ples. simonsi*, placing the North American sample in *Ples. tricuspidens* does not seem warranted.

Hypodigm.– Only two specimens of *Ples. simonsi* are known, both from the Big Horn Basin: PU 17814 (type) from the Sand Draw area (Middle beds), and PU 20091 from near the Clark Fork River, in Sec. 7, T 57 N, R 101 W, Park Co., Wyoming.

Plesiadapis cookei Jepsen

(Plates 5 H, K; 6 B, I)

Plesiadapis cookei Jepsen, 1930, p. 525; pl. 10: 1-7.
Plesiadapis cf. *cookei*, Gazin, 1942, p. 218.
Plesiadapis cookei (in part), Gazin, 1956c, p. 5; pl. 1: 5-8.

Type.– PU 13293, associated right and left mandibles, right maxilla, one upper and one lower incisor; from the Little Sand Coulee area (Sec. 32, T 57 N, R 101 W, Park Co.), Big Horn Basin, Wyoming.

Diagnosis.– *Plesiadapis cookei* is the largest known species of *Plesiadapis*, exceeding in size *Ples. simonsi*, *Ples. tricuspidens*, and *Ples. russelli* (compare measurements in Table A-13 with those in the other tables).

Description.– None of the maxillary specimens yet discovered is sufficiently complete to allow determination of the upper dental formula. By comparison with other closely related species it is almost certain that the upper formula is 2.0.3.3, which is the upper formula of *Ples. tricuspidens*. Sufficient bone is preserved in front of P_3 in five specimens to show that P_2 was not retained, making the lower dental formula consistently 1.0.2.3.

The upper central incisor of the type specimen (PU 13293) has a long anterocone and laterocone and a minute mediocone. It has no trace of a centroconule. Three other well-preserved upper incisors (PU 18118, 19623, 19624) show the same configuration of apical cusps. The upper incisor of the type specimen appears to lack a posterocone (see Jepsen, 1930, pl. 10:6-7), but considering that two other well-preserved incisors from the same beds have a strong posterocone, it seems likely that this cone has been broken off in the type specimen. A strong posterocone was probably a character of *Ples. cookei*, as it was in all other species of *Plesiadapis*.

No known specimens preserve the crowns of I^2, C (if present), or P^2. Only one known specimen (AMNH 16077) preserves the crown of P^3. This tooth has a high, pointed protocone and paracone, with no trace of a metacone or paraconule. P^4 is preserved in the type and two other specimens; each has a very small metacone and no paraconule. The upper molars have strong mesostyles and crenulated enamel on the lingual side of the protocone, forming a small lingual cingulum on M^3 and incipient cingula on the other molars. A small hypocone is present on the postprotocingulum of M^1 in the type specimen, but this structure is not present in most other specimens. The M^3 (USNM 21281) identified by Gazin (1956c, p. 6) as *Ples. cookei* probably belongs to *Phenacodus* or a related condylarth – it is not *Plesiadapis*.

Three lower incisors preserve the margoconid region (PU 17977, 19624). All three have distinct margocristids but lack the margoconid itself. $P_{3\text{-}4}$ are simple in structure, with a high protocone and small talonid. Paraconids and metaconids are not present on the premolars of any of the specimens. A distinct hypoconid and cristid obliqua are usually present, but there is no entoconid, so the talonids are open lingually and not basined as in *Ples. fodinatus*. The lower M_1 and M_2 are distinctive only in having a curved entoconid crest well developed. The talonid of M_3 is broad, rounded, and only weakly fissured in the type and some additional specimens (PU 18046, AMNH 57356), but it is broad, squared, and strongly fissured in other specimens (for example, AMNH 86787).

Measurements of the largest sample of *Ples. cookei*, that from the Little Sand Coulee type area, are summarized in Table A-13.

Discussion.– In describing *Plesiadapis cookei*, Jepsen (1930, p. 527) noted that it resembles *Platychoerops* in some characters, namely in lacking a paraconule on the upper premolars and in having strong mesostyles on the upper molars. The absence of a margoconid on I_1 is an additional important character suggesting that *Ples. cookei*, with *Ples. tricuspidens* and *Ples. russelli*, is closely related to the origin of *Platychoerops*.

Typodigm.– Most of the specimens of *Ples. cookei* come from the type area near Little Sand Coulee. These include: PU 13293 (type), 13307, 13308, 17893, 18046, 18056, 18093, 18097, 18098, 18118, 18138, 18312, 19538, 19547, 19551, 19590, 19621, 19623, 19624, 19819, 19846, 19851, 21003, 21009.

The following additional specimens also come from the Big Horn Basin: from the Paint Creek locality, PU 13342, 17934, 17936-17940, YPM 24616; from the southwest side of the McCullough Peaks, PU 17973; from the west side of Polecat Bench, PU 17977; from east of Foster's Gulch, PU 17825; from west of the Clark's Fork River, AMNH 16077; no specific locality, AMNH 21867. In 1975, 17 additional specimens were collected in Sand Coulee by a UM field party (including one, UM 65720, preserving both mandibular rami with practically a full lower dentition).

Two specimens come from the La Barge area Section 12 (Chappo-12): USNM 16698, 20785. The following specimens of *Ples. cookei* come from localities in the Togwotee Pass area: Main locality, AMNH 57224, 57236, 86787, 86788, 86790, 86816, 86817, 86825, 86842; Red Creek, UCMP 54003, AMNH 56121, 56123; Verland's locality, AMNH 88162, 86744, 86746; Susan locality, AMNH 88150, 88152; Locality 7, AMNH 88158; Locality 18, AMNH 57256, unnamed locality,

Table 5. Comparison of tooth length of *Plesiadapis insignis* with that of other species of *Plesiadapis*.
Figures in parenthesis are recalculated from photographs in Russell (1967a) as proportions of his total measured length of the lower tooth row.

		insignis	*praecursor*	*anceps*	*walbeckensis*
P_3	L	1.9 (2.0)	2.15	2.17	2.0
P_4	L	2.1 (2.1)	2.1	2.30	2.09
M_1	L	2.4 (2.5)	2.65	2.87	2.85
M_2	L	2.9 (2.7)	2.97	2.97	3.18
M_3	L	4.5 (4.5)	3.8	4.37	4.72

AMNH 57356. In addition, Gazin (1971, p. 14) mentions a locality "on Shotgun Butte proper" that includes *Plesiadapis* cf. *cookei*, but I have not seen these specimens.

European Species

Plesiadapis insignis (Piton)

(Plates 11; 12)

Sciurus feigouxi (in part), Launay, 1908, p. 393, fig. 1-2.
Sciuroides sp., Piton, 1940, p. 289, pl. 25: 3.
Menatotherium insigne Piton, 1940, p. 290; pl. 23; pl. 25: 25; pl. 26: 1-3. Simpson, 1948a, p. 165, fig. 1.
Plesiadapis insignis, Russell, 1967a, p. 488, pl. 1-3.

Type.– Unnumbered specimen in Muséum National d'Histoire Naturelle, Paris; from the Menat basin, Puy-de-Dôme, in central France (Auvergne). The counterpart of this same specimen is preserved in the Naturhistorishes Museum in Basel.

Diagnosis.– *Plesiadapis insignis* differs from all known European *Plesiadapis* in being significantly smaller and in having a relatively larger P_2. It cannot be adequately compared with the early North American forms, but *Ples. insignis* appears possibly to represent a slightly smaller species than *Ples. praecursor* and *Ples. anceps*. For this reason the name *Ples. insignis* is restricted at present to the specimens from Menat.

Description.– *Plesiadapis insignis* is one of three species of the genus for which the cranial and postcranial anatomy are known. The dentition, the element of greatest systematic significance, will be described first. This is followed by notes on the postcranial anatomy. The cranial anatomy will be discussed in a later chapter.

The dentition is best studied from Russell's (1967a) reversed stereophotographs. The upper dental formula of *Ples. insignis* is 2.1.3.3, as in all early plesiadapids. The lower dental formula in the only known skull is 1.0.3.3, which is identical to that in the early North American species of *Plesiadapis*.

Russell (1967a) has given a detailed description of the teeth of *Ples. insignis*. Only those aspects of particular importance are mentioned here. The upper central incisors of *Ples. insignis* have large anterocones, laterocones, and posterocones, and the mediocones appear to have been moderately large as well, but this cannot be stated with certainty. I^1 appears to be a relatively narrow tooth, compared to *Ples. walbeckensis* and later species of *Plesiadapis*. I^2 is a relatively large, single-cusped tooth separated by a diastema from both I^1 and the upper canine. The upper canine is similar in morphology to I^2, but it is considerably smaller. The remainder of the upper cheek teeth are typical of those found in the better known species *Ples. rex* or *Ples. walbeckensis*.

Small metacones are present on P^{3-4} (Russell, 1967a). Russell mentions a "mésostyle bien individualizé" on M^3. It is not clear whether this is a true mesostyle, formed at the juncture of the paracone and metacone blades of the centrocrista, or simply the small cuspule variably developed on the cingulum at this position in all early plesiadapids. Considering the primitive nature of the lower dentition, the latter appears to be more likely. M^{1-2} are too poorly preserved to permit a determination of whether or not they had mesostyles.

The lower incisors have a distinct margoconid, and a margocristid was undoubtedly developed as well, but the relative width of the lower incisors cannot be determined. The incisors appear to be relatively deep. A short diastema appears to separate I_1 from P_2, but this may be due to breakage, as Russell has noted. Considering that all the other teeth in the left half of the skull are in place and clearly visible, it is unlikely that either I_2 or a lower canine was present, or they would be visible too. As Russell notes, and as I have noted above in discussing the generic placement of this species, P_2 is much larger in *Ples. insignis* than it is in most species of *Plesiadapis*. Only some of the specimens of *Ples. praecursor* and *Ples. anceps*, judging from alveoli, could have had a tooth of comparable size.

The remaining cheek teeth resemble those of most early plesiadapids. M_3 has a distinct hypoconulid lobe, but it is unfortunately not possible to observe any other characteristics of this heel.

Russell (1967a, p. 487) lists measurements of the length of each of the lower cheek teeth P_3-M_3 of *Ples. insignis*. Because of the fragile nature of the original specimen, I did not attempt to measure the teeth directly, but instead have recalculated the lengths of the teeth of *Ples. insignis* from Russell's photographs as proportions of the sum of his measurements. Russell's measurements, the recalculated measurements, and the mean values of the corresponding measurements of the teeth of *Ples. praecursor, Ples. anceps*, and *Ples. walbeckensis* are listed in Table 5 for comparison. *Plesiadapis insignis* is clearly closest to *Ples. praecursor* in size.

Dimensions of the postcranial skeleton (where they can be determined) are listed in Table 6. Of particular interest, also, are the claws and bushy tail preserved in this species (see Plate 12).

Discussion.– The type specimen of *Plesiadapis insignis* is, as Simpson (1948a) noted, one of the most complete fossil mammals ever discovered. Both the type and a second specimen lacking the skull (actually the first of the two to be discovered and described) were long thought to be squirrels and identified as "*Scuirus feignouxi*," a Miocene squirrel well known in France from St. Gérand-le-Puy. Since the fossil plants and insects of the Menat deposit seemed to indicate an Eocene rather than Miocene age for the deposit, Piton (1940) noted that the headless specimen could as well represent the Eocene squirrel *Sciuroides*. The specimen with a skull, however, retained an upper canine and could, therefore, not be a rodent. Piton interpreted it as a tillodont (!) and gave no further thought to the possible relationships of his "rodent" and "tillodont."

The vertebrate fauna of Menat includes fish, amphibians, reptiles, and four mammal specimens. One of these is a carnivore the size of a small fox (Piton, 1940, p. 285). Another is a remarkably complete leptictid insectivore, described by Guth (1962). Piton's tillodont has been shown by Russell (1967a) to be a species of *Plesiadapis, Ples. insignis*. The remaining headless specimen is almost certainly a second specimen of *Ples. insignis*.

Piton's "*Sciuroides*" is slightly larger but otherwise identical to the type specimen of *Ples. insignis* in every comparable character. They share a similar trunk length, femur length, and tibia length. Both have an ulna, radius, fibula, and tibia of similar relative diameters, and both had a bushy tail. It seems very unlikely that two animals so similar in morphology and found in the same small deposit should represent different species. The second specimen is particularly important because it adds a number of important details to our knowledge of the postcranial anatomy of one of the earliest species of *Plesiadapis*. Certain implications of the limb proportions of *Plesiadapis insignis* are discussed in Chapter 8.

Typodigm.– The type specimen includes a main slab with the skull in the Muséum National d'Histoire Naturelle in Paris and its counterpart (lacking the skull, but with the postcranial anatomy better preserved) in the Naturhistorisches Museum in Basel. The main slab and counterpart of the referred specimen are both in the Paris museum.

Table 6. Dimensions of the postcranial skeleton of *Plesiadapis insignis*. All measurements from photographs, in millimeters.

	Type specimen		Referred specimen	
	Length	Min. width	Length	Min. width
Skull	50	–	–	–
Trunk	130	–	140	–
Humerus	33	5	–	6
Radius	–	3	31	4
Ulna	–	3	36	4
Hand length	–	–	32	–
Femur	45	6	49	6
Tibia	39	4	46	5
Fibula	39	2	46	3

Plesiadapis walbeckensis Russell

(Plates 3 E; 4 C)

Plesiadapis tricuspidens (in part), Weigelt, 1939, p. 526.
Plesiadapis walbeckensis Russell, 1964, p. 115, pl. 7: 6-7.

Type.– GH Wa287, a right mandible with I_1, P_4-M_3 intact and alveoli for P_3; from a Paleocene fissure-filling in middle Triassic limestone (Muschelkalk) near the town of Walbeck, NW of Magdeburg in Germany.

Diagnosis.– *Plesiadapis walbeckensis* differs from *Ples. insignis* in being significantly larger, and from the other European species of *Plesiadapis* in being smaller (see Tables 5, A14-A16 for comparative measurements). It is closest to the North American *Ples. anceps* and *Ples. rex* in size and morphology but differs from both in sometimes lacking P_2. *Plesiadapis walbeckensis* further differs from *Ples. anceps* in having a wider incisor and more crenulated enamel on the occlusal surface of the hypoconulid of M_3. *Plesiadapis walbeckensis* differs from *Ples. rex* in lacking a centroconule on the upper incisors and in generally having a more rounded, unfissured heel on M_3.

Description.– Several maxillae of *Plesiadapis walbeckensis* retain alveoli for the upper canine and P^2, and the premaxilla Wa297 preserves a relatively large alveolus for I^2. Thus the upper dental formula of this species is 2.1.3.3. The presence or absence of P_2 can be determined in 10 mandibles; of these five retain alveoli for P_2, and five do not. Thus the lower dental formula is 1.0.2-3.3, with P_2 being retained 50% of the time.

The upper incisors of *Ples. walbeckensis* have strong anterocones, laterocones, posterocones, and mediocones, but a small centroconule is only very rarely present. As in other species of *Plesiadapis*, I^2 is a relatively large tooth compared to the upper canine, and it is separated by a short diastema from both I^1 and the upper canine. Russell (1964, p. 116) noted two accessory denticles, one a very small cuspule anterior to the main cusp and the other a more distinct cuspule posterior to it, on the crown of I^2. The crowns of the upper canine and P^2 are not preserved. These two teeth were not separated by a diastema. The canine evidently had a single small root, while one or two alveoli are variably present for P^2. A distinct paraconule is present on $P^{3\text{-}4}$, but the metacone is usually only weakly developed on P^4, and it is absent from P^3. A distinct mesostyle is present on M^1 in one specimen and weakly developed on another, but it is usually not present on M^1. $M^{2\text{-}3}$ usually do have a distinct mesostyle, although it is weakly developed or absent in some specimens.

The lower incisors are similar to those of *Ples. rex* in appearance, being relatively wide and having a distinct margoconid and margocristid. The crown of P_2 is not preserved in any specimen. The alveolus for P_2, when present, is usually about .5 mm in diameter, but in one specimen (unnumbered) it is much smaller. $P_{3\text{-}4}$ are similar to those teeth in *Ples. rex* in lacking any but the strong protoconid cusp and in having a short, unbasined heel. $M_{1\text{-}2}$ also resemble those teeth in *Ples. rex* very closely in having squared, cusped entoconids and in lacking steeply sloping outer walls. M_3 usually has a broad, rounded heel, which is only weakly fissured. One specimen (Wa392) has a squared, fissured heel similar to that typical of *Ples. rex*.

Measurements of the dentition of *Plesiadapis walbeckensis* are summarized in Table A-14. The data given for the maxillary dentition is from Russell (1964, p. 296).

Discussion.– Russell (1964, p. 121) tentatively suggested that *Ples. walbeckensis* might be close to the ancestry of *Chiromyoides*; however, the discovery of a primitive species of *Chiromyoides* associated with *Ples. rex* in North America (described below) together with the probability that an unnumbered plesiadapid M_3 from Walbeck in the BMNH belongs to *Chiromyoides* would seem to rule this out. *Plesiadapis anceps* is a more likely ancestor of *Chiromyoides.*

Typodigm.– There are some 30 mandibles, 15 maxillae, and several hundred isolated teeth of *Ples. walbeckensis* known, all from the Walbeck fissure-filling, and virtually all in the collections of the Geiseltal Museum in Halle. The most important specimens are GH Wa282, Wa286-290, Wa297, and Wa392.

Plesiadapis remensis Lemoine

(Plate 5 A, B, I)

Plesiadapis remensis Lemoine, 1887, p. 192; 1891, p. 280, pl. 10: 58, 64. Schlosser, 1921, p. 104, pl. 15: 2, 9, 13.

Plesiadapis tricuspidens (in part), Teilhard, 1922, p. 21, pl. 1: 5, 7, 10. Russell, 1964, p. 84, pl. 7: 1a, 2b. Russell, Louis, and Poirier, 1966, p. 854.

Type.– MNHM Cl no. 13, a right mandible with $P_{3\text{-}4}$, $M_{1\text{-}3}$ ($P_{3\text{-}4}$ and M_1 have the buccal side of the teeth spalled off); from one of Lemoine's quarries in the Conglomérat de Cernay, near Reims in France.

Diagnosis.– Differs from *Ples. insignis* and *Ples. walbeckensis* in being larger and generally lacking P_2. Differs from *Ples. tricuspidens* (see Fig. 9) and *Ples. russelli* in being smaller (see Tables 5, 7, 8, and A14-A16 for comparative measurements). *Plesiadapis remensis* is distinguished from its closely related contemporary *Ples. tricuspidens* in having M_1 3.8 mm or less in length and 3.4 mm or less in width, in having a distinct margoconid on I_1, and possibly in sometimes retaining P_2. Differs from *Ples. simonsi* in being smaller, and from *Ples. churchilli* in consistently having curved entoconid crests on $M_{1\text{-}2}$, in having more crenulated enamel on occlusal surfaces, and in generally lacking P_2.

Description.– *Plesiadapis remensis* is known only from jaw fragments and isolated teeth, thus an independent determination of the upper dental formula of this species is impossible. The composite figure published by Lemoine (1889, p. 271), probably based on specimens of *Ples. remensis*, shows both I^2 and the upper canine in approximately their proper position. No specimens definitely showing this remain in the Lemoine collection (now in MNHN), so the presence of an upper canine cannot be confirmed. As I^2 is present in all other plesiadapid species, we can infer that it was retained in *Ples. remensis*, though no specimen definitely shows this. Several mandibles preserve the diastema between I_1 and P_3 and show that P_2 was not retained. One specimen (in the Pellouin collection from Lentille) does, however, have a very small alveolus, apparently for a short bristle-like P_2. For almost all specimens the dental formula of *Ples. remensis* can be written as $\frac{2}{1}\,\frac{?}{0}\,\frac{3}{2}\,\frac{3}{3}$, although a P_2 appears to have been retained in a very small proportion of the mandibles.

The upper central incisor of *Ples. remensis* differs from its counterpart in *Ples. tricuspidens* only in being smaller. All four major cusps are well developed. The centroconule is expanded to form a crest connecting the laterocone and mediocone. P^3 generally lacks both a paraconule and metacone, but these cusps may be weakly developed. P^4 generally has a distinct paraconule, but usually the metacone is absent or weakly developed. Strong mesostyles are consistently present on M^{1-3}, and a hypocone is sometimes present (but rarely) on the postprotocingulum of M^1 or M^2.

The lower incisor has a distinct margoconid and margocristid. A short diastema separates I_1 from the following cheek teeth. P_{3-4} have high, pointed protoconids, no accessory paraconid or metaconid, and a short unbasined heel. A weak hypoconid and cristid obliqua are sometimes present on P_4. M_{1-2} have curved, crested entoconids and are slightly narrower than the molars of most earlier species. This narrowing of the molars has resulted in slightly more vertical outer walls on the lower molars compared to those of earlier species of *Plesiadapis*. M_3 has a broad, squared, fissured heel with highly crenulated enamel in the talonid basin.

Measurements of the teeth of mandibles and maxillae from Cernay that undoubtedly represent *Ples. remensis* are summarized in Table A-15. Measurements of the type specimen of *Ples. remensis* are listed in Table 7 for comparison.

Discussion.— Considerable uncertainty regarding the validity of *Plesiadapis remensis* has existed since its description by Lemoine. This uncertainty was due to several factors: (1) Lemoine's figure of the type specimen bears little resemblance to any *Plesiadapis*, (2) the type specimen was unrecognized — no actual specimen appeared to match Lemoine's published figure, (3) until recently there was only a relatively small number of specimens known from Cernay, (4) the available specimens were never analyzed adequately (i.e., using teeth of low variability, bivariate plots, logarithmic axes, etc.), and (5) *Plesiadapis remensis* does appear to have been closely related to *Ples. tricuspidens*.

The type specimens of both *Plesiadapis tricuspidens* (figured by Gervais) and *Ples. remensis* were, until recently, thought to be lost. While measuring all of the Cernay specimens in the Lemoine collection of the MNHN, it was recognized by chance that one specimen (Crl-16) had the mandibular ramus broken in a distinctive and familiar way, exposing the mandibular canal. This left mandibular fragment with M_3 proved to the the type specimen of *Ples. tricuspidens*, reversed by the lithographic process of Gervais' time to appear in his figure as a right mandible. Because it was possible that a similar situation occurred with *Ples. remensis*, the collection was carefully reexamined. Each specimen was compared with Lemoine's figure (1891, fig. 64); the specimen Crl-13 proved without question to be the type specimen of *Ples. remensis*. M_{2-3} of this specimen are little damaged and undoubtedly belong to *Plesiadapis*. The other cheek teeth, however, have nearly the whole buccal half of each spalled away, resulting in the peculiar outline seen in Lemoine's figure. Further, there seems little question that Crl-1 is the specimen figured by Lemoine (1891, fig. 65) as the type specimen of *Ples. gervaisii*. It is the only left mandible in Lemoine's collection preserving P_4 through M_3.

Table 7. Measurements of the type specimen of *Plesiadapis remensis* (MNHN Crl-13). All measurements in millimeters.

	Length	Width
P_3	2.6	–
P_4	2.7	–
M_1	3.5	–
M_2	4.0	3.6
M_3	5.9	3.7

Fortunately, a large number of new specimens, mostly isolated teeth, have been collected by Russell, Louis, and Poirier from Lemoine's quarries in the Conglomérat de Cernay. When all of the specimens were analysed (see Gingerich, 1974e, and Chapter 2 of this report), it was clear that two species of *Plesiadapis* (*Ples. tricuspidens* and *Ples. remensis*) are represented at Cernay.

Russell, Louis, and Poirier (1966) analysed a rather large sample of *Plesiadapis* teeth from the Lentille de Berru locality (herein referred to simply as Lentille) and ascribed them all to *Ples. tricuspidens*. A histogram of the log of length multiplied by width of M_1 yields a distribution comparing closely with that from Cernay (see Fig. 9), indicating that *Ples. remensis* is present at Lentille, and that Russell, Louis, and Poirier are correct in estimating that the Lentille locality correlates with Cernay and underlies the main Berru level. The Lentille locality is possibly even slightly earlier than the Cernay locality.

Typodigm.— The following specimens from the type locality (Cernay) undoubtedly represent *Ples. remensis*: MNHN Crl-3, 7-10, 13 (type), 24, 77, 87, 1588, Cr-4267, 4268, and some isolated teeth in the collections of MNHN, Louis, Poirier.

In addition, small collections are known from Lentille (two mandibles and isolated teeth in collection of Louis, Pellouin, and Poirier), and from Berru (maxilla MNHN Cr-4272 only).

Plesiadapis aff. remensis

Plesiadapis sp. ind., Teilhard, 1927, p. 14, fig. 93.
Primate *incertae sedis*, Cooper, 1932, p. 465, pl. 12: 3.
Plesiadapis cf. *tricuspidens*, Russell, Louis, and Savage, 1967, p. 34, fig. 9.

Discussion.— The lower incisor described by Teilhard

(1927) from Erquelinnes has a distinct margoconid and margocristid and resembles closely those from Cernay and Lentille. It has a width of 2.6 mm and height of 4.4 mm, which is slightly narrower than most from the Cernay level.

Mr. Jeremy Hooker of the British Museum (Natural History) recently correctly determined that a tooth from Kyson, described by Cooper (1932) as an indeterminate primate, properly belongs to *Plesiadapis*.

The teeth described by Russell, Louis, and Savage (1967) from Pourcy as *Ples.* cf. *tricuspidens* are significantly smaller than the average for specimens of *Ples. remensis* from Cernay but are undoubtedly related to the latter species.

This small group of *Plesiadapis* teeth from Sparnacian localities in Europe undoubtedly represents an early Eocene descendant of the late Paleocene species *Ples. remensis*. The teeth are significantly smaller in almost every dimension than those of *Ples. remensis* from Cernay and when more complete material is discovered will almost certainly warrant recognition as a separate species. Until more complete specimens are discovered, the designation *Plesiadapis* aff. *remensis* is appropriate, as it shows that the species represented is probably distinct from *Ples. remensis* but closely related to it.

Plesiadapis tricuspidens Gervais

(Plates 5 C, D, G, J; 6 A, J; 8; 9)

Plesiadapis tricuspidens Gervais, 1877, p. 76, fig. 1-2. Lemoine, 1878, p. 9, pl. 2: 4, 5, 13. Russell, 1959, p. 312, pl. 18.

Plesiadapis gervaisii Lemoine, 1887, p. 192. Lemoine, 1891, p. 280, pl. 8: 65. Stehlin, 1916, fig. 355a. Schlosser, 1921, p. 105, pl. 15: 3,4,7, 12.

Plesiadapis rhemensis Rütimeyer, 1891, p. 124, pl. 8: 22.

Plesiadapis remensis, Stehlin, 1916, fig. 355b, 356a-d, 357, 358.

Plesiadapis trouessarti (in part), Schlosser, 1921, p. 104, pl. 15: 1, 6.

Plesiadapis tricuspidens (in part), Teilhard, 1922, p. 21, pl. 1: 6, 17. Russell, 1964, p. 84, pl. 7: 1b-c, 2a. Russell, Louis, and Poirier, 1966, p. 854.

Type.– MNHN Crl-16, a left mandibular fragment with M_3; from the Calcaires de Rilly, near Reims in France.

Diagnosis.– Differs from *Plesiadapis remensis* in being larger, with M_1 having a length of 3.9 mm or greater and a width of 3.5 mm or greater (see Fig. 9), and in generally lacking a margoconid on I_1. Differs from *Ples. insignis* and *Ples. walbeckensis* in being larger. Differs from the North American *Ples. simonsi* in generally having a deeper mandible and relatively narrower cheek teeth. Differs from *Ples. russelli* and *Ples. cookei* in being smaller, having a distinct centroconule on I^1, and generally having a distinct paraconule on P^4. (Comparative measurements are given in Tables 5, 7, 8, A13-A16, and in the discussion of *Ples. russelli* below).

Description.– *Plesiadapis tricuspidens* is, as a result of recent collecting by Russell, Louis, and others, the best known species of *Plesiadapis* in terms of its cranial anatomy. Several specimens consistently show that I^2 was retained, but the upper canine was lost in *Ples. tricuspidens*, giving an upper dental formula of 2.0.3.3. The lower formula is known from at least 40 specimens to be consistently 1.0.2.3.

The upper central incisor of *Ples. tricuspidens* has a large anterocone, laterocone, and mediocone, with a crestlike centroconule connecting the mediocone and laterocone. I^2 is a relatively large tooth with a simple pointed crown. The upper canine was not retained. P^2 in the Pellouin skull has two roots and an anteroposteriorly elongated crown measuring 2.5 mm long and 2.0 mm wide. The crown has a single cusp with short, distinct crests running anteriorly and posteriorly from it. P^3 in some specimens has a distinct paraconule and weak metacone, but in others both cusps are completely lacking. P^4 almost always has a well-developed paraconule and weak metacone (the paraconule is always of the type characteristic of *Plesiadapis*, not the molariform paraconule characteristic of *Platychoerops*). The upper molars consistently have well-developed mesostyles, and a distinct hypocone is sometimes (rarely) present on the postprotocingulum. M^3, particularly, has crenulated enamel, with the crenulations around the protocone often forming a weak lingual cingulum.

The lower incisor of *Plesiadapis tricuspidens* is distinctive in lacking a margoconid, though the margocristid is well developed. A relatively long diastema separates I_1 and P_3. $P_{3\text{-}4}$ have a slightly inflated, wedge-shaped protoconid, with a short heel. A distinct cristid obliqua is present on the back of the protoconid and on the heel in some specimens, most consistently developed on P_4. P_4 rarely has a distinct metaconid, but this cusp is very well developed in Louis Cm 336. $M_{1\text{-}2}$ have curved, crested entoconids, and M_3 has a broad, somewhat rounded, fissured hypoconulid lobe with a distinct posterior cingulid. An identical heel, including the posterior cingulid, is present on one specimen of *Ples. cookei* (AMNH 86787), but most *Ples. cookei* have an even more rounded heel and lack the posterior cingulid.

Measurements of the largest sample of *Ples. tricuspidens*, that from Berru, are summarized in Table A-16. Measurements of the type specimens of *Ples. tricuspidens* (Crl-16) and *Ples. gervaisii* (Crl-1) are listed here in Table 8 for comparison.

Discussion.– Much of the early confusion regarding

Ples. tricuspidens was caused by Lemoine's (1887) elevation of the species *tricuspidens* to subgeneric rank and its replacement at the species level by *Ples. gervaisii* and *Ples. remensis*, which were inadequately illustrated and described. The type specimens of *Ples. tricuspidens* and *Ples. gervaisii* are of nearly the same size, and they undoubtedly both represent the larger species of *Plesiadapis* at Cernay (see Chapter 2, and discussion above under *Ples. remensis*), with *Ples. tricuspidens* having priority.

Russell (1964, p. 85) states that *Ples. tricuspidens* is specialized in a direction different from that leading to *Platychoerops daubrei* and could not be ancestral to it. With more complete specimens of *Ples. daubrei* now available and *Ples. tricuspidens* more adequately diagnosed, it seems, on the contrary, almost certain that *Ples. tricuspidens* is part of the evolving lineage that subsequently led to *Plat. daubrei*. This will be discussed in more detail in a later chapter.

Finally, the peculiar lower incisors with a distinct margoconid and the tricuspid upper incisors from Berru figured by Russell (1964, pl. 3: 7) are very probably, as Schlosser (1921, Pl. 15: 8) noted, deciduous incisors of *Ples. tricuspidens*. Two similar lower incisors are present in the Mason Pocket sample of *Nannodectes gidleyi*, a sample including the deciduous cheek teeth of several specimens.

Hypodigm.– The M_3 (MNHN Crl-16) and I^1 figured by Gervais are the only specimens known from the type locality. The sample of *Ples. tricuspidens* includes the following specimens from the locality of Cernay: MNHN Crl-1, 15, and numerous jaw fragments and isolated teeth in the MNHN, Louis, Poirier, NHB, and UCMP collections. From Lentille: numerous isolated teeth in the Louis, Pellouin, and Poirier collections. From Berru: two nearly complete skulls, one in the MNHN (Cr-125) collection and one in the Pellouin collection; a partial skull, YPM 24618; and numerous mandibles, maxillae, and isolated teeth in the collections of MNHN, Louis, Pellouin, Poirier, NHB, and UCMP.

Plesiadapis russelli new species

(Plate 6 D, E)

"Renard" and "Civette?," Orbigny, 1836, p. 287.
Plesiadapis sp., Stehlin, 1916, p. 1489.
Plesiadapis inc. sp., Teilhard, 1922, p. 51, fig. 25.
Plesiadapis aff. *daubrei*, Teilhard, 1922, p. 80.
Platychoerops daubrei (in part), Russell, Louis, and Savage, 1967, p. 33.

Type.– Unnumbered upper right central incisor in the Laboratoire de Géologie, Université de Marseille; from the Conglomérat de Meudon (at the base of the Argile Plastique) at Meudon in France.

Table 8. Measurements of the type specimens of *Plesiadapis tricuspidens* and *Plesiadapis "gervaisii."* All measurements in millimeters.

		Ples. tricuspidens Crl-16 (type)	*Ples. "gervaisii"* Crl-1 (type)
P_4	L	–	3.3
	W	–	3.2
M_1	L	–	4.2
	W	–	3.7
M_2	L	–	4.6
	W	–	4.1
M_3	L	7.0	6.8
	W	4.2	4.1
Depth of Mandible		–	14.3

Diagnosis.– *Plesiadapis russelli* is intermediate between *Ples. tricuspidens* and *Platychoerops daubrei* in morphology. It differs from *Ples. tricuspidens* in being larger, in lacking *Plesiadapis*-type paraconules on $P^{3\text{-}4}$, and in lacking the centroconule crest and having a much smaller laterocone on I^1. *Plesiadapis russelli* differs from *Plat. daubrei* in retaining a small laterocone on I^1 and in having less molarized premolars, with the molar-type paraconule only incipiently developed on P^4. It differs from *Ples. cookei* in having a more reduced laterocone on I^1, in having an incipient paraconule on P^4, and in consistently having a posterocingulid on M_3.

Etymology.– Named for Dr. D.E. Russell of the Institut de Paléontologie in Paris, in recognition of his important contributions to our knowledge of the Plesiadapidae and in appreciation of his generous assistance to this study.

Description.– *Plesiadapis russelli* is known at present from only eight isolated teeth, but it is almost certain that the dental formula of this species is the same as that of the earlier *Ples. tricuspidens* and the later *Plat. daubrei*, which is $\frac{2}{1}\ \frac{0}{0}\ \frac{3}{2}\ \frac{3}{3}$.

Two upper central incisors are known, one with all apical cusps worn off. The other (the type specimen) has the anterocone partly broken off, but a small laterocone is present, no trace of the centroconule is retained, and it appears that a small mediocone was also present. A small interstitial wear facet is present medial to the position of the mediocone in the type specimen. Both upper incisors retain large functional posterocones. These incisors appear to differ from I^1 in *Ples. cookei* (PU 18118) only in having a much more reduced laterocone. The anteroposterior length and width at the base of the crown in the type specimen are 7.0 mm and 3.9 mm, respectively, and in the other upper incisor, 7.0 and 4.3 mm, respectively. A possible left I^2 has a crown measuring 3.6 mm by 2.6 mm. P^3 lacks any trace of a paraconule, has an incipient metacone, and measures 3.9 mm long and 5.4 mm wide. P^4 lacks any trace of the characteristic *Plesiadapis*-type paraconule, but it does have an incipient molar-type paraconule on the preprotocrista. The metacone is broken, but it appears to have been distinct and slightly separated from the paracone. No upper molars are yet known of this species. P^4 measures 4.0 mm in length and 6.3 mm in width.

Only one P_3 and two specimens of M_3 are known of the lower dentition. P_3 resembles this tooth in some *Ples. tricuspidens* and *Ples. cookei*. The main protoconid cusp lacks any accessory cusps, and the heel has the hypoconid and entoconid only very weakly differentiated. A small but distinct cristid obliqua is present. P_3 measures 4.0 mm in length, 3.6 mm in width. M_3 of *Ples. russelli* resembles that tooth in *Ples. tricuspidens*, but it more closely resembles M_3 in *Plat. daubrei* in having the enamel crenulations and fissuring on the talonid very strongly developed. A distinct posterior cingulid is present on the back of the hypoconulid lobe of both specimens. The Meudon specimens of M_3 measure in length and width: 9.0 mm and 4.7 mm, respectively, in one and 9.2 mm and 5.3 mm, respectively, in the other.

Discussion.— Several of the specimens of *Plesiadapis russelli* were briefly described by d'Orbigny in 1836, making them only the second fossil primate species (after *Adapis parisiensis* Cuvier) to be discovered and reported, although d'Orbigny thought the teeth belonged to a civet and/or a fox. It is not surprising, at that early date, that the significance of the specimens was not realized, but it is most unfortunate because Meudon is now an urban region of Paris and further collecting there is impossible. Lemoine seems to have been unaware of the Meudon specimens, perhaps because the distinctive incisors were in Marseille. Stehlin (1916) first noted that the Meudon specimens included tricuspid upper incisors of *Plesiadapis*. Taking a strictly typological approach, Teilhard (1922) suggested that perhaps two species were present at Meudon, one being of *Plesiadapis* (represented only by incisors), and the other of *Platychoerops* (represented only by cheek teeth). Russell, Louis, and Savage (1967) also failed to appreciate the significance of *Plesiadapis* incisors associated with "*Platychoerops*" molars at Meudon.

In Gervais' (1877, p. 76) original figures of the upper incisor of *Ples. tricuspidens*, three cusps are illustrated, the anterocone, laterocone, and posterocone. It is certainly to these three cusps that the "tricuspid" description applies, and Teilhard and Stehlin both used tricuspid in this sense in describing the Meudon incisors. One of the most significant differences between *Plesiadapis* and *Platychoerops* is the loss of the laterocone (and later the posterocone) in the latter genus. Since the incisor from Meudon has the three cusps characteristic of *Plesiadapis*, the *P. russelli* specimens have been placed in *Plesiadapis* rather then *Platychoerops* as Russell, Louis, and Savage (1967) advocated. This point is of less import, however, than the realization that *P. russelli*, whether included in *Plesiadapis* or in *Platychoerops*, links *Platychoerops daubrei* directly to the ancestral species *Ples. tricuspidens*. Moreover, in closely resembling the contemporaneous *Ples. cookei* from North America, the European *Ples. russelli* further demonstrates the very close relationship of the faunas of the two continents at the end of the Paleocene and beginning of the Eocene.

Typodigm.— The specimens of *Ples. russelli* are: LGM, unnumbered right upper central incisor (type), left I^1, left P^3, left M_3, right M_3; and MNHN, unnumbered left I^2, right P^4, and right P_3. This species is presently known only from the type locality.

CHIROMYOIDES Stehlin

Chiromyoides Stehlin, 1916, p. 1489. Type: *Chiromyoides campanicus* Stehlin.
Plesiadapis (in part), Teilhard, 1922, p. 21. Simpson, 1937b, pl. 9: 16. Schiebout, 1974, p. 17.
Nothodectes (in part), Gidley, 1923, pl. 3: 16.

Included species.— *Chiromyoides minor* Gingerich; *C. caesor* Gingerich; *C. potior* Gingerich; *C. major* Gingerich; *C. campanicus* Stehlin.

Known distribution.— Late Paleocene and early Eocene (Tiffanian and Clarkforkian) of western North America, and late Paleocene (Thanetian) of western Europe.

Diagnosis.— Differs from *Pronothodectes* in not retaining I_2 or the lower canine. Differs from *Nannodectes* in having broader cheek teeth. Differs from *Platychoerops* in being smaller. Differs from *Plesiadapis* and the other plesiadapid genera listed above in having extraordinarily robust central incisors and a very deep mandible, with relatively small but broad cheek teeth.

North American Species

Chiromyoides minor Gingerich

(Plate 7 A, F)

Plesiadapis gidleyi (in part), Schiebout, 1974, p. 17.
Chiromyoides minor Gingerich, 1975b, p. 142, pl. 1:5,9.

Type.— USNM 208976, a right upper central incisor; from the Chappo Member of the Wasatch Formation at the Chappo-17 locality (Sec. 17, T 26 N, R 113 W, Lincoln Co.), in the La Barge area of Wyoming.

Diagnosis.— *Chiromyoides minor* differs from the other species of *Chiromyoides* in being significantly smaller. The anteroposterior and transverse diameters at the base of the crown of I^1 are 5.6 and 2.7 mm, respectively, in the type specimen of *C. minor*, compared to 6.0 and 3.2 mm in *C. caesor. Chiromyoides minor* differs from *C. potior* and *C. major* in having a relatively narrower crown: the transverse diameter/anteroposterior diameter at the base of the crown in *C. minor* is .48, compared with .60 and .65 in *C. potior* and *C. major*, respectively. *Chiromyoides minor* differs from *C. campanicus* in lacking medial expansion of the posterocone to form a crushing platform.

Description.– The type specimen is a right I^1, with a distinct anterocone, laterocone, mediocone, and posterocone. It has no trace of a centroconule. Much of the cusp of the laterocone is broken, but all three apical cusps appear to be broader mediolaterally than in *Plesiadapis*. The posterocone is narrow and sharp, with a distinct posterocrista. The crown measures 5.6 mm in anteroposterior diameter at the base, 2.7 mm in transverse diameter at the base, and 3.3 mm in crown width measured half way between the posterocone and laterocone. A right I_1 (USNM 208977) from the type locality has a distinct margoconid and measures 5.1 mm in height at the base of the crown and 2.5 mm in crown width.

In addition, an edentulous mandible from Ray's Bonebed in the Black Peaks area of Texas, described by Schiebout (1974, p. 17-18), almost certainly represents *C. minor*. The ramus of this specimen (TMM 40537-37) is nearly complete, but unfortunately the crowns of all of the teeth are missing. The remaining root of I_1 measures approximately 5.0 mm by 2.7 mm, which is slightly smaller than the comparable measurements taken on the root of the lower incisor of *C. minor* from Chappo-17. The depth of the mandible below P_4 is 9.6 mm and below M_2 it is 9.0 mm, indicating that the deepening of the mandible characteristic of *Chiromyoides* was fully developed in this early species. M_1 length is estimated from the preserved roots to have been 2.4 mm. The bone between I_1 and P_3 is preserved intact, showing that in this species, the earliest yet known of *Chiromyoides*, P_2 was not retained.

An unnumbered, isolated lower third molar from Walbeck, in the fossil primate collections of the BMNH, is the right size (length, 4.1 mm; width, 2.3 mm) and morphology to represent this species, but in the absence of more complete material, this identification cannot be stated with certainty.

Typodigm.– Two specimens of *C. minor* are known from the type locality Chappo-17: USNM 208976 (type), and 108977.

A mandible from Ray's Bonebed in the Black Peaks area, TMM 40537-37, and an isolated M_3 from Walbeck (Germany) in the BMNH appear possibly to represent *C. minor*.

Chiromyoides caesor Gingerich

(Plate 7 B, G)

Chiromyoides caesor Gingerich, 1973a, p. 517, fig. 2.

Type.– PU 21575, a left upper central incisor; from the Croc Tooth Quarry (Sec. 5, T 54 N, R 95 W, Big Horn Co.), in the Big Horn Basin, Wyoming.

Diagnosis.– Differs from *C. minor* in being larger: the anteroposterior and transverse diameters at the base of the crown of I^1 are 6.0 and 3.2 mm, respectively, in the type specimen of *C. caesor*, compared to 5.6 and 2.7 mm in *C. minor. Chiromyoides caesor* differs from *C. potior* and *C. major* in having a relatively narrower crown: the transverse diameter/anteroposterior diameter at the base of the crown in *C. caesor* is .53, compared with .60 and .65 in *C. potior* and *C. major*, respectively. *Chiromyoides caesor* differs from *C. campanicus* in lacking medial expansion of the posterocone to form a crushing platform.

Description.– The type specimen is a complete left I^1 with all four major cusps well developed. The three apical cusps are mediolaterally broadened as in *C. minor*, and the mediocone is somewhat smaller than the laterocone (also seen in *C. minor*). The anterocone is worn flat, and the posterocrista is slightly worn in the type specimen. The base of the crown in PU 21575 measures 6.0 mm by 3.2 mm, and the crown is 3.4 mm wide (measured half way between the posterocone and laterocone).

A right I^1 (UCMP 36652) is slightly less well preserved than the type specimen, but it is otherwise virtually identical. The base of the crown of UCMP 36652 measures 6.1 mm by 3.2 mm, and the crown is 3.4 mm wide, measured as described above.

Hypodigm.– The type specimen, PU 21575, comes from the Croc Tooth Quarry in the Big Horn Basin. A second specimen, UCMP 36652, comes from the Mason Pocket locality in southern Colorado.

Chiromyoides potior Gingerich

(Plate 7 C, H)

Nothodectes gidleyi (in part), Gidley, 1923, pl. 3: 16.
Plesiadapis gidleyi (in part), Simpson, 1937b, pl. 9: 16.
Schiebout, 1974, p. 17, fig. 16d, i.
Chiromyoides caesor, Schiebout, 1974, p. 18, fig. 16a.
Chiromyoides potior Gingerich, 1975b, p. 143, pl. 1: 7, 11.

Type.– USNM 10639, a left upper central incisor; from Tiffany? beds, 5.5 mi E of Bayfield, Colorado.

Diagnosis.– Chiromyoides potior differs from *C. minor* and *C. caesor* in having an upper central incisor with a less elongated cross section anteroposteriorly, a relatively broader crown, and a smaller posterocone: in *C. potior* the transverse diameter/anteroposterior diameter at the base of the crown of I^1 is .60, compared with .48 and .53 in *C. minor* and *C. caesor*, respectively. *Chiromyoides potior* is similar to *C. major*, but it is significantly smaller and further differs in having the mediocone on I^1 approximately equal in size to the laterocone, not larger than the laterocone as it is in *C. major*. In *C. potior* the anteroposterior and transverse diameters at the base of the crown of I^1 are 5.3 and 3.2 mm, respectively, whereas the same measurements in *C. major* are 6.0 and 3.9 mm. *Chiromyoides potior* differs from *C. campanicus* in lacking medial expansion of the posterocone to form a crushing platform.

Description.– The type specimen of *C. potior* has the crown and most of the root preserved intact. The anterocone, laterocone, mediocone, and posterocone are all strongly developed and of approximately equal size. The mediocone of this species is distinctive in being the same size as the laterocone. There is no trace of a centroconule, in fact the mediocone and laterocone in this species are inflated to the extent that they contact each other, leaving no room for a centroconule. The posterocone of *C. potior* appears to be slightly smaller than that of *C. minor* and *C. caesor*. The anteroposterior and transverse diameters of the crown of the type specimen at its base are 5.3 mm and 3.2 mm respectively, and the crown measures 4.0 mm in width half way between the posterocone and laterocone.

Three isolated teeth belonging to this species have been collected in "Joe's Bonebed" in the Black Peaks area of Texas (Schiebout, 1974). One specimen (TMM 41365-826) is the broken crown of a right I^1 with cusps identical to those of the type specimen described above. Only the crown width half way between the posterocone and laterocone can be measured on this tooth – it measures 3.7 mm. An isolated P^4 (TMM 41365-327) has an inflated crown, with a distinct protocone, paracone, paraconule, and a small metacone and parastyle. The tooth has a very strong postprotocingulum, making the protocone essentially a strong crest. The enamel on this tooth is weakly crenulated. The tooth measures 2.2 mm long and 3.3 mm wide. The third tooth is an isolated M_2 (TMM 41365-191) measuring 2.6 mm long and 2.6 mm wide. It has a more inflated, rounded appearance than *C. campanicus* (or any other plesiadapid yet known) but otherwise resembles M_2 in that species.

The symphyseal region of a left mandible from the vicinity of the Big Horn Basin Schaff Quarry probably belongs to this species. It was described briefly in Gingerich (1973a, p. 518) and there provisionally assigned to *C. caesor*. On stratigraphic evidence it now appears more likely that this mandible belongs to *C. potior*. The fragment preserves the root of I_1 and the roots of P_3. The maximum and minimum diameters of I_1 are 5.6 mm and 3.2 mm, respectively. The diastema separating I_1 and P_3 is 3 mm long, compared with a diastema of 1.5 mm in the type specimen of *C. campanicus*. The anterior root of P_3 is 2.4 mm wide, compared with 1.7 mm in *C. campanicus*. P_3 of *C. potior* was significantly larger than that tooth in *C. campanicus*, and probably the remaining cheek teeth were larger as well. The preserved portion of the actual symphysis in this specimen of *C. potior* matches closely that of *C. campanicus* in form and size, although the latter is about 1 mm deeper (measured from the I_1-P_3 diastema).

Three additional incisors of *C. potior* are of significance. PU 17895 is the broken crown of an upper central incisor with all cusps intact from near the mouth of Little Sand Coulee in the Big Horn Basin. This specimen has a crown width of 3.5 mm measured in front of the posterocone. The second specimen is a lower central incisor from the Eagle Coal Mine at Bear Creek in Montana. This intact, unworn lower incisor is similar to those of *C. major* but smaller. Its total length is 21.0 mm, with an anteroposterior diameter at the base of the crown of 8.6 mm, a transverse diameter of 5.7 mm, and a crown width of 3.0 mm. The leading edge is relatively wide and sharp, with squared corners, as in *C. major*. The third specimen, UM 55126, is a lower incisor with the crown intact collected by J.A. Dorr from the Dell Creek locality in Wyoming.

Hypodigm.– The known specimens of *C. potior* include the type specimen from Bayfield: USNM 10639; three teeth from Joe's Bonebed in the Black Peaks area: TMM 41365-191, -327, and -826; a mandibular symphysis (PU 19125) from near the Schaff Quarry, an upper incisor (PU 17895) from the Little Sand Coulee area, and an upper incisor (PU 21590) from the Cleopatra Reservoir locality in the Big Horn Basin; a lower incisor (PU 18348) from Bear Creek; and a lower incisor (UM 55126) from Dell Creek.

Chiromyoides major Gingerich

(Plate 7 D, I, K)

Chiromyoides major Gingerich, 1975b, p. 143, pl. 1: 8, 12.

Type.– PU 21150, most of the crown of a left upper central incisor; from the Paint Creek locality (Sec. 11, T 55 N, R 103 W, Park Co.) in the Big Horn Basin, Wyoming.

Diagnosis.– *Chiromyoides major* differs from *C. potior, C. caesor*, and *C. minor* in having larger incisors, with a relatively larger mediocone on I^1. In *C. major* the anteroposterior and transverse diameters at the base of the crown of I^1 are 6.0 and 3.9 mm, respectively, compared to 5.3 and 3.2 mm in *C. potior*, 6.0 and 3.2 mm in *C. caesor*, and 5.6 and 2.7 mm in *C. minor*. *Chiromyoides major* differs from *C. campanicus* in lacking the medial expansion of the posterocone to form a crushing platform characteristic of that species.

Description.– Three upper incisors of *Chiromyoides major* are known from the type locality. All three have part of the crown missing. The most complete specimen (the type) shows that the incisors of this species are generally just a larger version of those of *C. potior*, with one further important difference. The type specimen shows that in *C. major* the mediocone is no longer equal to the laterocone in size, as it is in *C. potior*, but considerably larger – it is, in *C. major*, as wide as the anterocone, a development correlated with squaring and broadening of the leading edge of the lower incisor in this species.

The three upper incisors from Paint Creek measure 6.0 mm (type), 5.9 mm, and 6.2 mm, respectively, in anteroposterior diameter at the base of the crown. The latter two specimens measure 3.8 mm and 4.2 mm, respectively, in transverse diameter at the base of the crown, and 4.2 mm and 4.5 mm, respectively, in crown width half way between the posterocone and laterocone. A complete lower incisor of *C. major* from the type locality measures 24.3 mm in total length, 9.5 mm in crown length, 6.8 mm in crown height, and 3.6 mm in crown width. This tooth has a relatively weak margocristid, terminating posteriorly in a very small margoconid. The unworn anterior tip of the incisor differs from that of *C. campanicus* in having a nearly straight leading edge with squared corners, rather than the more blunt, rounded leading edge in the European species. Another complete lower incisor, identical to that from Paint Creek, was collected from an unrecorded stratigraphic level near Sand Draw in the Big Horn Basin.

Typodigm.– Three specimens of *Chiromyoides major* are known from the type locality, the Paint Creek locality in the Big Horn Basin: PU 21150 (including type), and 21587.

In addition, a specimen of *Chiromyoides major* is known from the Sand Draw area in the Big Horn Basin: PU 21588.

European Species

Chiromyoides campanicus Stehlin

(Plate 7 E, J, L-O)

Chiromyoides campanicus Stehlin, 1916, p. 1489, fig. 362-363. Russell, 1964, p. 120, pl. 8: 1a-c.
Plesiadapis campanicus, Teilhard, 1922, p. 21.

Type.– NMB Cy-153, a left mandible with I_1, $P_{3\text{-}4}$, and $M_{1\text{-}3}$; from the Conglomérat de Cernay, near Reims in France.

Diagnosis.– *Chiromyoides campanicus* differs from all North American species of *Chiromyoides* in having the region of the posterocrista on the upper central incisors expanded medially, forming a shelf, which prevented the tips of the lower incisors from passing between the posterocones of the upper incisors.

Description.– *Chiromyoides campanicus* is by far the best known species of *Chiromyoides*. Three partial mandibles (including the type specimen with all teeth in place), a maxilla, and several isolated teeth (including incisors) are known from Cernay and Berru in France. *Chiromyoides campanicus* has also been reported at Lentille (Russell, Louis, and Poirier, 1966), but I have not seen these specimens. The maxilla described by Russell (1964, p. 120) shows that at least P^2-M^3 were retained in this species. It is not known for certain if either I^2 or the upper canine was retained in this species. In view of the crowding of the anterior dentition caused by enlargement of the central incisors, it is unlikely that both of these teeth were retained. The lower dental formula is consistently 1.0.2.3.

The upper central incisor is similar to that of *C. caesor* in size and form but differs from it and the other known species of *Chiromyoides* in having the region of the posterocrista expanded medially. In MNHN Cr-357 a small accessory cusp is present on the expanded posterocrista, and the mediocone is of about the same size as the laterocone; whereas in a specimen in the Louis collection (figured in Gingerich, 1973a) there is no accessory cusp on the posterocrista, and the mediocone is very small. The crowns of $P^{2\text{-}3}$ are unknown. P^4 in the maxilla Cr-858 has a distinct paraconule but is too worn to determine whether or not a metacone was present. $M^{1\text{-}2}$ in this specimen are of note in having distinct mesostyles, as do three additional isolated specimens of M^2. Two of the latter (Cr-355, Cr-1288) have small but distinct hypocones on the postprotocingulum as well. The enamel on all of the teeth is generally smooth.

The lower incisor has a distinct margoconid and a weak margocristid. A diastema of 1.5 mm separates I_1 from P_3. The premolars have simple crowns with no accessory cusps and very short heels. P_4 is relatively much broader than in any species of *Plesiadapis*. The crowns of $M_{1\text{-}2}$ are only slightly more rounded than is characteristic of *Plesiadapis*, and the entoconid is squared and cusped. M_2 in *C. campanicus* is much less inflated and rounded than the M_2 of *C. potior* described above. M_3 in the type specimen has a broad, rounded hypoconulid lobe, with an unfissured posterior margin. Two slightly larger isolated M_3s (Cl-118, Cr-4450) have a somewhat more squared, distinctly fissured heel. If these

Table 9. Measurements of teeth of *Chiromyoides campanicus* from Cernay and Berru.

	I_1		P_3		P_4		M_1		M_2		M_3		Mandibular Depth
	A-P	T	L	W	L	W	L	W	L	W	L	W	
Lower Dentition													
Cernay Cy-153	6.6	3.3	1.8	2.1	2.0	2.8	2.5	2.7	2.7	3.0	4.2	2.8	12.5
Cernay Cr-4340	–	–	–	–	–	–	2.8	2.6	–	–	–	–	–
Cernay Cl-118	–	–	–	–	–	–	–	–	–	–	4.6	2.8	–
Berru Cr-859	–	–	–	–	–	–	2.5	2.7	2.7	3.1	–	–	13.0
Berru Cr-4450	–	–	–	–	–	–	–	–	–	–	4.8	3.0	–
	I^1		P^3		P^4		M^1		M^2		M^3		
Upper Dentition													
Cernay Cr-4343	–	–	–	–	–	–	–	–	–	–	2.4	3.5	
Cernay Cr-355	–	–	–	–	–	–	–	–	2.5	3.8	–	–	
Cernay Cr-4338	–	–	–	–	–	–	–	–	2.7	4.1	–	–	
Cernay Cr-1288	–	–	–	–	–	–	–	–	2.7	3.7	–	–	
Berru Cr-858	–	–	–	–	2.0	3.1*	2.6	3.7*	2.7	4.1*	–	–	
Berru Cr-357	6.5	3.9	–	–	–	–	–	–	–	–	–	–	
Berru ---	5.9	3.8	–	–	–	–	–	–	–	–	–	–	

*Estimated

teeth are in fact specimens of *C. campanicus* (which seems likely), the form of the hypoconulid lobe of M_3 in this species was rather variable.

The incisors of "*Chiromyoides campanicus*" figured by Schlosser (1921, pl. 15: 10, 11) are not deep enough to belong to *Chiromyoides* and the specimens more likely represent *Plesiadapis remensis*.

Measurements of the teeth of *Chiromyoides campanicus* are listed in Table 9.

Typodigm.– The type sample of *C. campanicus* from Cernay includes: NMB Cy-153 (type), MNHN Cl-118, Cl-227, Cr-355, Cr-1288, Cr-4338, Cr-4340, Cr-4343.

Additional specimens are known from Berru: MNHN Cr-357, Cr-858, Cr-859, Cr-4450; and an unnumbered upper incisor in the Louis collection.

PLATYCHOEROPS Charlesworth

Platychoerops Charlesworth, 1855, p. 80. Type: *Platychoerops richardsonii* Charlesworth.
Miolophus Owen, 1865, p. 339. Type: *Miolophus planiceps* Owen.
Plesiadapis (in part), Lemoine, 1880, p. 588.
(*Subunicuspidens*) Lemoine, 1887, p. 193. Type: *Plesiadapis (S.) daubrei* Lemoine.
Platychaerops (in part), Hill, 1953, p. 722.

Included species.– *Platychoerops daubrei* (Lemoine), and *Plat. richardsonii* Charlesworth.

Known distribution.– Early Eocene (Sparnacian and Cuisian) of western Europe only. *Platychoerops* is not known from North America, as Savage (1971, p. 156) tentatively suggested.

Diagnosis.– Species of *Platychoerops* differ from those of the other plesiadapid genera in having more molarized premolars, in having more complicated molars with highly crenulated enamel, and in lacking the laterocone (and usually the posterocone) on the upper central incisors.

Comments.– As was discussed above in connection with the diagnosis of *Plesiadapis* and the generic placement of *Ples. russelli*, the transition from *Plesiadapis* to *Platychoerops* was a continuous and gradual one, making any diagnosis of the two genera necessarily arbitrary. Lemoine's (1887) separation of "*Tricuspidens*" and "*Subunicuspidens*" was the first supraspecific diagnosis of species close to the *Plesiadapis–Platychoerops* boundary, and I have followed Lemoine in placing all species with tricuspid upper central incisors in *Plesiadapis*.

The name *Platychoerops* has occasionally been spelled *Platychaerops* (see Hill, 1953, p. 722; and Simons, 1972, p. 284; among others). This confusion results from the use of an ambiguous ligature in Charlesworth's original publication of the name. The situation is complicated by the fact that *Platychoerops* was proposed as a new genus of fish before a definitive spelling of the mammalian genus was published. A complete discussion of this problem, together with a request for validation of Charlesworth's spelling as *Platychoerops*, has been submitted to the International Commission on Zoological Nomenclature (Gingerich, 1974d).

Platychoerops daubrei (Lemoine)

(Plate 6 C, G, H)

Plesiadapis daubrei Lemoine, 1880, p. 588. Lemoine, 1891, p. 278, pl. 10: 49, 51, 53, 68.
Plesiadapis daubrei (in part), Teilhard, 1922, p. 59, fig. 29a, d-e; pl. 3: 3, 4, 9-14.
Platychoerops daubrei, Simpson, 1929, p. 11. Russell, Louis, and Savage, 1967, p. 28, fig. 7, 8.
Platychoerops richardsonii (in part), Hill, 1953, p. 723.

Type.– MNHN Al-5156, a right mandible with I_1, P_{3-4} and M_{1-3}; the type is apparently from Sparnacian lignites somewhere near Reims, in France, in spite of Lemoine's (1887, p. 192) statement that it came from "sables à Térédines" (these horizons he failed to differentiate in his studies of early Eocene mammals, see Teilhard, 1922, p. 80).

Diagnosis.– *Platychoerops daubrei* differs from *Plat. richardsonii* in being significantly smaller (compare measurements in Tables 11 and A-17). Differs from *Plat. ?richardsonii* in having a distinct fissure in the lingual crest on the heel of M_3, in lacking a direct protoconid-paraconid crest on the trigonid of the lower molars, and in being smaller.

Description.– A broken premaxilla of *Plat. daubrei* figured by Lemoine (1891, fig. 49) and Teilhard (1922, pl. 3: 3) preserves I^{1-2} intact. No known maxilla of *Plat. daubrei* has more than two teeth in place, but several isolated specimens of P^2 are known, showing that the upper dental formula was probably 2.0.3.3, as it is in *Ples. tricuspidens*. Seven mandibles of *Plat. daubrei*, including the type specimen, have a lower dental formula of 1.0.2.3.

Several beautifully preserved upper central incisors of *Plat. daubrei* are known from Mutigny. They have a single apical cusp (homologous with the anterocone in *Plesiadapis*). A long curving anterocrista connects the anterocone with the medial border of the tooth. The incisors from Mutigny and those in Lemoine's original collection have a very weak enamel fold in the position formerly occupied by the posterocone. Two upper central incisors of *Plat. daubrei* are known from Pourcy, both in private collections. One has the posterocone broken off but preserves a typical *Plat. daubrei*-like apex with a single large anterocone, while the other has the apex broken off but preserves a well-developed posterocone similar to that in *Plesiadapis*. This is additional evidence supporting the recent suggestion of Louis (1970) that the fauna from Pourcy is older than that from Mutigny.

The upper cheek teeth of *Plat. daubrei* are very variable in crown morphology. The following description applies to the specimens of the largest sample, that from Mutigny. Some specimens of P^3 have a molar-type paraconule strongly developed, while in others it is completely lacking. Similarly, some have a distinct metacone, others lack it. P^4 consistently has a well-separated metacone and usually has a distinct paraconule. M^{1-2} consistently have strong mesostyles and almost always have a small but distinct hypocone on the postprotocingulum. M^3 consistently has a very strong mesostyle and usually has a distinct lingual cingulum connecting the anterior and posterior cingula.

Table 10. Measurements of the type specimen of *Platychoerops daubrei*.
All measurements in mm.

		MNHN Al-5156 (type)
I_1	H	5.5
	W	3.6
P_3	L	4.8
	W	4.1
P_4	L	4.9
	W	4.1
M_1	L	4.9
	W	4.3
M_2	L	5.3
	W	4.5
M_3	L	8.1*
	W	5.0
Mandibular depth		15.0

*Estimated

The lower incisor of *Plat. daubrei* lacks any trace of a margoconid, and the margocristid is only very weakly developed. The unworn tip of the incisor in *Platychoerops* is more pointed than that of any species of *Plesiadapis*. P_3 in the type specimen has a distinct paraconid and an incipient metaconid, in addition to the central protoconid. A well-developed cristid obliqua runs down the back of the trigonid of P_3, but the hypoconid and entoconid are only very weakly developed. P_4 is usually the size and form of a molar but differs from the molars in lacking a strong entoconid, making the heel less basined. M_1 has a relatively narrower trigonid than M_2, but the two are otherwise very similar. Both have the entoconid crest continuous with the posterior basal cingulum, an independently derived condition in which they resemble the North American species *Plesiadapis dubius*. M_3 has a broad, rounded, deeply fissured heel, with a small but distinct posterior basal cingulum.

Measurements of the Mutigny sample of *Platychoerops daubrei* are summarized in Table A-17. The dimensions of the type specimen of *Platychoerops daubrei* are listed in Table 10 for comparison.

Discussion.– Almost all of the upper teeth of *Platy-*

Table 11. Measurements of the teeth of the type specimen of *Platychoerops richardsonii*. All measurements in millimeters.

		YM 520 (type) Left side	YM 520 (type) Right side
P^4	L	–	5.4
	W	–	8.5
M^1	L	–	5.6*
	W	–	–
M^2	L	6.3	6.3
	W	9.0	9.1
M^3	L	–	6.7
	W	9.4	–

*Estimated

choerops daubrei are isolated, and it may prove helpful to note the following points when attempting to identify them as to tooth position. The upper premolars lack mesostyles, and P^4 has a distinct postprotocingulum continuous with the back of the protocone. M^1 is narrower and more square than M^2. In outline, M^2 is more rhomboidal than M^1 because in M^2 the metacone is generally positioned relatively more medially on the crown. M^3 is distinctive in having an expanded, curved posteromedial border.

Russell, Louis, and Savage (1967) noted that the cheek teeth of *Platychoerops* from Pourcy and from the Cuisian locality of Grauves tend to be larger than those in the Mutigny sample. Measured as outlined in the introductory section, only two of the Pourcy teeth (Louis Py-104, Py-96) exceed the observed size range at Mutigny, and these by only .1 mm and .2 mm. The two specimens of M_3 of *Ples. russelli* from Meudon are significantly larger than those teeth in the Mutigny sample of *Platychoerops*. If the Meudon teeth are representative, it would not be surprising if the Pourcy teeth also average slightly larger than those from Mutigny, though this would imply a slight reversal of the general evolutionary tendency for the *Platychoerops* lineage to become larger over time.

An M^2 identical to those of *Platychoerops daubrei* has recently been collected from the Belgian locality of Dormaal by Dr. P. Gigase. The tooth, measuring 4.8 mm in length and 7.1 mm in width, is the first record of a plesiadapid from the Dormaal locality, and it appears to further confirm a Sparnacian age for this deposit.

An M_3 of *Platychoerops* from Grauves (Louis Gr-209) is significantly larger than any tooth from Mutigny and lacks the fissure in the lingual crest on the heel. For this reason the teeth from Grauves are referred, together with several others from Lemoine's early Eocene "Ageian" collection, to *Plat. ?richardsonii*.

Hypodigm.– The sample of *Plat. daubrei* in Lemoine's collection includes several jaw fragments and isolated teeth, all in the MNHN. The best of these are: Al-5156 (type), Al-5157, and Al-5171. The sample from Mutigny includes seven mandibles and numerous isolated teeth in the collection of MNHN, UCMP, Louis, and Poirier. From Pourcy only isolated teeth are known, in the Louis and other private collections. Small samples from Condé-en-Brie and Avenay are in the MNHN and Louis collections. The M^2 from Dormaal is in the private collection of Dr. Gigase.

Platychoerops richardsonii Charlesworth

(Plate 6 K)

Platychoerops richardsonii Charlesworth, 1855, p. 80. Lydekker, 1887, p. 4. A. Woodward, 1890, p. 35, pl. 1: 1a-b. Russell, Louis, and Savage, 1967, p. 27, fig. 6.
Miolophus planiceps Owen, 1865, p. 341, pl. 10: 1, 3.
Plesiadapis daubrei (in part), Teilhard, 1922, p. 59.
Platychaerops richardsoni (in part), Hill, 1953, p. 723, pl. 34.

Type.– YM 520, a palate preserving P^4, M^{2-3} on the right side, and M^{2-3} on the left; from the London Clay at Herne Bay, in England.

Diagnosis.– *Platychoerops richardsonii* differs from *Plat. daubrei* in being significantly larger (see Tables 11 and A-17 for comparative measurements).

Description.– The type and only specimen of *Platychoerops richardsonii* is a palate with alveoli for six upper cheek teeth on each side, although it has not yet been sufficiently cleaned to clearly show all of these. Most of the major cusps on the teeth are slightly damaged, but they are very similar to those of *Plat. daubrei* in morphological details, differing only in being larger and possibly in having slightly more crenulated enamel.

Measurements of the type specimen of *Plat. richardsonii* are listed in Table 11.

Discussion.– *Miolophus planiceps* Owen, 1865, is a junior objective synonym of *Platychoerops richardsonii* Charlesworth, 1855. Both names are based on the same type specimen, a fact that was first realized by W.S. Dallas, the Keeper of the Yorkshire Museum, shortly after publication of Owen's (1865) description. After its mention by Charlesworth (1855), the specimen had been borrowed from the Yorkshire Museum by Dr. Falconer, who sent it to Monsieur Lartet in France for examination. M. Lartet returned the specimen to England by way of a Mr. Christy, who, Dr. Falconer having died, left it with a Mr. Roberts, who in turn submitted it to Prof. Owen for description (see H. Woodward, 1866). The brevity of Charlesworth's description, together with the circuitous route by which the specimen reached Prof. Owen, would seem to explain how it came to be named twice.

Platychoerops richardsonii was the first plesiadapid species to be named, and it was one of the first described species of fossil primates, though it was not suspected of being a primate until 1922. Owen (1865) believed it to be an early perissodactyl. Lydekker (1885) believed *Platychoerops* to be identical to Cope's North American tillodont *Esthonyx*, a view Cope (1885) immediately challenged. Teilhard (1922) correctly recognized the affinity of *Platychoerops* with archaic primates.

Teilhard (1922), Hill (1953), and others have synonymized *Plat. richardsonii* and *Plat. daubrei*, but the large collection of *Plat. daubrei* recently collected and described by Russell, Louis, and Savage (1967) demonstrates beyond doubt that *Plat. richardsonii* represents a species significantly larger than *Plat. daubrei* (see Tables 11 and A-17 for comparative measurements). The teeth described below as *Platychoerops ?richardsonii* are also significantly larger than those of *Plat. daubrei*, and they probably represent *Plat. richardsonii*, though this cannot yet be confirmed beyond question.

Typodigm.– The only specimen undoubtedly belonging to *Plat. richardsonii* is the type specimen, YM 520.

Platychoerops ?richardsonii

(Plate 6 F)

Plesiadapis daubrei (in part), Teilhard, 1922, p. 61, fig. 29b, c.

Platychoerops daubrei (in part), Russell, Louis, and Savage, 1967, p. 28.

Diagnosis.– The specimens here referred to *Platychoerops ?richardsonii* differ from those of *Plat. daubrei* in being larger, in having a new crest on the lower molars connecting the protoconid and paraconid directly, and in lacking the distinct fissure in the crest bordering the lingual margin of the talonid of M_3. The specimens are of about the same size as *Plat. richardsonii* but cannot otherwise be compared to that species.

Description.– Teilhard (1922, p. 61) first noted the presence of a distinctive straight trigonid crest connecting the protoconid and paraconid in two isolated M_3s of *Platychoerops* from Lemoine's Ageian collection. These specimens, originally labelled MNHN Al-H and Al-I, are extraordinarily large, measuring respectively 8.9 mm and 8.5 mm in length. Both have the distinctive trigonid crest well developed. Among the other isolated teeth in Lemoine's Ageian collection was found a mandible fragment (Al-5170) with an M_2 in place having the same distinctive protoconid-paraconid crest on the trigonid. The tooth described above as Al-I proved, fortunately, to belong to this same mandible. An M_1 labelled Al-F also belongs to this mandible. The teeth of the resulting mandible are at the upper limit of the tooth measurements of the Mutigny sample. The distinctive trigonid crest is present on M_{2-3}, and M_3 has an unfissured crest on the lingual border of the heel – a characteristic uncommon in *Ples. tricuspidens* and unknown in *Ples. russelli* or *Plat. daubrei*.

The two good teeth of *Platychoerops* from Grauves, described by Russell, Louis, and Savage (1967, p. 31), as well as an additional M_3 (Louis Gr-209) collected subsequently, all fall at the upper size limit of the Mutigny sample of *Plat. daubrei*. The M_3 lacks the fissure in the lingual crest on the heel characteristic of *Plat. daubrei*, but it does not have the trigonid crest connecting the paraconid to the protoconid.

Discussion.– The three characters in which the teeth here referred to *Plat. ?richardsonii* differ from *Plat. daubrei* (large size, trigonid crest on M_{2-3}, absence of a lingual fissure on the heel of M_3) are all apparently advanced characters. The small number of specimens now available is not sufficient to prove that the species represented is *Plat. richardsonii*, but the specimens suggest that this might well be so.

One of the major achievements of Teilhard's 1922 study was the demonstration that Lemoine's "Ageian" fauna included a mixture of specimens from beds of both Cuisian and Sparnacian age. Considering the advanced character of the specimens here referred to as *Plat. ?richardsonii* and the recent discovery of Cuisian *Platychoerops* at Grauves, it seems probable that the advanced "Ageian" specimens are of Cuisian age as well. It is also very probable that the type specimen of *Plat. richardsonii* from the London Clay at Herne Bay is of Cuisian age. This raises a potential problem, as the type species of *Hyracotherium* comes from the London Clay at Herne Bay. An even more detailed study of early Perissodactyla than the recent report of Savage, Russell, and Louis (1965) will be necessary to clarify the relationships of *Hyracotherium, Propachynolophus*, etc.

Hypodigm.– The following specimens are referred to *Plat. ?richardsonii*, from Lemoine's "Ageian" collection: MNHN Al-5170, Al-H; from Grauves: MNHN Gr-6686, Louis Gr-177, Gr-209.

NOMINA ADDENDA

A number of additional names have been proposed as species of *Plesiadapis* or *Platychoerops*. These are listed below, and the correct allocation of each discussed.

"Plesiadapis" curvicuspidens Lemoine, 1878, p. 12. Lemoine (1880) subsequently placed this species in a new genus *Protoadapis.*

"Plesiadapis" crassicuspidens Lemoine, 1878, p. 13. This species was placed in *Protoadapis* by Lemoine (1880) but never mentioned subsequently. No specimen was ever designated to bear this name and it is thus a *nomen nudum.*

"Plesiadapis" recticuspidens Lemoine, 1878, p. 14. Lemoine (1880) subsequently placed this species also in his new genus *Protoadapis.*

"Plesiadapis" chevillionii Lemoine, 1880, p. 588. This species was never mentioned subsequently by Lemoine, no specimen was ever designated to bear the name, and it is consequently a *nomen nudum.*

"Plesiadapis" trouessarti Lemoine, 1891, p. 280. The specimen on which this species is based was later recognized as an arctocyonid, and it is now the type species of *Arctocyonides.*

"Plesiadapis" orsmaelensis Teilhard, 1927, p. 13. Hill (1953) placed this species in *Platychoerops*. Restudy of the type specimen (IRSNM 1428) has shown that it is an incisor of microsyopoid rather than plesiadapoid type. Suggestively, it and several identical specimens are approximately the right size to belong with the numerous mandibles of the small primate *Teilhardina belgica* from the same deposit.

Notes are added here concerning several isolated teeth of uncertain identity.

L. Russell (1958, p. 99, pl. 1:6-7) described an isolated M_1 from Calgary as *Pronothodectes* sp. Judging from his measurements (L=2.1 mm, W=1.6 mm), the specimen is too small to belong to any plesiadapid species yet described. Definite identification of the tooth will require additional specimens from the Calgary locality.

Similarly, Dorr (1958, p. 1222) reports *Pronothodectes matthewi* in the Hoback Battle Mountain fauna. The only tooth on which this identification was based, an isolated M^2 (UM 34766), is of about the same size as M^2 in *Pro. matthewi*, but it is of fundamentally different construction with a relatively much reduced metacone and extraordinarily large posterior cingulum. It appears that a postprotocingulum is present, but this appearance may be only a result of the very heavy wear to which the tooth has been subjected. The tooth may be an M^3 rather than an M^2, and it is unlike any tooth in *Pronothodectes*.

Krishtalka (1973, p. 40, fig. 19) recently described and figured a single isolated P^4 from Police Point in Alberta as *Plesiadapis fodinatus*. It may represent *Ples. fodinatus* (or possibly *Ples. churchilli*), but until diagnostic evidence is discovered, it is best referred to as *Plesiadapis* sp.

IV

NORTH AMERICAN BIOSTRATIGRAPHY AND PHYLOGENY

The Paleocene stratigraphic record in western North America is much more complete than the European record, and it is only in North America that the details of the early evolution of the Plesiadapidae can be worked out. Accordingly, the phylogeny of the North American species of Plesiadapidae is presented in this chapter. In the following chapter the relationships of the European species to their North American counterparts and the phylogeny of the European species are discussed.

The major part of the phylogeny of North American plesiadapid species presented here has been determined by a direct application of the stratophenetic method outlined in Chapter 2. A number of plesiadapid-bearing localities are isolated and thus of no use in working out stratigraphic relationships. Fortunately, in several areas the relative ages of plesiadapid species are known because of the direct superposition of one locality above another. The stratigraphy of the published areas with superposed localities is reviewed, and several important additional stratigraphic sections in the Big Horn Basin are discussed in more detail. Finally, a composite stratigraphic column is built up by correlating localities sharing the same guide species. The relationships of the species of Plesiadapidae were determined by phenetic linking within this composite biostratigraphic matrix. Only the position of *Pronothodectes jepi* relative to *Pro. matthewi* could not be determined on stratigraphic evidence alone – *Pro. jepi* is intermediate between *Pro. matthewi* and later plesiadapid species in morphology, and it has thus been placed above *Pro. matthewi* biostratigraphically.

BIOSTRATIGRAPHY

The stratigraphic position of the localities in each of the major geographic areas is described here, beginning with those in Montana.

Crazy Mountain Field.– Fossil mammals were first collected from Paleocene rocks in the Crazy Mountain Field of central Montana by Douglass in 1901. Subsequently, intensive work in this area by Douglass, Silberling, Gidley, and Simpson has yielded a large fauna, including plesiadapids from several levels. The monographic publication by Simpson (1937b) on the Crazy Mountain faunas remains a model faunal study. Simpson's careful documentation of the relative stratigraphic position of the important fossil localities in that area is of particular importance to our knowledge of plesiadapid evolution. Following the completion of Simpson's monograph, additional collections were made at the Scarritt Quarry (Locality 56, see Simpson, 1936, 1937a) and at the Douglass Quarry (Locality 63, see Bell's unpublished thesis, 1941).

The result is a sequence of four fossil localities yielding plesiadapids, with the relative age of each locality established on stratigraphic grounds. The lowest locality in the measured stratigraphic section, the Gidley Quarry, yields *Pronothodectes matthewi*. Some 1650 ft above the Gidley Quarry, the Douglass Quarry fauna includes both *Nannodectes intermedius* and *Plesiadapis praecursor*. Approximately 500 ft higher in the section, the Scarritt Quarry yields *Ples. anceps*. The final locality, Locality 13, is 1000 ft above the Scarritt Quarry and yields *Ples. rex*. The relative position of each of these localities is illustrated diagrammatically in Figure 15.

Medicine Rocks.– A number of important new Paleocene localities have been discovered in recent years by Mr. Marshall Lambert in a shallow syncline between the towns of Ekalaka and Baker in southeastern Montana. The Medicine Rocks Site 1 and Mehling Site have yielded two maxillary fragments of *Pro. matthewi*. To the north of these localities and demonstrably overlying them, three additional localities (White Site, 7-up Butte, Highway Blowout) contain *Ples. anceps*. The sequence here is thus the same as the lower part of the section exposed in the Crazy Mountain Field.

Big Horn Basin.– As a result of the collecting efforts of the late Prof. G.L. Jepsen of Princeton, Paleocene collections and stratigraphic associations in the Big Horn Basin are the most extensive known anywhere. The

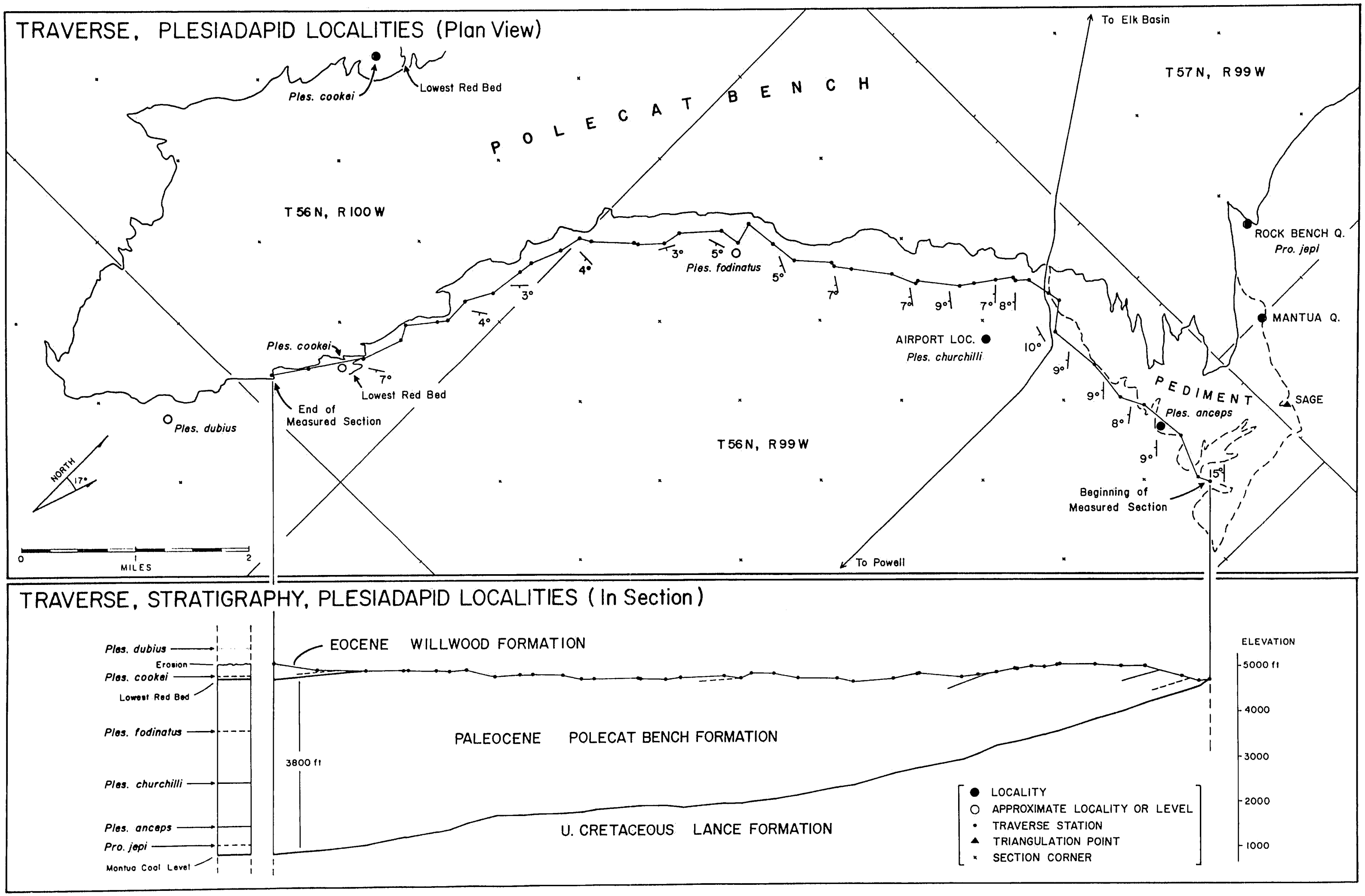


Figure 13. Stratigraphic position of Plesiadapidae in the type section of the Polecat Bench Formation. Measured traverse shown in plan view, and in section. Stratigraphic position of each station in the traverse is shown in cross section, and the relative position of each plesiadapid locality is similarly indicated. See text for further discussion.

general stratigraphy of the Paleocene and earliest Eocene rocks of the Big Horn Basin has been described by Jepsen (1930, 1940) and by Van Houten (1944). To summarize, in the northern part of the basin the upper Cretaceous Lance Formation (containing dinosaur specimens almost to its uppermost level) is conformably overlain by the Polecat Bench Formation. The Polecat Bench Formation was originally described by Jepsen (1940) as being bounded below by *Triceratops*-bearing beds and above by *Homogalax*-bearing beds, and was estimated to be 3500 ft thick. As recognized here and defined lithologically, the Polecat Bench Formation includes the drab sandstones, shales, lignites, and limestones in the Big Horn Basin lying above the base of the Mantua coal seam and below the lowest red bed of the overlying Willwood Formation.

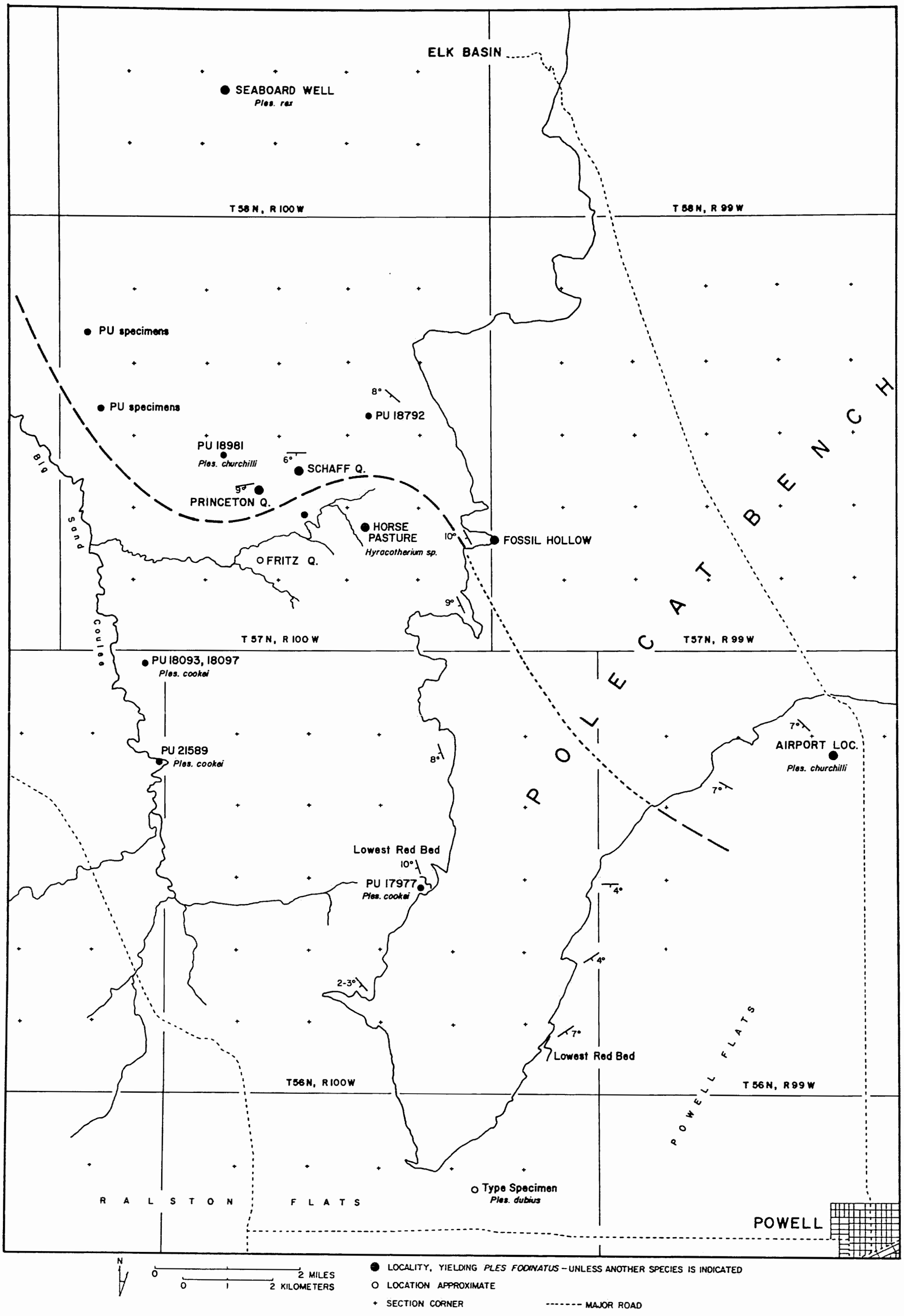
The type section of the Polecat Bench Formation is well exposed on the south side of Polecat Bench in the northern part of the basin. The thickness of the formation was measured by the author in 1967 using a plane table and alidade. The total traverse measured covered a distance of approximately 10 miles, and the attitude of the sediments was measured, by alidade, at 18 stations in the traverse (see Fig. 13). The total thickness of the formation was computed to be 3817 ft, which rounded to the nearest 50 ft gives a thickness of 3800 ft (1160 m) for the type section of the Polecat Bench Formation. The sediments in the lower third of the formation (and probably the rest as well) are clearly cyclic, and these cycles have been interpreted as a natural result of sedimentation by meandering rivers rather than a result of rhythmic mountain uplift (Gingerich, 1969).

Specimens of six plesiadapid species can be referred with certainty to the type section of the Polecat Bench Formation and to the lower strata of the Willwood Formation exposed on Polecat Bench. The lowest plesiadapid-bearing locality, the Rock Bench Quarry, is about 200 ft above the base of the Mantua coal (Jepsen, 1940, p. 234) and yields *Pro. jepi*. A single mandible of *Ples. anceps* (PU 17816) was found very near the measured traverse in Section 2, T 56 N, R 99 W (see Fig. 13), which is approximately 500 ft above the level of the Rock Bench Quarry. The Airport Locality, yielding several specimens of *Ples. churchilli* (viz. PU 19158), is approximately 800 ft above the level of the *Ples. anceps* mandible. No specimens of *Ples. fodinatus* have been found on the south side of Polecat Bench, but considering the measured attitude of the strata on both sides of the bench, the relative position of the beds bearing *Ples. fodinatus* can be projected from the Fossil Hollow locality across Polecat Bench to a level about 1000 to 1500 ft above the level of the Airport Locality (see Fig. 14). This compares well with the height of the Silver Coulee level (Princeton Quarry) above the base of the Polecat Bench Formation (2400 ft), as calculated by Jepsen (1940, p. 236). The *Ples. fodinatus* beds of Fossil Hollow and the Sand Coulee basin unquestionably lie above those bearing *Ples. churchilli*.

The lowest occurrence of *Plesiadapis cookei* near Polecat Bench is on the west side of the bench, where a number of teeth (PU 17977) were found in an area just above the lowest red bed (see Fig. 14). The lowest red bed occurs immediately above the top of the Polecat Bench Formation, at a distance of 3800 ft above the Mantua coal, and thus well above the level of the known occurrences of *Ples. fodinatus*. The label with the type specimen of *Ples. dubius* (AMNH 16073) says only "bluff base northeast of Ralston, Wyo., 1912," and Matthew's description of the specimen (1915, p. 482) gives no additional information. Granger's (1914, p. 204) description of the area leaves little question that the "bluff northeast of Ralston" is in fact Polecat Bench, but he has not indicated the precise localities of any particular fossils found there. Granger's field map for 1911 and 1912 (published by R. Wood, 1967) leaves little doubt that the type specimen of *Ples. dubius* came from Section 36 in T 56 N, R 100 W, or Sections 1, 2, or 11 in T 55 N, R 100 W – all well above the level from which *Ples. fodinatus* is known, and at approximately the level yielding *Ples. cookei*. The relative stratigraphic positions of the six species known from Polecat Bench are compared with those from other sections in Figure 15.

The area west of Polecat Bench in the Big Sand Coulee drainage again confirms the *Ples. cookei*/*Ples. fodinatus*/*Ples. churchilli* stratigraphic sequence (Fig. 14). In addition, a mandible fragment of *C. potior* (PU 19125) comes from Section 22 near the Schaff Quarry. An upper incisor of this species (PU 17895) has also been found just east of the mouth of Little Sand Coulee, near the type locality of *Ples. cookei*. The species from the Sand Coulee area are plotted in proper superpositional sequence in Figure 15.

The Big Sand Coulee area is of particular interest, as it contains the best documented "Paleocene" record of the characteristically Eocene horse *Hyracotherium* (Jepsen and Woodburne, 1969). Considering the strike and dip of the strata in this area (plotted in Fig. 14, all carefully measured in 1973 using a brunton compass), it is clear that the Horse Pasture Locality yielding *Hyracotherium* is in a downwarped area between the *Ples. fodinatus*-bearing Princeton Quarry, Schaff Quarry, and Fossil Hollow localities. The Horse Pasture Locality and the Schaff Quarry are at very nearly the same elevation (4500 ft above sea level), and the dip of the strata between the Schaff Quarry and the Horse Pasture indicates a significant stratigraphic difference, with the *Hyracotherium* locality being several hundred feet above


ELK BASIN
SEABOARD WELL
Ples. rex
T 58 N, R 100 W
T 58 N, R 99 W
PU specimens
PU specimens
8°
PU 18792
PU 18981
Ples. churchilli
6°
SCHAFF Q.
9°
PRINCETON Q.
HORSE PASTURE
Hyracotherium sp.
10°
FOSSIL HOLLOW
O FRITZ Q.
9°
Big Sand Coulee
T 57 N, R 100 W
T 57 N, R 99 W
POLECAT BENCH
PU 18093, 18097
Ples. cookei
PU 21589
Ples. cookei
8°
7°
AIRPORT LOC.
Ples. churchilli
7°
Lowest Red Bed
10°
PU 17977
Ples. cookei
4°
4°
2-3°
7°
Lowest Red Bed
T 56 N, R 100 W
T 56 N, R 99 W
POWELL FLATS
O Type Specimen
Ples. dubius
RALSTON FLATS
POWELL
N
0 2 MILES
0 1 2 KILOMETERS
● LOCALITY, YIELDING PLES FODINATUS – UNLESS ANOTHER SPECIES IS INDICATED
O LOCATION APPROXIMATE
+ SECTION CORNER
------- MAJOR ROAD

the Princeton Quarry-Schaff Quarry level. Several isolated teeth of *Plesiadapis* from the Horse Pasture area appear to represent advanced *Ples. fodinatus* or primitive *Ples. dubius*. The significance of this association will be discussed further in the following chapter.

Several localities south of Lovell, Wyoming, are important in establishing the relative ages of *Ples. rex* and *Ples. churchilli*. The Cedar Point Quarry (Sections 23-26, T 55 N, R 96 W) and the Jepsen Quarry (Section 25, T 55 N, R 96 W) both yield *Ples. rex*. Further south, the Croc Tooth Quarry (Section 5, T 54 N, R 95 W) and the Divide Quarry (Section 16, T 54 N, R 95 W) both yield *Ples. churchilli*. The Croc Tooth Quarry also yields *Chiromyoides caesor*.

The stratigraphic relationships of these four quarries were studied during the summer of 1973. The Cedar Point and Jepsen quarries are about 1.5 miles apart and lie very nearly on strike. Several miles further south, the Croc Tooth and Divide quarries are about two miles apart. Both of these sites lie just below the top of a prominent ridge striking about N 20° to N 30° W. Both quarries are very nearly on strike and possibly lie within the same sandstone bed. The changing strike and dip of the beds indicates that the *Ples. churchilli* interval strikes in a progressively more westerly direction, passing approximately a mile south of, and clearly overlying, the Cedar Point-Jepsen Quarry beds bearing *Plesiadapis rex*.

A fourth area of interest in the Big Horn Basin includes a number of localities in the Sand Draw area, also south of Lovell. The specimens (most from Section 24, T 54 N, R 97 W) include PU 17787, a mandible of *Ples. churchilli* from the lower Sand Draw beds; PU 17814, the type specimen of *Ples. simonsi*; and PU 21588, a lower incisor of *Chiromyoides major*.

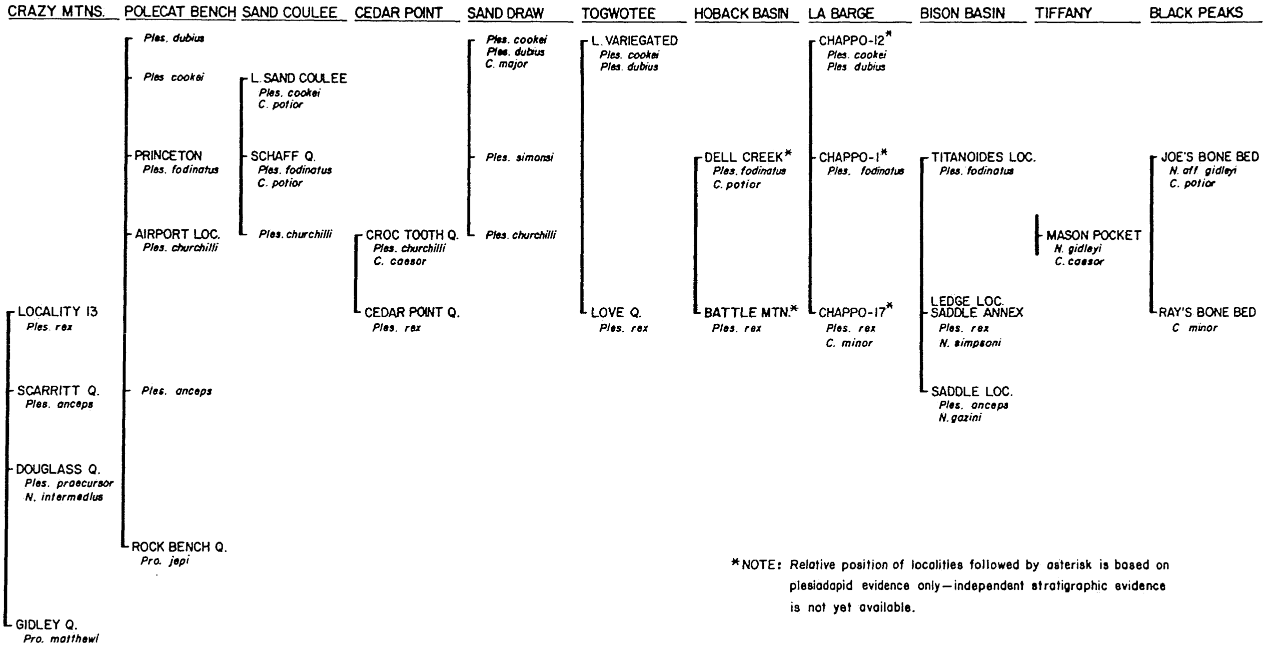
Section 24 was restudied and prospected for two days in 1973. The strata in this section dip at about 10°-20° to the southeast. The only good exposures are all east of the Sand Draw ravine itself. In the northern part of the section, the lower part stratigraphically, there are a number of ridge-forming sandstones exposed. The *Ples. churchilli* mandible is yellow in color, as are all specimens in this region preserved in sandstone, and could only have come from one of the sandstone ridges in the lower part of the section. The beds in the southern half of Section 24, and extending on for miles to the south, are drab gray mudstone with none of the massive yellow sandstones found in the northern half of the section. The few scraps of mammal and reptile teeth and bone found in prospecting in these beds are all black in color, as are the *Ples. simonsi* and *C. major* specimens, which undoubtedly came from the southern higher levels of the Sand Draw area.

The *Ples. simonsi* and *C. major* specimens both bear the same field number, indicating that they came from the same general area (which, in such sparsely-fossiliferous country as this, could be rather large), but not necessarily the same horizon. Further to the south of the Sand Draw area, in the higher levels of the drab gray mudstones, both *Ples. cookei* (PU 17825) and *Ples. dubius* (UW 6118) are found. Because *C. major* is found with the latter two species at the Paint Creek Locality north of Cody, Wyoming, it seems almost certain that it comes from a higher level in the Sand Draw area than the type specimen of *Ples. simonsi*. Of particular importance is the demonstration in the Sand Draw area that *Ples. simonsi* comes from a higher stratigraphic level than *Ples. churchilli*, and from a lower level than *Ples. cookei* and *Ples. dubius*. Furthermore, the relatively slight advancement of *Ples. simonsi* over *Ples. churchilli* suggests that *Ples. simonsi* is probably a species contemporaneous with *Ples. fodinatus*, although the two species have not yet been found together. These stratigraphic relationships are indicated in Figure 15.

Togwotee Pass.– The fossil vertebrates of the Togwotee Pass area have been described in a preliminary report by McKenna (1972b). Two distinct faunas including *Plesiadapis* are known. The lower fauna, from Love Quarry, contains *Ples. rex*. A number of additional localities in beds described by McKenna (1972b) and Love (1973) as the Lower Variegated sequence yield a fauna with both *Ples. cookei* and *Ples. dubius*. The superposition of the Lower Variegated beds (Tlv) over those of the Love Quarry (V) is spectacularly illustrated in Love's figure 31 (Love, 1973).

Hoback Basin.– As a result of Dorr's (1952, 1958) stratigraphic studies in the Hoback Formation, two *Plesiadapis*-bearing localities in this area were included in a measured stratigraphic section. The Dell Creek locality, yielding *Ples. fodinatus*, was thought to be approximately 8,000 feet stratigraphically above the Battle Mountain locality, which yields *Ples. rex*. However, more recent work has shown that the two localities are separated by complex thrust faulting (Guennel, Spearing, and Dorr, 1973), and thus this section does not give independent evidence that *Ples. fodinatus* beds overlie those yielding

Figure 14. Approximate geographic distribution of beds yielding *Plesiadapis fodinatus* on the west side of Polecat Bench in the Big Horn Basin, and their relationship to beds yielding other species of *Plesiadapis* and a specimen of *Hyracotherium*. The heavy dashed line shows the approximate trend of beds yielding *Plesiadapis fodinatus*. These beds dip gently to the south or southwest at from 7° to 10°, as indicated by strike and dip symbols on the map. Beds yielding *Plesiadapis cookei* specimens form a parallel trend on the map at a higher stratigraphic level.



*NOTE: Relative position of localities followed by asterisk is based on plesiadapid evidence only—independent stratigraphic evidence is not yet available.

Figure 15. Correlation chart of North American plesiadapid-bearing fossil localities. The stratigraphic evidence for the sequence in each area is discussed in detail in the text.

Ples. rex.

La Barge.— Plesiadapids have been described from the La Barge (Buckman Hollow) area by Gazin (1942, 1956c, 1962 in Oriel). The three known localities are here designated Chappo-1, Chappo-12, and Chappo-17 to distinguish them clearly. All are in the Chappo Member of the Wasatch Formation. Chappo-1 and Chappo-12 are in Sections 1 and 12, respectively, of T 26 N, R 114 W. Chappo-17 is in Section 17, T 26 N, R 113 W. The stratigraphic relationships of the three localities have never been described, but they probably conform to the sequence seen elsewhere, with Chappo-12 (*Ples. cookei* and *Ples. dubius*) overlying Chappo-1 (*Ples. fodinatus*), which in turn overlies Chappo-17 (*Ples. rex, C. minor*). The latter association of *Ples. rex* with *Chiromyoides minor* is of particular importance in establishing the relative age of the latter species. The Chappo localities are listed in their inferred relative order in Figure 15.

Bison Basin.— The Bison Basin faunas have been described in detail by Gazin (1956a). Subsequently, a small number of new species have been added to the Bison Basin faunas, but no revision of Gazin's stratigraphic determinations has been proposed. Gazin described four localities, named Saddle, Ledge, Titanoides, and West End. On stratigraphic evidence, he noted that the Ledge locality is higher than the Saddle locality, and that the Titanoides locality is significantly higher than the West End locality. Gazin believed on the basis of the fossil faunas that the West End locality was approximately equivalent in age to the Ledge locality (Gazin, 1956a, p. 4). Although some revision of Gazin's species identifications has been necessary, this study has further substantiated his views regarding the relative ages of each of the Bison Basin faunas.

The name Saddle Annex has been given to the locality mentioned by Gazin (1956a, p. 3) in the area of the Saddle locality, but some 50 ft stratigraphically higher than it. The Saddle Annex yields *Nannodectes simpsoni*, and as Gazin noted, it clearly overlies the Saddle Locality proper, which yields *Nannodectes gazini*. The Saddle Annex and the Ledge Locality both include *N. simpsoni*, and the Ledge and West End localities both yield *Ples. rex*, so these three localities appear to be correlative. The relative stratigraphic position of each of the Bison Basin localities is shown in Figure 15.

Tiffany.— The best known species from the isolated Mason Pocket locality, *Nannodectes gidleyi*, has not yet been found in any other locality. Fortunately, the presence of *C. caesor* in this important locality suggests that it is correlative with the Croc Tooth Quarry in the Big Horn Basin.

Black Peaks.— In an important recent study, Schiebout (1974) has described seven superposed mammalian faunas, two of which include plesiadapids. Joe's Bonebed, with *Nannodectes* aff. *gidleyi* (a still poorly known species apparently more advanced than *N. gidleyi*) and

	NORTH AMERICAN PLESIADAPID ZONE	ADDITIONAL SPECIES	MAJOR LOCALITIES
CLARKFORKIAN	*Plesiadapis cookei*	*Plesiadapis dubius* [1]*Chiromyoides major* [2]*Chiromyoides potior*	[2]Bear Creek, Chappo-12, [2]Little Sand Coulee, [1]Paint Creek, Plateau Valley, Togwotee lower variegated seq., [1]Upper Sand Draw.
TIFFANIAN	*Plesiadapis simonsi*	*Plesiadapis fodinatus* *Nannodectes aff. gidleyi* *Chiromyoides potior*	Bayfield, Chappo-1, Dell Creek, Fossil Hollow, Middle Sand Draw, Princeton Q., Schaff Q., Titanoides Loc.
	Plesiadapis churchilli	*Nannodectes gidleyi* *Chiromyoides caesor*	Airport Loc., Croc Tooth Q., Divide Q., Long Draw Q., Lower Sand Draw, Malcolm's Locality, Mason Pocket.
	Plesiadapis rex	*Nannodectes simpsoni* *Chiromyoides minor*	Battle Mountain, Cedar Point Q., Chappo-17, Erickson's Landing, Ledge Loc., Love Q., Melville-13, Saddle Annex, Twin Creek, West End Loc.
	Plesiadapis anceps	*Nannodectes gazini*	Highway Blowout, Saddle Loc., Scarritt Q.
	Plesiadapis praecursor	*Nannodectes intermedius*	Douglass Q., Keefer Hill.
TORREJONIAN	*Pronothodectes jepi*		Rock Bench Q.
	Pronothodectes matthewi		Gidley Q.

[1] Upper part of zone only.

[2] Lower part of zone only.

Figure. 16. Sequence of plesiadapid range zones in western North America. Each zone is based on the largest species to be found in that zone. Additional species found in each zone are listed in the following column. The *Plesiadapis cookei* zone appears to be subdivisible, with *Chiromyoides potior* occurring in the lower part and *C. major* occurring in the upper part. Based on Figure 15, with some additional important localities listed. Localities are listed in alphabetical order within each zone.

Chiromyoides potior, overlies by some 100 ft the Ray's Bonebed level yielding *C. minor*. These localities correlate with the more northern localities approximately as shown in Figure 15.

PHYLOGENY

Eight distinct biostratigraphic zones are apparent in the correlation chart presented in Figure 15. Each of these range zones is defined by, and named after, the largest contained plesiadapid species, and the sequence of zones is outlined in Figure 16. All of the evidence thus far discovered indicates that any given North American plesiadapid species is confined to one of these named range zones, with one exception. *Chiromyoides potior* is apparently associated with *Ples. cookei* in Little Sand Coulee, indicating that this species survived beyond the *Ples. simonsi* zone. The larger species *C. major* appears only in the later part of the *Ples. cookei* zone.

Knowledge of the distribution of species in each of the North American plesiadapid zones is fundamental to determining the phylogenetic relationships of the species. A single species is present in each of the lower two zones. Two coexisting lineages first appear in the *Ples. praecursor* zone. One species, *Ples. praecursor*, is characterized by robust premolars and the loss of the lower canine. The other, *N. intermedius*, retains the lower canine and has very narrow incisors and cheek teeth. Both are near *Pro. jepi* in size and morphology, and there is no reason to reject the simplest hypothesis, i.e., that they were directly derived from that species.

In the overlying *Ples. anceps* zone one species of *Plesiadapis* is present, as is one species of *Nannodectes*. They were almost certainly derived from their respective congeneric species of the underlying zone. Similarly, the two *Ples. rex* zone species, *Ples. rex* and *N. simpsoni*, were very probably derived from *Ples. anceps* and *N. gazini*, respectively. *Chiromyoides minor* could have evolved from either *Ples. anceps* or *N. gazini* in the underlying zone, but considering its reduced dental formula and its dental morphology, *C. minor* was almost certainly derived from the similar species *Ples. anceps*.

The three plesiadapid species in the *Ples. churchilli* zone appear to have been derived from their respective congeneric species in the *Ples. rex* zone. In the overlying *Ples. simonsi* zone, *N.* aff. *gidleyi* and *C. potior* link most closely to *N. gidleyi* and *C. caesor*, respectively. There is at present no reasonable alternative to the hypothesis that both *Ples. simonsi* and *Ples. fodinatus* evolved from the older but very similar species *Ples. churchilli*.

In the *Plesiadapis cookei* zone, *Chiromyoides major* is probably derived from *C. potior. Plesiadapis cookei* is larger but otherwise very similar to *Ples. simonsi*, and *Ples. dubius* is smaller but similar to *Ples. fodinatus*. There appears to be little question that *Ples. cookei* is derived from *Ples. simonsi* and that *Ples. dubius* is derived from *Ples. fodinatus*.

The resulting phylogeny of North American Plesiadapidae is outlined diagrammatically in Figure 17. *Pro. jepi* is thought to be derived from *Pro. matthewi* because it is intermediate in size between *Pro. matthewi* and the derived *Ples. praecursor*, but this relationship has not yet been substantiated stratigraphically. The relationships of all of the remaining species are those suggested by stratigraphic evidence and phenetic linking. The order of appearance and disappearance of various morphological characters in each of the lineages is consistent with the phylogeny presented in Figure 17 – to postulate any other relationship of the species would require at least one additional lineage, for which there is neither a need nor any positive evidence. The mammalian faunas of this period show no evidence of massive extinctions or migrations, and all appear to represent basically similar ecological associations. In this setting, it is quite reasonable that successive species of evolving lineages would be discovered, such as those outlined in Figure 17. Eight plesiadapid zones are known in western North America, spanning approximately eight or nine million years (Berggren, 1972, p. 202). If the zones prove to be of about equal duration, each would span approximately one million years. As additional groups of mammals are studied in this zonal context, the relative time duration of each zone should become more clear.

CLARKFORKIAN MAMMAL AGE

H. Wood et al. (1941, p. 9) proposed the name Clarkforkian for a provincial or mammal age in North America intermediate between the Paleocene Tiffanian provincial age and the Eocene Wasatchian provincial age. In their proposition, the Wood committee noted only one species, *Plesiadapis cookei*, as an index fossil for the Clarkforkian. Subsequently, R. Wood (1967) reviewed the Clarkforkian fauna and concluded (1967, p. 28) that the "Clark Fork" mammal fauna consisted of only four specimens referable to four mammalian genera, each from a different locality and not confined to a lithologically distinguishable Clark Fork stratigraphic interval. He thus felt that recognition of the Clarkforkian as a mammal age or faunal zone was unwarranted. However, in reducing the Clark Fork fauna to four specimens of four genera, R. Wood eliminated from further consideration all specimens coming from beds of equivocal Paleocene or Eocene age, in other words, the specimens of greatest importance – specimens coming from beds above those containing Tiffanian faunas and below those containing Wasatchian faunas. This procedure eliminated from further consideration all specimens

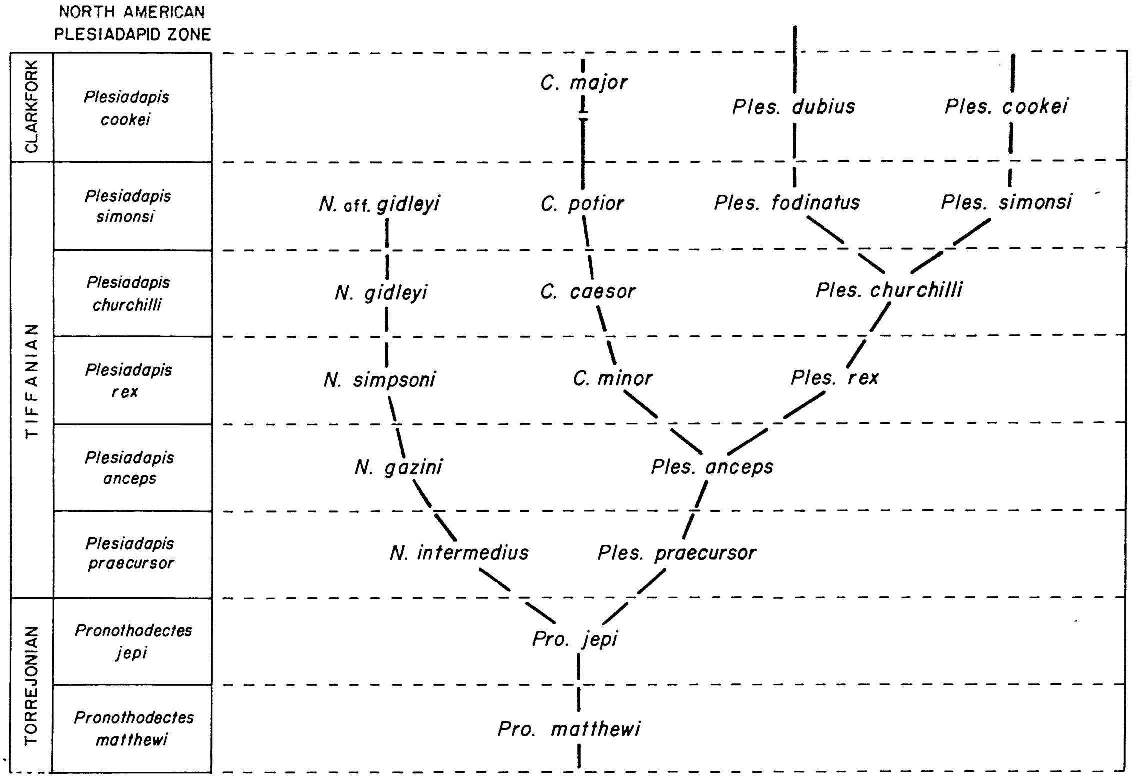


Figure 17. Phylogenetic relationships of the North American species of *Pronothodectes, Nannodectes, Chiromyoides,* and *Plesiadapis*. Species of the major lineage from *Pro. matthewi* to *Ples. cookei* have been chosen to define the sequence of superposed biostratigraphic range zones listed at the left of the figure. The total amount of time represented by the Torrejonian (part), Tiffanian, and Clarkforkian in the figure is about 8-9 million years (from approximately 62 my to 53 my ago; modified from Berggren, 1972, fig. 4). Lacking evidence to the contrary, the zones are depicted as approximately equal in duration, although additional study of other lineages will be necessary to confirm this.

of the originally designated index species of the Clarkforkian, *Plesiadapis cookei*, since all localities yielding this species are in beds that have sometimes been called Paleocene and sometimes Eocene.

Quite apart from the question of whether the species is Paleocene or Eocene in age, the stratigraphic data in Figure 15 and the phylogeny illustrated in Figure 17 leave little doubt that there is a distinctive *Plesiadapis cookei* zone. *Plesiadapis dubius* comes from the same stratigraphic interval as *Ples. cookei* (see Fig. 15-17), and *Carpolestes nigridens* comes from this interval also (Rose, 1975, 1976). In 1975, a major program of careful collecting was begun in the Sand Coulee area of Wyoming, the type area of the Clark Fork fauna. Some 15 new specimens of *Plesiadapis cookei* have been discovered from eight localities within a restricted stratigraphic interval that is overlain by beds containing a typical *Hyracotherium*-dominated Sand Coulee or lower Gray Bull fauna. On the basis of these new collections, it appears that distinctive species of many genera and a unique faunal association are characteristic of the *Plesiadapis cookei* zone, and thus continued use of a Clarkforkian provincial or mammal age in North America appears to be justified.

Faunas from beds of Clarkforkian age include genera usually found in the Paleocene as well as genera characteristic of the Eocene, and there is thus a problem in deciding whether the Clarkforkian is the last Paleocene mammal age in North America or whether it should be considered the first Eocene mammal age. The boundary between the Paleocene and Eocene is defined in the Paris Basin in Europe, where it is generally placed between the Thanetian and Sparnacian (see Gingerich, 1975c, for discussion and references). The mammal fauna of the late Thanetian is well known from the localities of Cernay and Berru in the Paris Basin. The lowest locality stratigraphically in the Sparnacian is the locality of Meudon, also in the Paris Basin. No good faunas between Berru and Meudon are known, and there is a marked change from one to the other. The following six mammalian taxa are known from the Conglomérat de Meudon:

Plesiadapis russelli
Phenacolemur sp. (incisor only)
Paramys sp. (incisors)
Oxyaena sp. ("*Palaeonictis*")
Hyracotherium sp.
Coryphodon oweni

Of these, *Plesiadapis russelli* is a more advanced descendent of *Ples. tricuspidens*. The remaining genera make their earliest appearance in the European fossil record at Meudon; i.e., the beginning of the Eocene in the Paris Basin (where the Paleocene-Eocene boundary is defined) is marked by the first appearance of rodents (*Paramys*), oxyaenid creodonts (*Oxyaena*), perissodactyls (*Hyracotherium*), and the genus *Coryphodon*.

A new fauna collected in 1975 from a locality in the Sand Coulee basin of Wyoming (Univ. Michigan Loc. SC-19), in the type area of the Clark Fork beds, included the following taxa:

Plesiadapis cookei
Phenacolemur sp.
Carpolestes sp.
Paramys, 2 sp.
Didymictis sp.
Oxyaena sp.
Esthonyx sp.
Ectocion sp.
Phenacodus sp.
Dissacus sp.
Arctostylops steini
Coryphodon sp.
Probathyopsis sp.

Hyracotherium has not yet been found at locality SC-19, but it has been described from beds apparently in the very upper part of the *Plesiadapis simonsi* zone or the lower part of the *Plesiadapis cookei* zone (see discussion and Fig. 14 above; also Jepsen and Woodburne, 1969).

Comparison of the fauna from the Clarkforkian locality SC-19 and that from Meudon indicates that *Plesiadapis cookei* itself is very similar to *Ples. russelli*, although it is not so specialized in the direction of *Platychoerops* as the latter species. *Phenacolemur* is present at both SC-19 and Meudon, but it is known from earlier localities in the Sand Coulee area as well. The remaining four genera in the Meudon fauna are the four mammalian genera marking the beginning of the Eocene in Europe, and all make their first appearance in North America in the *Plesiadapis cookei* zone. Thus it seems probable that the *Plesiadapis cookei* zone is largely, if not entirely, correlative with the lower part of the Sparnacian sequence in Europe. For this reason, the Clarkforkian is here regarded as the earliest Eocene mammal age in North America rather than the latest Paleocene mammal age as it has generally been regarded in the past.

V

EUROPEAN STRATIGRAPHY, PHYLOGENY, AND CORRELATION

The evolution of Plesiadapidae in Europe can unfortunately not be documented in the detail possible in North America. All of the localities are isolated – there is no area where two or more localities can be shown to be directly superposed. A problem of facies changes also complicates lithological correlations of the upper Paleocene and lower Eocene sediments of western Europe. These drawbacks are, however, partly compensated by the fact that the plesiadapid-bearing sediments of Europe are interbedded with marine sediments, permitting a correlation of early Tertiary marine and nonmarine stratigraphy not possible in North America.

The close relationship of the European and North American plesiadapid species has greatly assisted interpretations of the phylogeny and relative ages of the European forms. Because the Paleocene-Eocene boundary is defined in the Paris Basin (see Pomerol, 1969), understanding the correlation of North American plesiadapids with their European counterparts is of special importance. Russell (1975) provides a concise review of the Paleocene and early Eocene mammal faunas of Europe.

BIOSTRATIGRAPHY

The species of *Plesiadapis* from Menat and Walbeck are important in showing that the genus had a long evolutionary history on the European continent and in demonstrating the close relationship of this early history to that of North American species; but Menat and Walbeck are completely isolated occurrences and thus of little assistance in understanding the phylogeny of European plesiadapids.

The only possible approach to the stratigraphic history of European plesiadapids is to try to place each species in the context of the general early Tertiary stratigraphy of either the Paris, London, or Belgian basins. The correlation chart presented in Figure 18 is compiled from a number of sources, including especially Curry (1965, 1967) and Curry, Gulinck, and Pomerol (1969). Within each basin the sequence of beds is well established, but because of the great number of local facies involved, it is not possible to be completely certain of the correlations between basins before the appearance of *Nummulites planulatus*. The correlation of the London Clay with the Paris basin sequence is particularly important and difficult. On the basis of the advanced species *Platychoerops richardsonii*, at least part of the London Clay would appear to have been deposited later in time than the Sparnacian *Plat. daubrei* beds, and it has been tentatively correlated with the lower part of the Cuisian Sables â Unios et Térédines.

The Belgian mammalian faunas from Dormaal and Erquelinnes have sometimes been regarded as Paleocene rather than early Eocene in age, but the recently discovered upper molar of *Platychoerops daubrei* from Dormaal suggests a Sparnacian age for the Belgian fauna.

PHYLOGENY

Only the Paris Basin sequence is of any value in interpreting the phyletic evolution of European plesiadapids. Three species (*Plesiadapis tricuspidens, Ples. remensis,* and *Chiromyoides campanicus*) coexisted at Cernay and Berru, and it is thus clear that at least three plesiadapid lineages were evolving in Europe at that time. No evidence suggests more than three lineages. At the next higher stratigraphic level, the Conglomérat de Meudon includes a slightly larger, more advanced species, *Ples. russelli*, similar to and almost certainly derived from *Ples. tricuspidens*.

In the next higher stratigraphic level, at Pourcy, two species are present. The smaller of the two is a small species of *Plesiadapis* very similar to and almost certainly derived from *Ples. remensis*, although no intermediate connecting form is known in the small fauna from Meudon. The larger species at Pourcy is identical to typical specimens of *Plat. daubrei*, except that a relatively large posterocone is retained on one of two upper central incisors known, a characteristic present in *Ples. russelli* but lost in all Mutigny level *Platychoerops*.

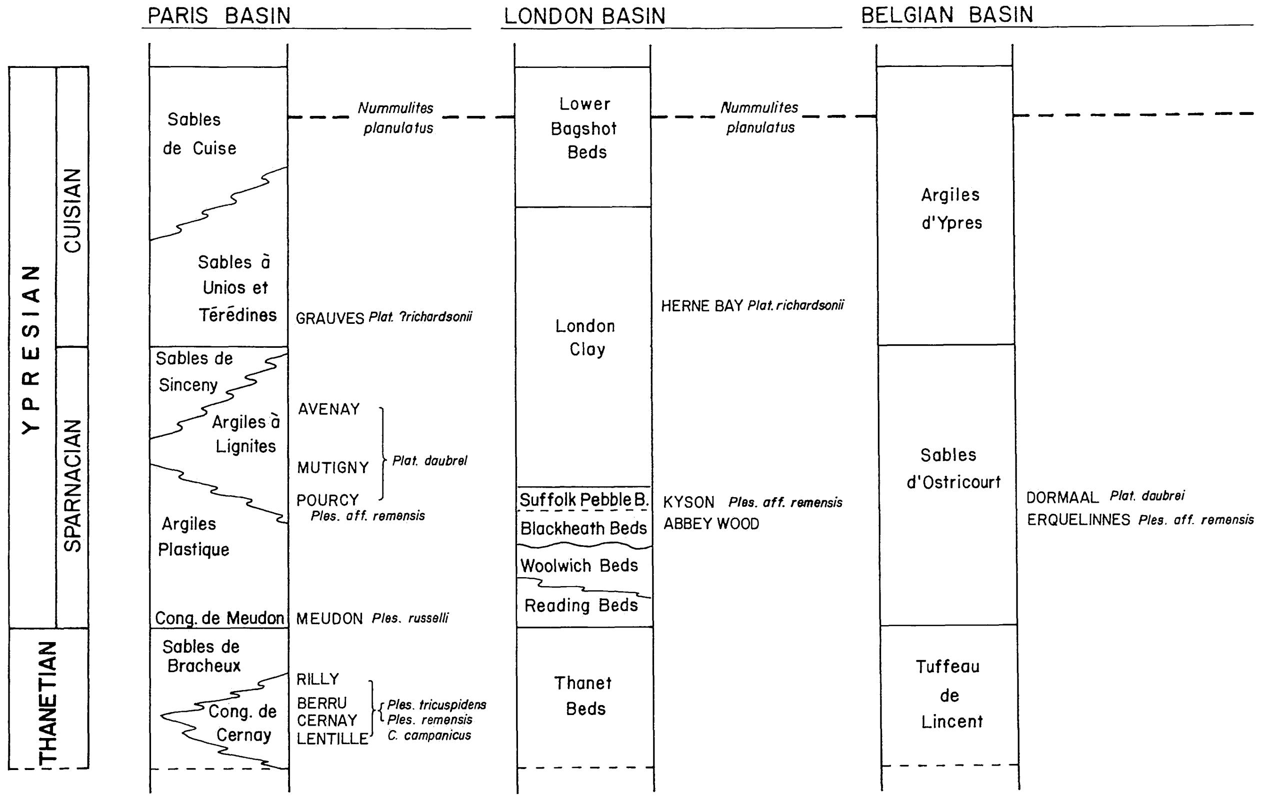


Figure 18. Tentative correlation of upper Paleocene and lower Eocene sediments in the Paris, London, and Belgian Basins. The relative position of plesiadapid species and localities are listed to the right of each stratigraphic column. Stratigraphic successions and correlation modified from Curry (1967) and Curry, Gulinck, and Pomerol (1969).

This intermediate Pourcy *Platychoerops* almost certainly links *Plat. daubrei* to an origin from *Plesiadapis russelli*. Several specimens from the Cuisian locality of Grauves are larger than *Plat. daubrei* and appear to represent the large London Clay species *Plat. richardsonii* in France.

The few specimens of *Ples.* aff. *remensis* from Pourcy, Kyson, and Erquelinnes show that a lineage of small *Plesiadapis* unquestionably survived into the Eocene in all three European basins.

As was noted in the chapter on systematics, the European species are all very similar, but not identical, to a corresponding species in western North America: *Ples. insignis* resembles closely *Ples. praecursor, Ples. walbeckensis* resembles closely *Ples. rex*, both *Ples. remensis* and *Ples. tricuspidens* resemble closely *Ples. simonsi*, and *Ples. russelli* is close to *Ples. cookei*. Of greater importance is the apparent congruency of the major part of the phylogeny of the European species with the phylogeny of their North American counterparts.

The probable phylogeny of the European Plesiadapidae is presented in Figure 19, together with a system of plesiadapid range zones paralleling those proposed for the North American record. Major gaps exist between each of the Paleocene zones. In the Ypresian the record is much more complete, and the evolution of *Plat. richardsonii* from *Ples. tricuspidens* and *Ples. russelli* is much better documented.

CORRELATION

The sequence of plesiadapid zones in Europe is compared with that in North America in Figure 20, where the European species are correlated with their most similar counterparts in North America. As was noted above, *Ples. insignis* is, insofar as they can be compared, close to *Ples. praecursor. Plesiadapis walbeckensis* is close to *Ples. rex* but retains a number of characters of *Ples. anceps* not seen in *Ples. rex*, and seems best correlated somewhere between the *Ples. anceps* and *Ples. rex* zones. *Plesiadapis tricuspidens* is close to *Ples. simonsi*, and the two zones are probably nearly equivalent in age.

The close relationship of *Ples. russelli* to *Ples. cookei*

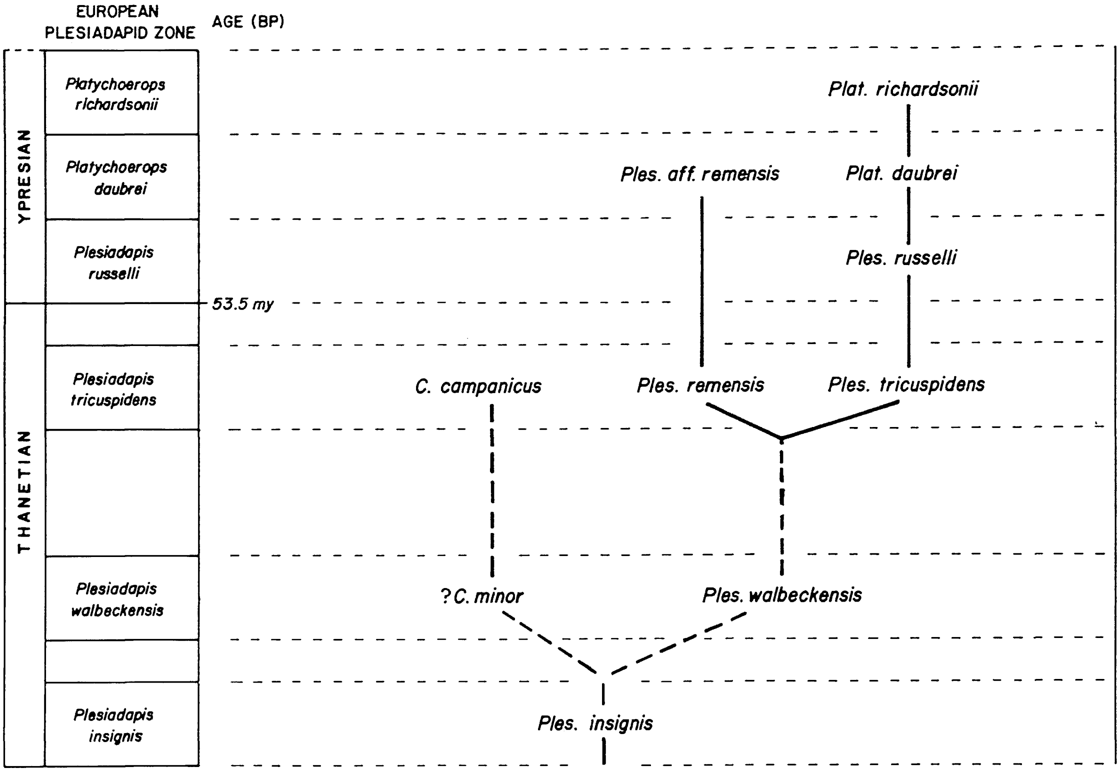


Figure 19. Phylogenetic relationships of European species of Plesiadapidae. European plesiadapid range zones are listed at left. As in North America, these range zones are based on the largest plesiadapid species present in each stratigraphic interval.

is of special importance. As was discussed in the previous chapter, the fauna from the Conglomérat de Meudon is the earliest Eocene mammalian fauna from the Paris Basin, type area for definition of the Paleocene-Eocene boundary. The Meudon fauna includes *Plesiadapis russelli* and the earliest European *Hyracotherium, Coryphocon*, and Rodentia. The North American Clarkforkian stage includes a *Plesiadapis* species very close to *Ples. russelli*, and the earliest North American occurrence of *Hyracotherium* (Jepsen and Woodburne, 1969), of *Coryphodon* Simons (1960b), and of Rodentia (Jepsen, 1937). Thus it seems probable that the Clarkforkian mammal age in North America is in large part (and possibly entirely) correlative with the earliest Eocene of the Paris Basin.

The presence of identical or closely similar species in Europe and North America is much stronger evidence of intercontinental connections than the absence of similar species is of continental separation. Thus, the close similarity of the European and North American Paleocene species listed in Figure 20 suggests a broad connection of the two continents throughout the Paleocene. The fact that the North American *Nannodectes* lineage is unknown in Europe, and the European *Ples. remensis* lineage unknown in North America, is negative and weak evidence by comparison.

In conclusion, the similar *Plesiadapis* and *Chiromyoides* species present in Europe and North America suggest the possibility of a pangeographic distribution of these genera spanning both continents during the Paleocene and provide strong evidence for a close continental connection between Europe and North America throughout this epoch.

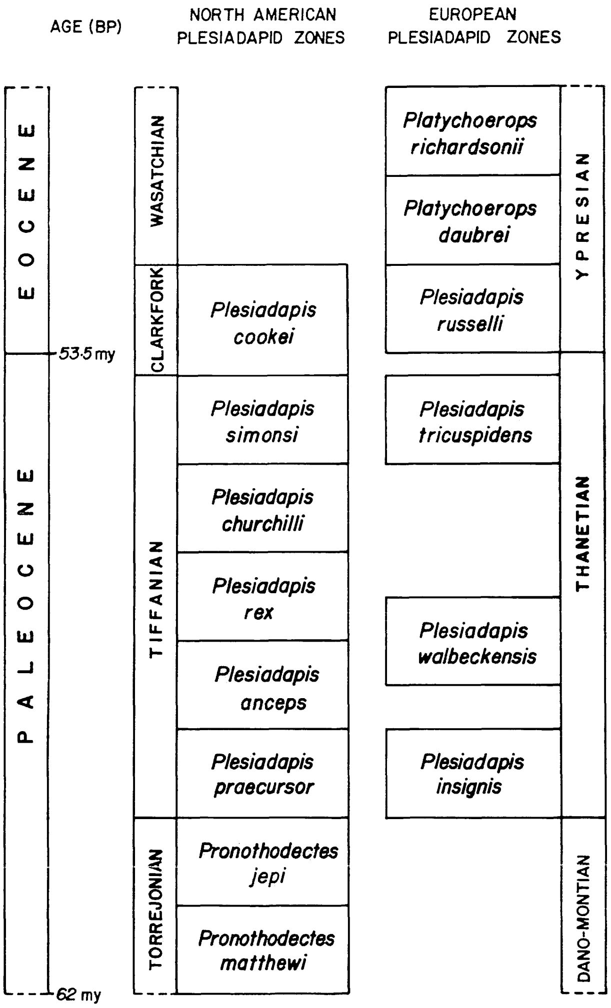


Figure 20. Tentative correlation of the plesiadapid zones of North America and Europe. Dates from Berggren (1972).

VI

DENTAL FUNCTION AND EVOLUTION

In the previous chapters the stratigraphic distribution and relationships of the species of Plesiadapidae have been reviewed, providing the phylogenetic context necessary for an interpretation of evolutionary trends in the dental evolution of plesiadapids. In this chapter, the function of various elements of the plesiadapid dentition is considered, providing the basis for a functional interpretation of the observed evolutionary changes. Previous work on the function of the dentition of *Plesiadapis rex* (Gingerich, 1974f) is reviewed, with annotations on important features observed in other species. This is followed by a detailed consideration of the most important aspects of evolutionary change in the plesiadapid dentition. The functional implications of each of the observed morphological trends and possible functional reasons or explanations for the trends are discussed following their descriptions.

DENTAL FUNCTION

Much effort has been devoted in recent years to the study of dental function in primates and other mammals. Mills (1955, 1963) has described wear facets on the teeth of living primates, and a number of important cineradiographic and electromyographic studies of chewing in living mammals have recently been published (Hiiemae and Ardran, 1968; Crompton and Hiiemae, 1970; Hiiemae and Crompton, 1971; Hiiemae and Kay, 1972, 1973; Kallen and Gans, 1972; Herring and Scapino, 1973; Kay and Hiiemae, 1974a, b). These studies, together with the interpretation of wear facets on the teeth of fossil mammals (Crompton and Jenkins, 1968; Crompton, 1971; Gingerich, 1972b, 1973b, 1974b,f), lead to a relatively simple model of mammalian molar function.

The occlusal surfaces of the molars of living primates bear a number of points (cusps), lines (crests), and planar areas (basins). These function, respectively, to puncture, cut, and grind food. Furthermore, the progression of increasing geometrical complexity (from points to lines to planes) reflects the order of steps by which food is masticated and the order in which each functional component was added phylogenetically to the mammalian dentition (which is in turn probably correlated with the differentiation of masticatory musculature in early mammals).

As a further generalization, the incisors and canines of a generalized mammal function to separate food items for ingestion, the premolars as a rule are conical puncturing teeth, and the molars are predominantly cutting and grinding teeth. Thus the above mentioned progression of geometrical complexity is seen proceeding from the front to the back of the cheek dentition.

Incisor Function.– The functional evolution of the incisors of primates has never been considered in detail, but the conclusion of Hiiemae and Kay (1972) that incisal biting is a specialization of higher primates is clearly at variance with the fossil record. The incisors of all of the Paleocene and Eocene primates are strongly developed, and they were undoubtedly of primary importance in ingestion of virtually all food items in the diet.

The upper incisor of *Plesiadapis rex* (illustrated in Figure 5) has three apical cusps, the anterocone, mediocone, and laterocone, together with a large posterocone. Most of the other species of *Plesiadapis*, as well as the species of *Pronothodectes, Nannodectes,* and *Chiromyoides*, have this basic four-cusped upper incisor pattern. The posterocrista is the largest, most heavily worn crest on the incisors of all but the most specialized species of Plesiadapidae.

The lower incisor of *Ples. rex* is also typical of most plesiadapid species. The most important features of the crown of the lower incisor are the well-developed margocristid and distinct margoconid on the lateral margin of the crown.

Three distinct types of incisor occlusion are possible in *Ples. rex*. The anterior tip of a lower incisor can oppose the anterocone of the upper incisor directly, producing flattening and blunting of the tips of both

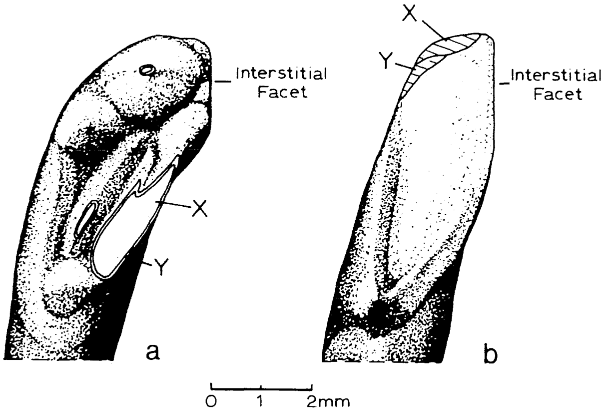


Figure 21. Wear facets on the incisors of *Plesiadapis rex*. Upper (a) and lower (b) incisors in occlusal view, showing matching x and y facets. Striations on the facets parallel the direction of movement. From Gingerich, 1974f.

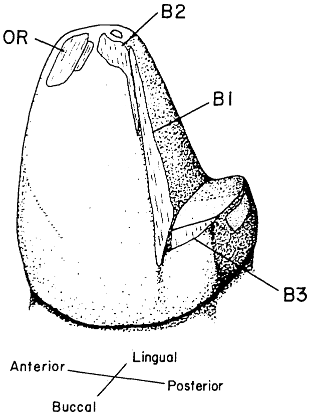


Figure 22. Wear facets on a lower premolar of *Pronothodectes jepi*. Figure shows left lower P_4 of PU 14782 in oblique lateral view. Striations shown on facets are parallel to the direction of mandibular movement.

incisors. The tip of a lower incisor can pass just behind the anterocone, occluding against the mediocone, centroconule, and laterocone in the final occlusal position. The function of the laterocone, centroconule, and mediocone in this case is possibly analogous to the seed cup in the upper bill of some birds – and possibly thus an indication that small seeds were an important component of the diet. The third possibility is that the tips of the lower incisors occluded behind the apical cusps of the upper incisors and were then drawn upward and backward, passing between the posterocones of the upper incisors. The heavy wear on the posterocrista of the upper incisors and on the lateral edge of the tips of the lower incisors indicates that the latter was by far the most important functional mode of the incisors of *Plesiadapis rex* and most of the related species as well.

Wear facets on two of the best preserved incisors of *Ples. rex* are illustrated in Figure 21. Two distinct striated wear facets are present on the lower incisor, labelled respectively x and y. The most heavily worn area of the upper incisor is between the mediocone and posterocone. From manipulation of the upper and lower incisors it is clear that the x facet on the lower incisor was made as the tip of the lower incisor was drawn upward and backward across the region labelled x on the large facet on the upper incisor (Fig. 21). The posterocone acted as a stop at y, forcing the lower incisor more medially and thus producing the y facet on the lower incisor. Such a movement was equally possible on either the left or the right side, but both sides could not occlude simultaneously.

In this predominant form of incisor occlusion in *Ples. rex*, the lower incisor forms the third side of a closing triangle, the other two sides being the surface of the crown and the anterior edge of the posterocone. Such a pinching device is clearly not adapted to cutting pieces from fruits or seeds but seems well adapted to cutting small pieces from a larger, stem-shaped food mass. While the first two incisor occlusal positions described above might be useful in killing small animals and in eating fruits and seeds, the predominant type of occlusion in *Plesiadapis rex* (and all of the early plesiadapid species) functions most efficiently in cutting stems. Presumably soft vegetation in the form of stems constituted a predominant fraction of the diet of early plesiadapids.

The second incisors, canines, and anterior premolars (P_2^2) were already so reduced that uppers and lowers did not occlude in the earliest plesiadapids yet known, the species of *Pronothodectes*.

Premolar and Molar Function.– As was noted above, the functional components of the molar crown of mammals include cusps (points), crests (lines), and basins (planes), the functions of which are respectively puncturing, shearing, and grinding. In primates a distinct set of wear facets and a characteristic direction of mandibular movement are associated with each of the three functional components (Gingerich, 1972b). The cusps puncture as the mandible is drawn upward and backward. The crests shear as the mandible is forced upward and forward. Grinding is accomplished in the basins as the mandible is forced forward and slightly downward. Each of these mandibular movements also has a small medial component.

The mandibular movements can be further classified as parts of two distinct masticatory cycles or stages of chewing. The upward and backward movements are part of an initial Orthal Retraction (OR) stage of puncturing and crushing. The two types of forwardly directed

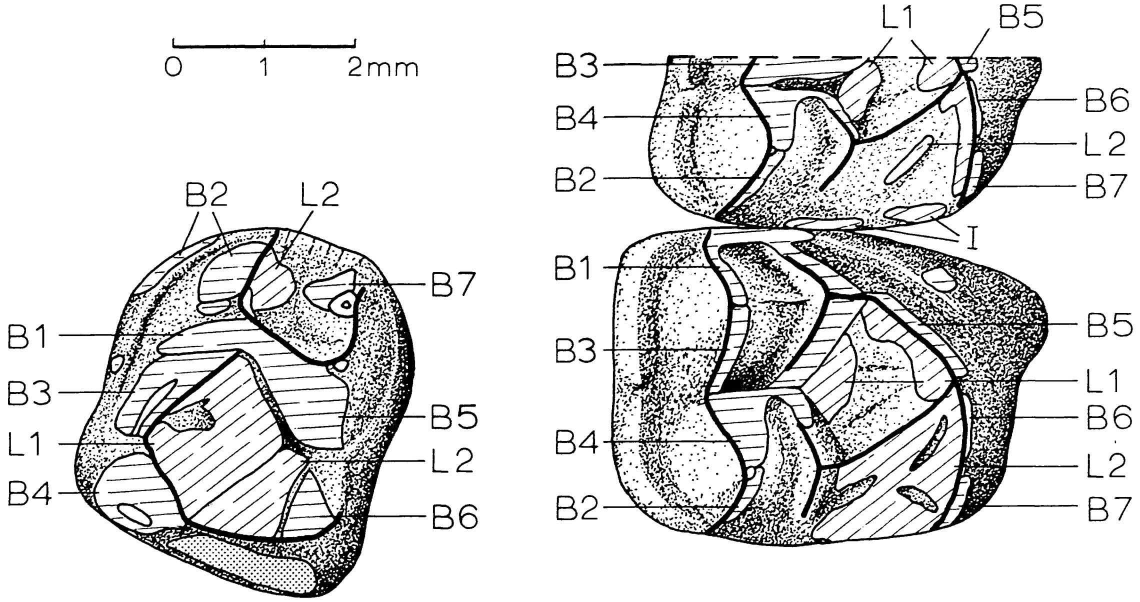


Figure 23. Wear facets on the upper and lower molars of *Plesiadapis rex*. Figure shows a left lower molar (M_2, at left) with right upper molars (M^{1-2}, at right) in occlusal view. Striations shown on facets are parallel to the direction of mandibular movement. From Gingerich, 1974f.

occlusion are parts of a subsequent transverse stage of shearing and grinding – the transverse stage consisting of two sequential phases, the Buccal Phase (BP, shearing) and the Lingual Phase (LP, grinding).

The wear facets on primate premolars and molars can thus be mapped on the basis of the orientation of their striations and the associated geometrical feature (cusp, crest, or basin) as belonging to the OR stage, B phase, or L phase. A map of the lower fourth premolar of *Pronothodectes jepi* is presented in Figure 22, and a more complex map of wear facets on upper and lower molars of *Ples. rex* is presented in Figure 23.

Kay and Hiiemae (1974a) have suggested that OR facets are the result of accidental balancing side contact during mastication. However, it seems very unlikely that the OR facets are accidental, given their antiquity and their strong development in numerous fossil and living mammals, including the Triassic *Eozostrodon* (=*Morganucodon*; Gingerich, in prep.), Jurassic *Docodon* (Gingerich, 1973b), Paleocene *Phenacolemur* (Gingerich, 1974b), Eocene *Adapis* (Gingerich, 1972b), and living *Cercopithecus* (Gingerich, in prep.). Also, Crompton (1972) has described similar facets in Triassic mammal-like reptiles.

Kay and Hiiemae (1974a) believe that because Mills (1955, 1963) confused the interpretation of wear facets on the molars of primates, it is necessary to discard his descriptive terminology as well. They substitute "Phase 1" and "Phase 2" for the Buccal Phase and Lingual Phase, respectively. The two sets of terminology are for all practical purposes synonymous, and I have rightly or wrongly continued to use the earlier terminology here. It might be noted also that following a very complicated geometrical analysis, Kay and Hiiemae (1974a) reject Mills' (1955) conclusion that during the Buccal Phase the mandible rotates about the ipsilateral condyle. However, Mills' simple suggestion appears to be easily demonstrated on a dried mandible of practically any species: if one point of a dividers is placed on the mandibular condyle, the other point will trace out the Buccal Phase striations on the ipsilateral molar wear facets.

The premolars of early plesiadapids are all relatively simple teeth, with a large, robust conical protoconid and a small heel but no additional accessory cusps. The simple crowns of the lower premolars of *Pronothodectes* have sometimes been assumed to represent the primitive condition in early plesiadapiform primates, but the species of *Palaechthon* are generally more primitive in cheek tooth structure (Bown and Gingerich, 1973), and a simple conical premolar appears to be a derived condition. While the premolars of plesiadapids are not as enlarged as the premolars of *Phenacolemur* (Gingerich, 1974b), they probably have a simplified puncturing crown for the same functional reason.

The functional similarity of the premolars of *Pronothodectes* to those of *Phenacolemur* is indicated especially by the orthal retraction (OR) facet developed at the apex of the protoconid (see Fig. 22) in both forms. This facet is not present on all specimens, but as in *Phenacolemur*, its strong development on some indicates that the general function of the pointed premolars of primitive plesiadapids was puncturing with an upward and backward mandibular movement. Such puncturing movements were presumably powered chiefly by the largest masticatory muscles, the temporalis muscles, drawing the mandible directly upward and backward (Gingerich, 1971a).

The pattern of wear facets on the molars of *Ples. rex* (Fig. 23) is somewhat more complicated than the pattern of wear on the premolars. Seven distinct, matching Buccal Phase facets (B1-B7) can be identified on well-preserved upper and lower molars, as well as two distinct Lingual Phase facets (L1, L2). Facets with striations oriented in a direction intermediate between those of the B and L facets are labelled I; they show that the Buccal and Lingual facets represent two phases of a single transverse jaw movement.

The Buccal Phase performs primarily a cutting function, with crests on the lower molars shearing past those on the upper molars. To better serve this function, the number of cutting edges on the molars was increased by two means. Cutting edges were added by developing new crests parallel to the previously existing ones. Thus the B1 protocristid cutting edge on the lower molars sheared past first the paracrista, then the anterior crista on the paraconule, and finally past the lingual cingulum on the corresponding upper molar. As development of the posterior crista on the metaconule on the upper molars was limited by the L2 facet, a second B2 cutting edge was added, developing from the buccal cingulid of the lower molars.

The second means of adding cutting edges is illustrated by both the B3 and B4 facets on the lower molars, as shown in Figure 23. Here the enamel has been worn through relatively early, resulting in two resistant enamel cutting edges on a single crest. On heavily worn teeth, almost all the crests bear two cutting edges as a result of wear having perforated the enamel.

The molar teeth of *Ples. rex* occluded in such a way that they formed a series of three compression chambers on the active chewing side for expressing juices. At the beginning of the Buccal phase, the B3, B4, and L1 facets on the upper molars and the L1, L2, B5, and B6 facets on the lower molars completely enclosed a space, the volume of which was progressively reduced as the teeth approached centric occlusion. The pulp remaining after this compression was then ground during the lingual phase.

The lingual phase performs primarily a grinding function. Food is ground between opposing planar areas of the matching lingual phase facets. In *Ples. rex* and in later species, the crenulated surface of the enamel in the areas where lingual phase facets developed (illustrated in Figure 23) caused windows to remain in the facets until they became heavily worn. These windows would function as cutting edges, suggesting that in advanced species of *Plesiadapis* the lingual phase performed a cutting as well as a grinding function, at least in younger individuals.

Any attempt to determine the general function of the dentition and the diet of an extinct mammal must consider the morphology of all the teeth: incisors, canines, and premolars, as well as molars. The incisor mechanism of *Plesiadapis rex* indicates a cropping mode of food acquisition. The reduction and loss of canines and premolars in *Plesiadapis*, leaving a large diastema between the incisors and cheek teeth, is also consistent with a cropping incisor mechanism. The canine and premolar teeth of many mammals are used to shear and puncture large pieces of food when they are first injested. Reduction and loss of canines and premolars, with a resulting large diastema, is correlated with initial injestion into the mouth of small pieces of food. Grazing mammals have a large diastema because they feed on food that is by its nature already in small pieces. Rodents have a large diastema because they gnaw a series of small pieces from a larger piece of food rather than injesting the larger piece (Hiiemae and Ardran, 1968). The reduction of canines and anterior premolars already present in the earliest plesiadapids suggests that the entire family injested food in small pieces, although the primitive species would have been able to feed on a relatively more omnivorous diet than the later highly specialized species.

DENTAL EVOLUTION

It is not possible to discuss every aspect of the dental evolution of plesiadapids here, rather the discussion will center on five of the most interesting and important aspects: size change through time, progressive reduction of the dental formula, evolution of the central incisors, evolution of the upper premolars, and finally the evolution of the lower third molar.

Evolution of Size.— For reasons outlined in Chapter 2, the log of the crown area of M_1 is one of the best measurements for comparing the size of two or more closely related species of fossil mammals. This quantity is plotted in Figure 24 for the best samples of *Pronothodectes, Nannodectes,* and *Plesiadapis* from each North American plesiadapid zone. Unfortunately, there are too few known cheek teeth of the North American species of *Chiromyoides* to even estimate the size of M_1, and these species could not be included in the diagram.

It is apparent from Figure 24 that the lineage from

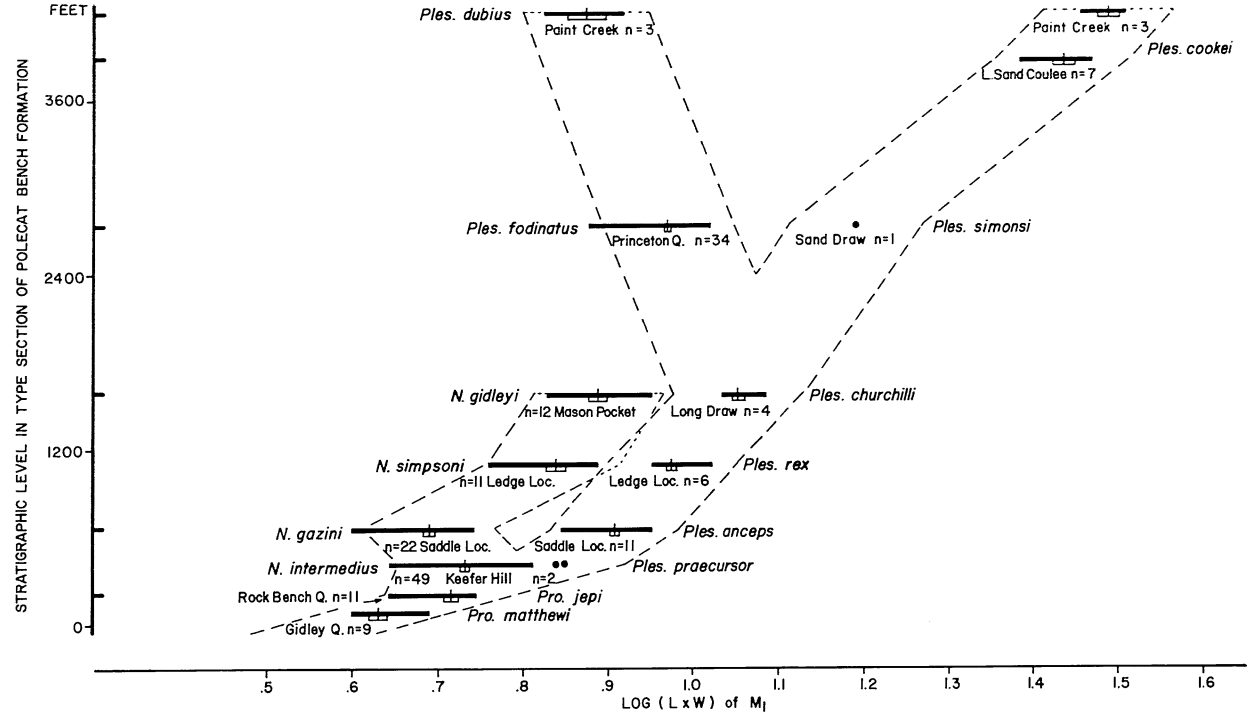


Figure 24. Evolutionary change in the size of M_1 in North American Plesiadapidae. Mean (vertical line), range (black bar), and standard error of mean (open bar) are plotted for the species of *Pronothodectes, Nannodectes,* and *Plesiadapis* from each plesiadapid zone. The vertical axis shows the position of six species in the type section of the Polecat Bench Formation (see Fig. 13); the remaining species are correlated or interpolated into this section on the basis of information given in Figure 15. Considering that there is an early Puercan fauna (Mantua Quarry) at the base of the Polecat Bench Formation, the time duration represented by the lower 600 ft of sediment is probably relatively longer than that represented by 600 ft intervals higher in the section. Dashed lines bracket the mean ± two standard deviations (estimated from the Cedar Point sample of *Plesiadapis rex*, see Fig. 11), thus enclosing the probable range of 95% of the specimens in each lineage.

Pronothodectes matthewi to *Plesiadapis cookei* underwent a continuous, gradual increase in size. Such a lineage, increasing continuously in size, can be termed an *incremental* lineage. The species of the short lineage leading from *Ples. churchilli* to *Ples. dubius* became progressively smaller. Such a lineage, decreasing continuously in size, can be termed a *decremental* lineage. The species of the *Nannodectes* lineage first became smaller, and then progressively larger. Such a reversed lineage, ultimately increasing in size, can be termed an *inverted* lineage. The opposite, a reversed lineage finally decreasing in size, can be termed a *deverted* lineage.

While their size cannot be measured directly, the teeth of the edentulous mandible of *Chiromyoides minor* (TMM 40537-37) were clearly significantly smaller than those of their ancestor *Ples. anceps*. Thus, at all three branching points one lineage became larger and the other became smaller. This is the same pattern as that seen in *Hyopsodus* (Gingerich, 1974a) and seems best interpreted as size divergence to minimize competition between two sympatric, closely related, but genetically isolated populations. Since body size is one of the most important components of an animal's morphological adaptation, it is not surprising that character divergence first appears in this morphological characteristic.

In the evolution of early Eocene *Hyopsodus*, there was a single incremental lineage and four decremental lineages (Gingerich, 1974a, 1976). A similar decremental lineage is apparent here in the *Ples. dubius* lineage. However, in the two plesiadapid lineages that diverged sufficiently in form to be placed in different genera (*Nannodectes* and *Chiromyoides*), the lineages became inverted. Evidently, if a decremental lineage becomes sufficiently different in form from its sister incremental lineage, it can invert and become progressively larger, thus paralleling the incremental lineage. Decremental lineages that remain close in form to their sister incremental lineage may, for reasons of competition, necessarily always become smaller. These ideas remain to be tested further, of course, by the discovery of a much

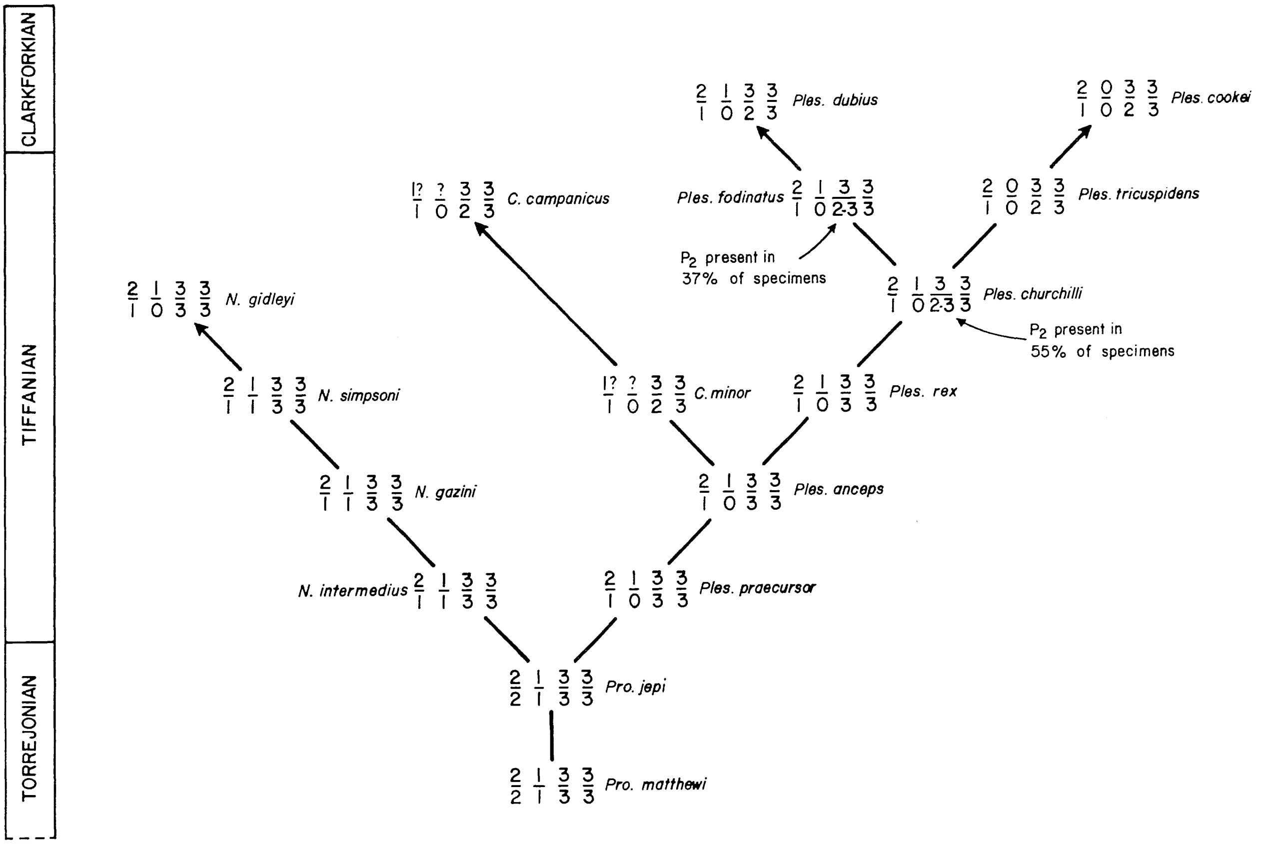


Figure 25. Evolutionary reduction of the dental formula in North American Plesiadapidae. The formulae of *Ples. tricuspidens* and *C. campanicus* have been substituted for those of their less well known North American counterparts *Ples. simonsi* and *C. caesor-C. minor*. Note particularly the loss of P_2 from *Ples. rex* to *Ples. dubius* through gradual change in the frequencies of a dimorphism in number of premolars.

larger number of branching points in stratigraphically documented evolutionary lineages.

An additional point should be noted regarding rates of evolution. The average increase in the log (L x W) of M_1 in both of the increasing plesiadapid lineages in Fig. 24 is approximately .10 per million years. When absolute rates of change in *darwins* are calculated (change in ln x per million years, see Haldane, 1949), the area of M_1 increased in the lineage from *Pronothodectes matthewi* to *Plesiadapis cookei* at a rate of .23 darwins. Area of M_1 decreased at a rate of -.20 darwins from *Ples. churchilli* to *Ples. dubius* and increased at a rate of .23 darwins from *Nannodectes gazini* to *N. gidleyi*. These figures are in the same range as figures calculated for the Eocene condylarth *Hyopsodus* and primate *Pelycodus* (data from Gingerich, 1976), where rates of size change in both incremental and decremental lineages vary from about .20 to .30 darwins.

Reduction of Dental Formula.— The changes in dental formula during the course of evolution of the Plesiadapidae are outlined in Figure 25. North American species are shown, except for substitution of the well-known European species *Chiromyoides campanicus* and *Plesiadapis tricuspidens* for correlative and inadequately known North American species.

The earliest plesiadapids yet known, species of *Pronothodectes*, already show the loss of one incisor (I_3) and one premolar (P_1) from the general eutherian complement of 3.1.4.3. The loss of these two teeth, a loss shared by all other plesiadapiform primates, is presumably related to the relative enlargement of the central incisors. As is generally true during mammalian evolution (but not necessarily so, the bat-eared fox *Otocyon* being an obvious exception), the dental formula of plesiadapids underwent progressive reduction.

Reduction of the lower formula from 2.1.3.3 to 1.0.3.3 happened independently in two lineages. This lower formula of 1.0.3.3 was further independently reduced to 1.0.2.3 in three lineages. The full upper dental formula of 2.1.3.3 was retained except in the

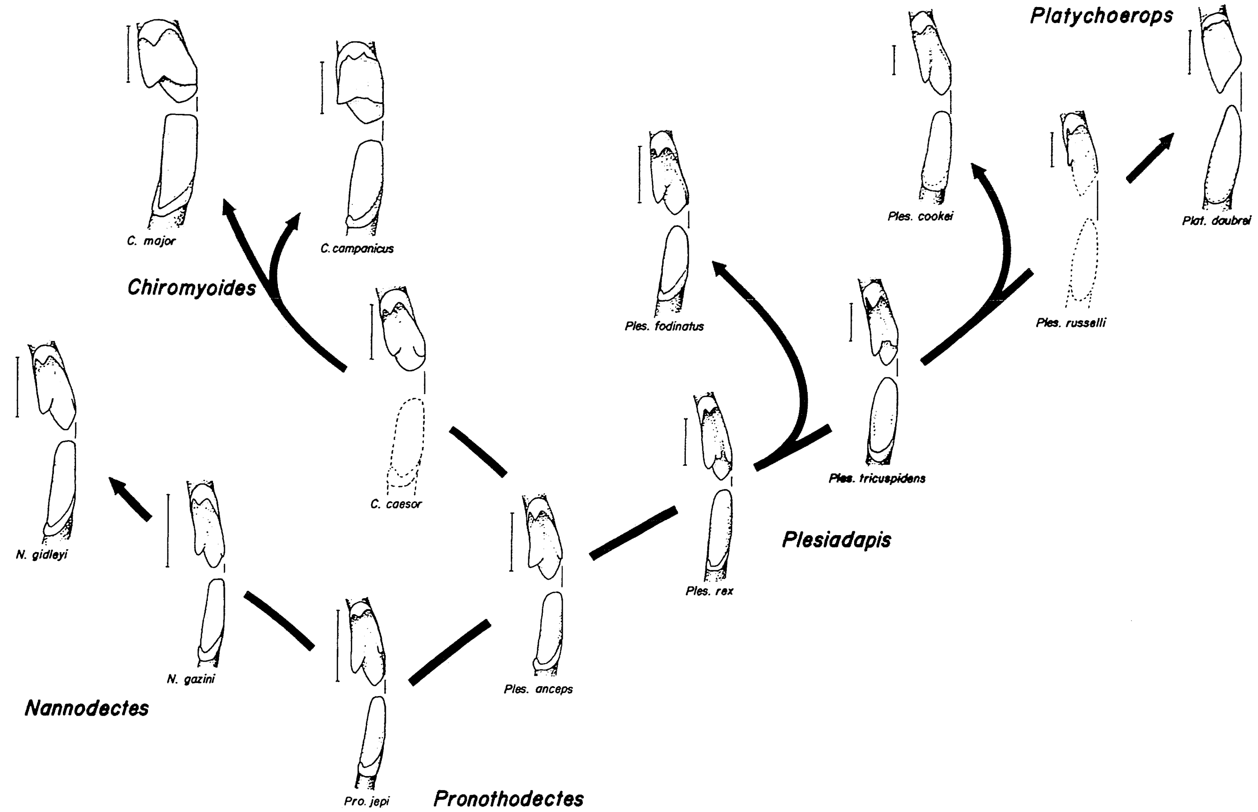


Figure 26. Evolutionary diversification of the incisors of Plesiadapidae. Diagrams of upper and lower incisors of the most important stages of evolution in the five genera of Plesiadapidae, all brought to the same crown length of the upper incisor. All are left incisors in posterior view, with midline at the right. Scale line at left of each pair represents 5 mm. Note particularly the gradual loss of centroconule, mediocone, and laterocone in sequence from *Ples. tricuspidens* to *Plat. daubrei*.

Ples. tricuspidens–Ples. cookei–Platychoerops group, and considering the gross enlargement of the upper central incisor, loss of one or two of the following teeth in *Chiromyoides* seems likely.

The presence or absence of a tooth is a discrete characteristic – in a given specimen the tooth is either present or it is absent. Generally, the retention or loss of the tooth at a given position is determined by functional requirements; thus the loss of a tooth from the dental formula could be expected to happen relatively rapidly, and the result might appear as a series of abrupt discontinuities in the fossil record. Presumably if enough stages were sampled, even the rapid loss of a tooth would appear gradual at the population level, with intermediate polymorphisms connecting the primitive and derived states of, respectively, 'tooth present' or 'tooth lost.'

Such a gradual sequence of polymorphisms does in fact appear in the evolution of *Ples. dubius* from *Ples. rex*. The alveolus for the second lower premolar (P_2) is consistently present in all 80 mandibles of *Ples. rex* preserving this region. The alveolus for P_2 was retained by 50-60% (4 of 7) of the specimens of *Ples. churchilli*. Two large samples of *Ples. fodinatus* are known: 37% of the specimens (9 of 21) from the Princeton Quarry retained P_2, and 37% of the specimens (7 of 19) from the Schaff Quarry retained this tooth. No specimens of *Ples. dubius* have yet been discovered with an alveolus for P_2 (two are known that definitely did not have it). This example shows that where the number of sample levels is large relative to the rate of change of even a discrete character, gradual change through polymorphism can be documented.

Incisor Evolution.– One of the initial reasons for interest in the evolution of Plesiadapidae was the sudden appearance in the fossil record of the genus *Platychoerops*, with unicuspid incisors radically different from the tricuspid incisors characteristic of other plesiadapids. This appears to be a good example of what Simpson (1953) and others have called "quantum evolution."

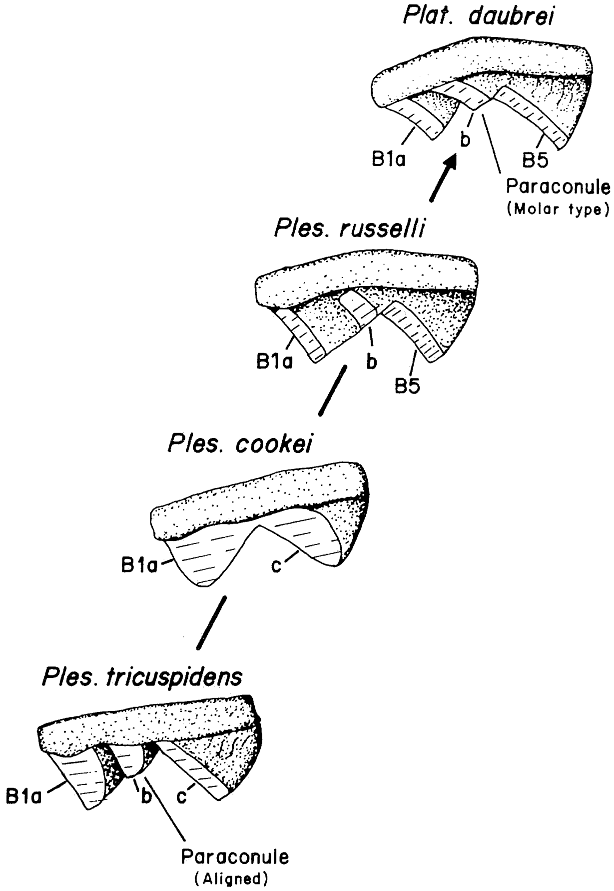


Figure 27. Gradual molarization of P^4 from *Plesiadapis tricuspidens* to *Platychoerops daubrei*. All figures are right P^4 in anterior view. Note progressively more vertical mandibular movement indicated by striations on the wear facets. See text for discussion.

The major stages of incisor evolution in the Plesiadapidae are illustrated in Figure 26. For comparison, all have been brought to the same upper crown length – it should be remembered that the incisors of the earlier species are much smaller than those of most later species.

The incisors of *Pronothodectes* are fully tricuspid, with an anterocone, laterocone, and posterocone. In the *Nannodectes* lineage a small mediocone was added, then subsequently reduced to a ridge of enamel. The mediocone added in the *Plesiadapis* lineage became a strong apical cusp, which in *Chiromyoides* eventually expanded completely across the occlusal surface of the upper incisor to join the laterocone. The strong mediocone of early *Plesiadapis* species was subsequently lost independently in the lineage leading to *Ples. dubius* (via *Ples. fodinatus*) and *Platychoerops*. The centroconule first appearing in *Ples. rex* became stronger in *Ples. tricuspidens* before it was ultimately lost. The centroconule was gradually reduced in *Ples. fodinatus* and is absent in its descendant *Ples. dubius*. In *Chiromyoides major* and *Ples. tricuspidens* the margoconids on the lower incisors were lost independently.

The incisors of *Ples. cookei* and *Ples. russelli* shed considerable light on the evolutionary transformation of the tricuspid upper incisor of *Ples. tricuspidens* into the unicuspid incisor of *Platychoerops daubrei*. The tip of the lower incisor of *Ples. tricuspidens* occluded (as described above in *Ples. rex*) either (a) against the tip of the upper incisor, (b) shearing past the tip of the upper incisor to occlude against the centroconule crest, or (c) shearing against the posterocone. *Plesiadapis cookei* represents the next morphological (if not ancestral) stage in the evolution of the upper incisors. Here the centroconule crest was lost and the mediocone reduced to a crest of enamel. In *Ples. russelli*, the next stage, the laterocone was reduced to a vestigial cusp. An incisor from an early population of *Plat. daubrei* (from Pourcy, not illustrated) shows that initially some individuals of this species retained a large posterocone, which was subsequently lost (Mutigny sample, illustrated in Fig. 26), resulting in the much altered final form characteristic of *Plat. daubrei*. The alteration that previously seemed an inexplicable quantum evolutionary change is thus clearly recorded in the five stages of plesiadapid evolution just described. The change was relatively rapid, but nevertheless continuous and gradual.

The functional shift associated with this morphological change reflects progressive specialization for cropping with the lower incisor shearing only against the anterocrista (see Fig. 5) and not against the posterocrista. In addition, the seed cup formed by the three apical cusps was lost. The end result, in *Platychoerops daubrei*, is a much more specialized incisor mechanism, presumably adapted to a smaller range of food items but able to injest them more efficiently.

Evolution of the Fourth Premolar.– In the section on systematics, notes were given on the relative molarization of the upper fourth premolar in each plesiadapid species. To review briefly, all the species of *Pronothodectes* have a characteristic, well-developed paraconule, or "centroconule," aligned directly between the paracone and protocone. A distinct metacone is usually present as well. Through the course of plesiadapid evolution these two accessory cusps, the paraconule and metacone, are variably present. Of particular interest in this regard is the origin of the molarlike paraconule seen in *Platychoerops*.

Plesiadapis tricuspidens generally has a well-developed aligned paraconule on P^4, although it is absent in a few specimens. In *Ples. cookei* the paraconule is lost entirely on P^4, leaving only the protocone and metacone. *Plesi-*

adapis russelli has an incipient molar-type paraconule, and the paraconule of the molarized P^4 of *Ples. daubrei* is as well developed as that on the true molars. As in the molars, it is no longer aligned with the protocone. These evolutionary stages are outlined diagrammatically in Figure 27.

The functional changes involved provide a partial explanation for the observed morphological changes. During the buccal phase of mastication in *Ples. tricuspidens*, the back of the protoconid (B1 facet) sheared across three successive matching facets on P^4 – these successive facets are numbered B1a, B1b, and B1c in Figure 27. In *Ples. cookei* the paraconule was lost, leaving only the cutting edges of facets B1a and B1c. In *Ples. russelli* the B1a facet remains well developed, followed by a small facet (B1b) on the new incipient paraconule. The facet on the protocone of the P^4 in *Ples. russelli* now no longer follows B1a but corresponds to the B5 facet on the molars, indicating that a metaconid was at least partially developed on P^4. This same pattern is more strongly developed on P^4 in *Plat. daubrei*, a tooth that is virtually fully molariform.

The loss of the aligned paraconule in *Ples. cookei* is evidently the result of its merger with the paracone, resulting in a broader, more open P^4. This is plausibly the result of a simple shift to a slightly more vertically directed buccal phase jaw movement. The original length of shearing crests was then restored by development *de novo* of a paraconule of the molar type, in association with a more molarized P_4. While it is impossible to say for certain which came first, the change in mandibular movement or the change in tooth morphology, it seems more plausible that a simple change in mandibular movement led to the relatively complicated change in tooth morphology.

Evolution of the Third Molar.– One of the most diagnostic features of the dentition of various plesiadapid species is the third lower molar. An outline of its evolution is presented in Figure 28.

The shape of the hypoconulid lobe, or heel, of M_3 shows a number of interesting evolutionary changes. The heel is round and unfissured in the species of *Pronothodectes* and generally remains so in the *Nannodectes* and *Chiromyoides* lineages. In *Ples. rex*, however, the heel becomes more squared, and distinct posterior and medial fissures divide the heel. This pattern of fissures appears in all of the derived species, though the heel becomes less squared in later species.

The later species of *Nannodectes* and *Plesiadapis* have highly crenulated enamel in the talonid basins of M_3. These crenulations evolved independently in *N. gidleyi*, and in *Ples. churchilli* and its derivatives. As with changes in the dental formula and incisor morphology, the evolution of crenulated enamel was gradual, with successive species showing increasingly more crenulated enamel.

DISCUSSION

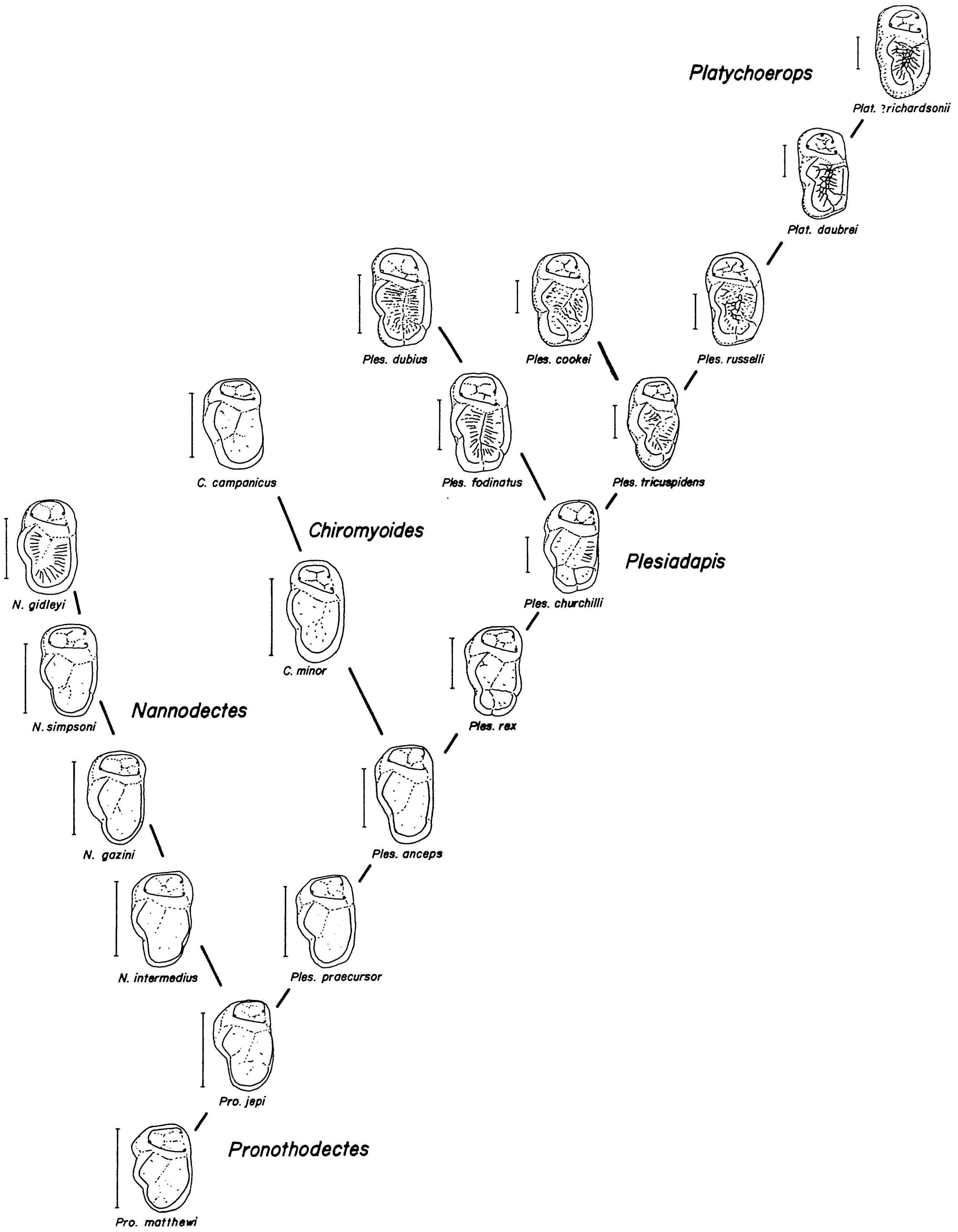
The radiation of plesiadapids led to four evolutionary lineages in North America and three related, but ultimately distinct, lineages in Europe. In four of these lineages (leading to *N. gidleyi, C. major, Ples. cookei, Plat. richardsonii*) the species increased in size. In two lineages (*Ples. dubius, Ples. remensis*) the lineages decreased in size. The final lineage, leading to *C. campanicus*, is inadequately known, so possible changes in size cannot be investigated. The divergent changes in size that inevitably followed the origin of a new lineage would appear to have been adaptive in minimizing competition between two closely related species, but no more general explanation for changes in size can yet be advanced.

The remaining four evolutionary trends described above include reduction of the anterior cheek teeth, diversification of the incisors, molarization of the premolars in the line leading to *Platychoerops* (which happened to a lesser extent in the *Ples. dubius* lineage as well), and complication and crenulation of the enamel on the third lower molar. Apart from the *Chiromyoides* lineages, which perhaps reflect progressive specialization for seed eating (especially in *C. campanicus*), the evolutionary trends all seemingly indicate increasing specialization for a diet of herbaceous vegetation. The cropping specializations of the diverse incisor types are consistent with this view. Loss of occlusion in the anterior cheek teeth and development of a mandibular diastema indicate that the food matter was being ingested in small pieces – the typical method of ingesting herbaceous vegetation. Finally, increasing molarization of premolars, addition of mesostyles, and crenulation of enamel on occlusal surfaces are specializations generally seen in herbivorous mammals.

The fact that the later members of plesiadapid lineages were highly specialized herbivorous feeders does not mean that they fed exclusively on vegetation, nor does it imply that the species of *Pronothodectes* even fed predominantly on herbaceous vegetation. The presence of a greater number of teeth in *Pronothodectes* suggests that the species of this genus were more omnivorous than the later, more specialized plesiadapids.

Finally, it should be clear from this chapter and the previous systematic descriptions that the dental characters of plesiadapids are highly mutable (as presumably are most other characters in Plesiadapidae and other Mammalia as well). The number of independent acquisitions or losses of morphological characters and the number of times a feature was acquired and then lost in the same lineage (minor evolutionary reversals) would make it very difficult to understand the genealogical relationships of the species of Plesiadapidae without a sound, independent stratigraphic framework.

Figure 28. Evolution of M_3 in Plesiadapidae. All figures of left M_3, in occlusal view, with specimens brought to the same length. Scale line at left of each is 3 mm in length. Note particularly the independent evolution of enamel crenulation in three lineages and the fissuring of the hypoconulid lobe characteristic of *Ples. rex* and species derived from it.


Platychoerops
Plat. ?richardsonii
Plat. daubrei
Ples. dubius
Ples. cookei
Ples. russelli
C. campanicus
Ples. fodinatus
Ples. tricuspidens
Chiromyoides
N. gidleyi
Plesiadapis
Ples. churchilli
C. minor
Nannodectes
N. simpsoni
Ples. rex
N. gazini
Ples. anceps
N. intermedius
Ples. praecursor
Pro. jepi
Pronothodectes
Pro. matthewi

VII

CRANIAL ANATOMY

Lemoine's (1887) comments would seem to indicate that he had in his collection a significant portion of the skull of *Plesiadapis*, but since this was never adequately figured and is now apparently lost, it is impossible to confirm his observations. Simpson (1935a) was thus the first to describe in detail significant portions of the skull of a plesiadapid, that of *Nannodectes*. More recently Russell (1959) discovered a nearly complete, though flattened skull of *Plesiadapis tricuspidens* at Berru. Russell (1959; 1964, p. 87-114) has given a very complete description and comparison of the skull from Berru (MNHN Cr 125), as well as several fragments of other skulls of *Ples. tricuspidens* found at Berru. The purpose of this chapter is not to review Russell's descriptions but rather to add supplemental information on several regions of the skull of *Plesiadapis* that are of particular interest. The skull fragments of *Nannodectes* from the Mason Pocket at Tiffany are unfortunately all badly broken and add no information of significance.

The reconstructed skull of *Plesiadapis tricuspidens* is illustrated in Figure 29, which should be compared with Figure 35 to appreciate the remarkable breadth of the skull. In general appearance the skull of *Plesiadapis* resembled that of broad-skulled rodents more closely than it resembled any living primate.

The major masticatory muscles have been added to the skull in Figure 29b. A distinct projecting ridge following the temporal-parietal suture indicates that the temporalis was divided into anterior and posterior parts, a development to be expected whenever the incisors are separated from the cheek teeth by a large diastema. In *Plesiadapis*, as in mammals in general (Gingerich, 1971a), the fibers of the posterior temporalis were aligned with the incisor region and provided the chief force pulling the lower incisors upward and backward against the uppers during incisor biting. The muscle fibers of the anterior temporalis are aligned with the cheek teeth and no doubt provided much of the bite force in this region.

The masseter muscle probably consisted of three parts, as shown in Figure 29b. The first portion, the superficial masseter, was relatively large as evidenced by the large, roughened process at the base of the anterior end of the zygomatic arch for its tendinous origin. The superficial masseter inserted along the posterior and ventral portion of the mandibular angle and pulled the mandible forward. Underlying the superficial portion, the medial part of the masseter muscle originated along the base of the zygomatic arch and inserted on the lateral surface of the ascending ramus of the mandible. Its action elevated the mandible. The deep masseter originated from the posterior part of the zygomatic arch and inserted in the masseteric fossa of the ascending ramus, thus it was functionally a part of the posterior temporalis, retracting the mandible. Significantly, the masseteric fossa is gradually reduced and lost in the lineage leading to *Platychoerops*, indicating that the deep masseter was progressively reduced in mass and suggesting that mandibular retraction was of less importance in *Platychoerops* (as is true of most other specialized herbivores as well). Although not shown in the figure, the orientation of the medial pterygoid muscle shows that it was functionally equivalent to the medial masseter, and the lateral pterygoid muscle was functionally equivalent to the superficial masseter in producing force in a parasagittal plane.

As discussed in the previous chapter, the buccal and lingual phases of a transverse mandibular movement involved first upward and forward, then slightly downward and forward movements. Following the principle that masticatory muscle fibers are, where possible, aligned with the bite they produce, it is to be expected that the deeper fibers of the masseter and the medial pterygoid would provide the greatest power to the buccal phase, and the superficial masseter and lateral pterygoid would provide the greatest power to the lingual phase of a transverse mandibular movement. This is essentially the pattern shown by Kallen and Gans (1972) in their electromyographic study of mastication in the little brown bat *Myotis*.

Szalay (1972b, p. 19) asserted that the mandibular

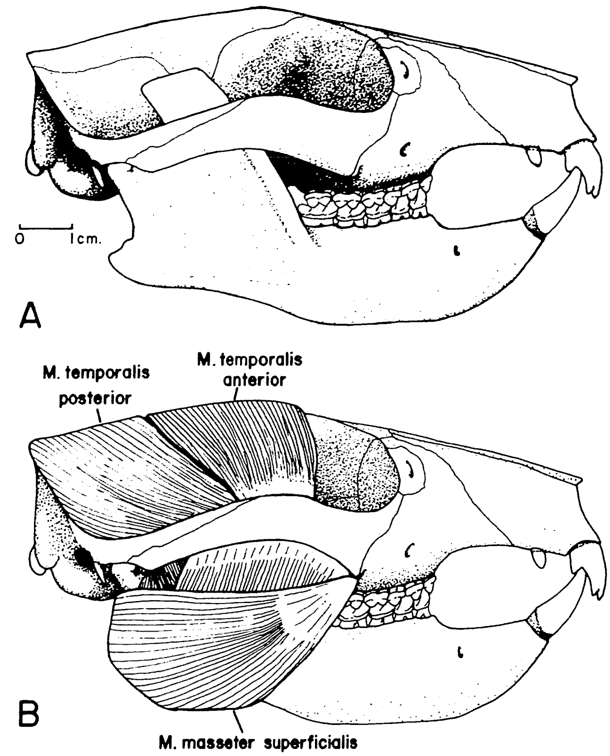


Figure 29. Reconstruction of the skull of *Plesiadapis tricuspidens*. (A) Lateral view, modified from Russell, 1964, fig. 13. (B) Lateral view with generalized temporalis and masseter musculature restored.

symphysis of *Chiromyoides* was probably fused during at least part of its ontogeny, but the symphyseal morphology of all of the known plesiadapid mandibles (including those of *Chiromyoides*) show clearly that the symphysis remained mobile throughout the life of the animal.

In the remaining sections of this chapter several specific problems of dental homology, tooth replacement, and relationships of bones in the nasal, orbital, and basicranial regions will be discussed, and observations will be presented on a new skull of *Ples. tricuspidens* (in the collection of M. Pellouin) and a partial skull of *Ples. anceps* (PU 19642).

DENTITION

Dental Formula.– Throughout the discussion in the preceeding chapters the full dental complement of primitive Plesiadapiformes was assumed to be $\frac{2}{2}\,\frac{1}{1}\,\frac{3}{3}\,\frac{3}{3}$, and confirmation of this was deferred to this section. Species of the most primitive plesiadapid, *Pronothodectes*, have nine teeth in the upper and lower jaws. In the upper jaw, the two most anterior teeth are in the premaxilla (as determined from specimens of *Nannodectes* and *Plesiadapis*), and they are thus regarded as incisors. The three most posterior upper teeth have no deciduous precursors and are thus true molars.

Recently, a specimen of the microsyopoid primate *Palaechthon* was described (Wilson and Szalay, 1972), which shows that the third tooth in the upper dentition followed immediately behind the premaxilla-maxilla suture and that it was relatively larger than the following tooth, both of which are general characteristics of canine teeth. The upper dental formula of the dentally primitive *Palaechthon* (and "*Plesiolestes*," see Szalay, 1973) was thus almost certainly 2.1.3.3. Considering the enlargement and occlusion of the third lower tooth of *Palaechthon* (Fig. 30a), that tooth is almost certainly a lower canine, making a lower dental formula of 2.1.3.3 as well. Comparing the dentition of *Pronothodectes matthewi* with that of *Palaechthon problematicus* (Fig. 30) suggests that $\frac{2}{2}\,\frac{1}{1}\,\frac{3}{3}\,\frac{3}{3}$ was almost certainly the dental formula of *Pronothodectes* as well.

Previous interpretations of the dental formula of microsyopids (Bown and Gingerich, 1972; 1973) assumed a lower formula of 2.1.3.3, and the skull of *Palaechthon* shows that the upper formula was 2.1.3.3. This would appear to make derivation of Microsyopidae from "*Plesiolestes*" or *Palaechthon* (advocated by Bown and Gingerich, 1973) impossible, since the dental formula of a well-preserved skull of *Microsyops* was interpreted as 1.1.4.3 by Szalay (1969, p. 264, fig. 16). Reexamination of the *Microsyops* skull (AMNH 55284) clearly shows that the upper dental formula of this genus was 2.1.3.3, as McKenna's (1966) figure 8 also indicates. The critical region of the skull is shown in Figure 30c, with the course of the premaxilla-maxilla suture indicated. An additional maxilla (AMNH 13041) figured by Matthew (1915; and partially figured by Szalay, 1969, pl. 46) also indicates an upper dental formula of 2.1.3.3. Thus, there is no reason to bar *Palaechthon (="Plesiolestes")* from the ancestry of *Microsyops*, and their very close similarity supports such a relationship (Bown and Gingerich, 1973).

The dental formulae and homologies given here are those conventionally used in mammalogy, where teeth are identified according to the following definitions:

1. Incisors are teeth erupting in the premaxillae (upper jaws), or teeth occluding with teeth in the premaxillae (lower jaws).
2. The canine is an enlarged tooth erupting at the front of the maxilla (upper jaw), or an enlarged tooth occluding with and just in front of this tooth (lower jaw).
3. Premolars are the anterior series of postcanine teeth that generally have deciduous precursors.
4. Molars are the posterior series of postcanine

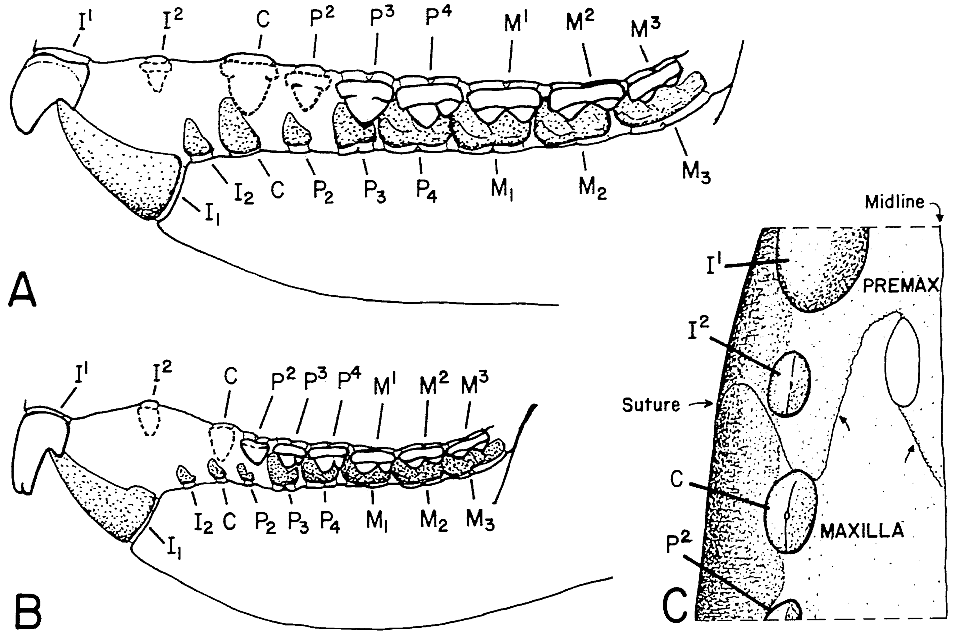


Figure 30. Homologies of the teeth of *Pronothodectes* by comparison with the dentition of *Palaechthon*. (A) Left dentition of *Palaechthon problematicus* in lateral view, with dashed crowns restored from figure in Szalay, 1973. (B) Left dentition of *Pronothodectes matthewi* in lateral view. (C) Right upper anterior dentition of *Microsyops lundeliusi* in occlusal view, with the course of the maxilla-premaxilla suture indicated by arrows. See text for discussion and rules of homology employed here.

teeth that lack deciduous precursors.

When it was not possible to precisely apply an appropriate above definition to teeth in a fragmentary specimen, the teeth in this specimen were identified by comparing them to similar teeth thought to be homologous in closely related, more complete specimens.

West (1973, citing McKenna) published revised identifications of the large anterior teeth of apatemyid insectivores as canines rather than incisors, and Schwartz and Krishtalka (1976) recently stated that they believe the enlarged anterior teeth in *Plesiadapis* and its relatives to be canines rather than incisors. These new interpretations are based on a new and different set of definitions, and rules of homology different from those conventionally accepted. The new interpretations will apparently alter much of what has been written about tooth homologies in the previous literature, and it seems imperative that a new terminology be introduced by Schwartz et al. to avoid confusion over the meaning of such standard terms as incisor, canine, premolar, and molar. Having studied all of the relevant fossil specimens, it is clear that *according to conventional definitions* the enlarged anterior tooth in both apatemyids and plesiadapids is the central incisor, not the canine.

Tooth Eruption.– Lemoine (1887) mentions a specimen of *Plesiadapis* with the incisor partially erupted, but his specimen was never figured and it has evidently been lost. As Schlosser (1921) noted, incisors of a rudimentary plesiadapid type (figured by Russell, 1964, pl. 3:7) are almost certainly deciduous incisors of *Plesiadapis tricuspidens*. Simpson (1935a) has figured deciduous cheek teeth of *Nannodectes gidleyi*, and the Mason Pocket collection of *Nannodectes* includes deciduous incisors as well.

About a dozen mandibles and maxillae of *Plesiadapis* and *Nannodectes* in North American collections show deciduous teeth being replaced. The most interesting of these are illustrated in Figure 31. The order of eruption indicated by the specimens thus far discovered (based on AMNH 17372, 17387; PU 13968, 17603, 17615, 17621, 17622, 20799; UW 1701) is as follows:

Upper Dentition: $dP^2, dP^3, dP^4/M^1/M^2/P^2, M^3/P^3/P^4$

Lower Dentition: $dP_3, dP_4/M_1/M_2/P_2, M_3/P_3/P_4$

Plesiadapis thus resembles *Adapis, Tupaia, Microcebus*, and *Lemur* in having P3 and P4 consistently erupt after

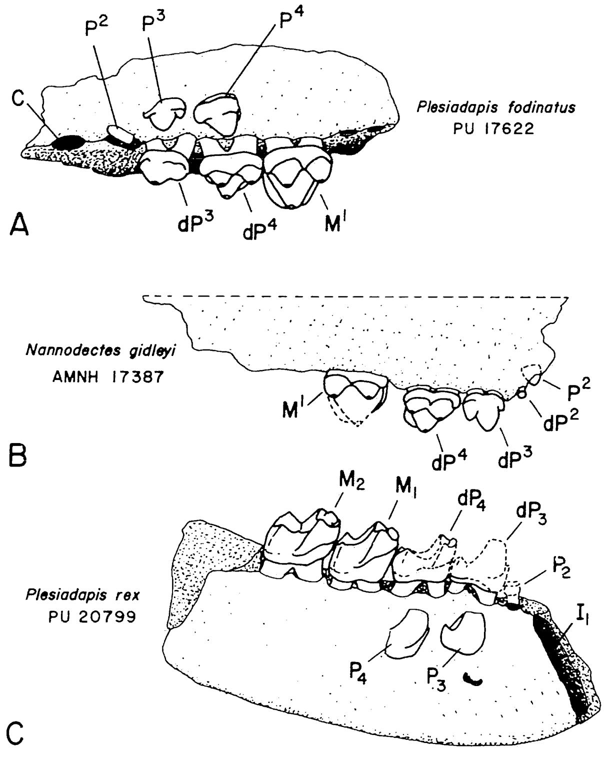


Figure 31. Specimens of *Nannodectes* and *Plesiadapis* showing teeth in the process of eruption. See text for sequence of eruption inferred from these and other specimens.

the three molars are in place (Bennejeant, 1936, p. 69-88; Schultz, 1956, p. 937). This is presumably the primitive pattern in primates, whereas *Tarsius*, some Lemuriformes, and higher primates have retarded the eruption of M3 as a result of shortening the jaws.

It should be noted that the upper canine in *Plesiadapis* erupted before P^2 (see Fig. 31a); dP^2 was a minute tooth in *Nannodectes* (Fig. 31b); and P_2 was probably more important functionally in the early stages of tooth eruption (Fig. 31c) than it was once the full permanent dentition was in place in those species of *Nannodectes* and *Plesiadapis* that retained P_2.

NASAL REGION

The nasal region of *Plesiadapis* is distinctive in having a very large premaxilla, which extends back parallel to the nasal bones to contact the frontals. Russell (1959, p. 312) first described this remarkable (for a primate) enlargement of the premaxillae, and later elaborated further:

> L'écrasement subi a rendu difficile la détermination de la limite postérieure et dorsale des prémaxillaires. Les deux os ont été brisés de la même manière et au même niveau, au-dessus et en avant de P^2. La configuration actuelle semble indiquer que la cassure s'est produite le long d'une suture, bien qu'aucune trace n'en soit visible. On peut suivre, au contraire, latéralement, une vraie suture qui se prolonge loin vers l'arrière, témoignant ainsi d'un large contact prémaxillo-frontal. Il est certain que les nasaux n'occupent pas cette région, car leurs sutures sont parfaitement visibles. (Russell, 1964, p. 88)

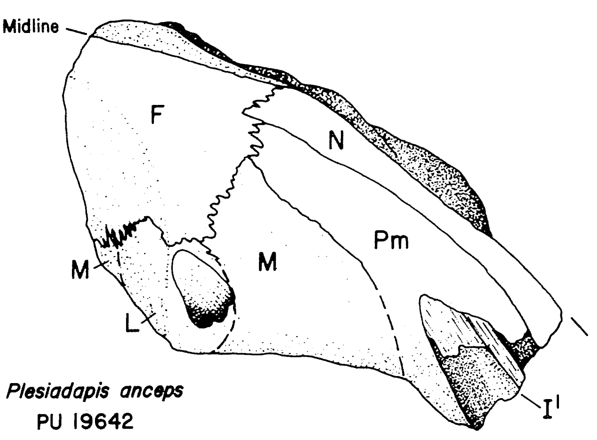


Figure 32. Premaxilla-frontal contact in *Plesiadapis anceps*. Figure is of the right side of a broken snout, in oblique lateral view. Note also the partially preserved lacrimal canal, which opened well out on the face. Figure approximately twice natural size.

Nevertheless, Szalay (1971) proposed that the premaxillae actually ended where they are broken, and that they did not extend back to contact the frontals as Russell had observed. Restudy of the skull in question (MNHN Cr 125) has shown that Russell's observations are correct – the premaxillae are enlarged and contact the frontals exactly as he described them (see also Plate 8). Szalay's assertion is simply incorrect. In addition, the frontal of the Pellouin skull shows the sutures for the premaxillary-frontal contact clearly.

Of interest also is a broken skull of *Plesiadapis anceps* (Figure 32) collected by Marshall Lambert at the 7-up Butte locality in the Medicine Rocks area of Montana. The premaxillae in this species clearly contacted the frontals also, although they were not so greatly enlarged as the premaxillae of *Ples. tricuspidens* (Fig. 34). The premaxillae appear not to have contacted the frontals at all in *Carpolestes dubius* (PU 19422; see Rose, 1975, fig. 32) or in *Phenacolemur pagei* (PU 19498), but they did contact the frontals in the related paromomyid *Ignacius graybullianus* (UM 65569, Gingerich and Rose, in prep.). As was noted elsewhere (Gingerich, 1971b), enlarged premaxillae contacting the frontals are characteristic of marsupials (*Dactylopsila*), primates (*Daubentonia*), Rodentia, and Lagomorpha that have enlarged, procumbent central incisors.

ORBITAL REGION

Virtually the entire orbital region of *Plesiadapis* can be reconstructed from the skull of *Plesiadapis tricuspidens* (MNHN Cr 125) and several additional unflattened skull fragments, all from Berru. Russell's (1964, fig. 19) reconstruction of this region is illustrated here in Figure 33. Of particular interest are the facial exposure of the lacrimal and the absence of an ethmoid component (os planum) in the orbital wall.

As shown in Figure 33, a large portion of the lacrimal bone in *Plesiadapis tricuspidens* extended onto the face, and the lacrimal foramen was well out on the face as well. The same appears to have been true in *Ples. anceps* (Fig. 32), although this skull is not so well preserved. In having the lacrimal foramen well out on the face, *Plesiadapis* resembles *Necrolemur* (see Simons and Russell, 1960) and differs from *Adapis* and *Notharctus*, which have the lacrimal foramen near or in the orbital margin.

Figure 33 shows the relationship of bones within the orbit. The frontal clearly contacted the maxilla behind the lacrimal, and there is no trace of an intervening ethmoid component (os planum). Presence of an os planum is sometimes considered a primitive character of primates, but primitive mammals in general lack it, as do all Eocene primates, so an os planum is unlikely to represent a primitive state in those primates that have it. As Cartmill (1971) noted, ethmoid exposure in the orbit is a simple result of having relatively large orbits positioned close together – this condition has probably developed independently in *Tarsius*, in cheirogaline lemurs, in Lorisoidea, and in Anthropoidea, and an os planum may thus have evolved independently four or more times.

BASICRANIAL REGION

The basicranial region of *Plesiadapis tricuspidens* has been described in detail by Russell (1959, 1964). The major features of the basicranial region of the most complete skull (MNHN Cr 125) are illustrated here in Plate 8. The basicranium of an additional skull (in the private collection of M. Pellouin) is illustrated in Plate 9.

The Pellouin skull preserves the entire right auditory bulla virtually complete and uncrushed (several small fragments were removed to permit cleaning the interior of the bulla). The auditory bulla of *Plesiadapis tricuspidens* was completely ossified and continuous with the petrosal, as in tree-shrews (Spatz, 1966) and all primates. These are important characters in which *Plesiadapis* differs from most of the Insectivora. Miocene and various later hedgehogs have an ossified bulla, but it is continuous medially with, and largely formed from, the basisphenoid and not the petrosal (Butler, 1948; Rich and Rich, 1971). Similarly, the bulla of the late Eocene European apatemyid *Heterohyus* was continuous with the basisphenoid (Hürzeler, 1949). The Oligocene leptictid insectivore *Leptictis* (=*Ictops*, see Fig. 41) had an ossified bulla continuous with the petrosal, resembling in the latter character both tree-shrews and primates.

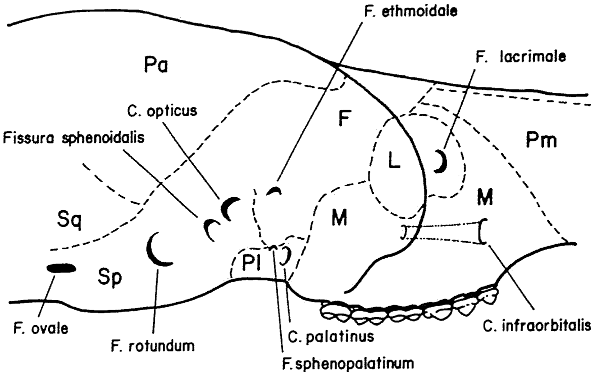


Figure 33. Orbital foramina in *Plesiadapis tricuspidens*. The relationships of the bones comprising the orbital region are indicated, as well as the contained foramina (F.) and canals (C.). Note particularly the facial position of the lacrimal foramen, and the absence of an ethmoid element between the orbital components of the frontal and maxilla. F, frontal; L, lacrimal; M, maxilla; Pa, parietal; Pl, palatine; Pm, premaxilla; Sp, sphenoid; Sq, squamosal. Redrawn from Russell, 1964, fig. 19.

Since the Pellouin skull represents a relatively old individual of *Plesiadapis tricuspidens*, it is not possible to determine whether an independent entotympanic center of ossification was present or not, but the important fact is that the bulla was completely ossified and continuous with the petrosal. The lateral wall of the bulla was apparently formed in large part by the ectotympanic, but all sutures are obliterated, and the precise contribution of this element cannot be determined. The lateral extension of the ectotympanic to form an external auditory tube is of considerable interest and importance. This is a character in which *Plesiadapis* resembles Eocene Tarsiiformes and differs from Eocene Lemuriformes.

Middle Ear.– The left and right middle ear of the Pellouin skull of *Plesiadapis tricuspidens* are illustrated in Plate 9. As was noted above, the right auditory bulla is preserved uncrushed and almost intact. By removing a small portion of the ventral wall of the bulla it was

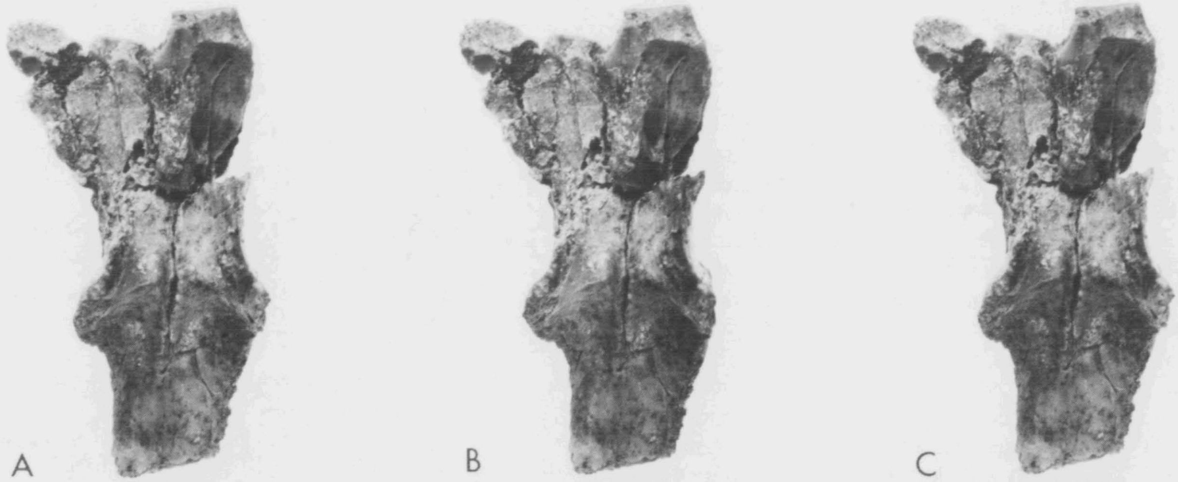


Figure 34. Frontal fragment of skull of *Plesiadapis tricuspidens* from Berru, in ventral aspect (YPM 24618, gift of M. P. Louis). (A-B) Stereophotographs showing actual specimen. (B-C) Reversed stereophotographs showing external morphology of brain fitting frontal fragment (technique suggested by M. R. Lavocat). Figure 1.5 times natural size.

possible to clean the interior. The ectotympanic ring holding the ear drum was uncovered, and it is virtually intact. The skull described by Russell (1964) preserves part of the ectotympanic ring, so it was previously known that the ring was fused into the lateral wall of the bulla, but the Pellouin skull shows this more clearly than any previous specimen. Of considerable interest is the suspended position of the ring – the ring itself is not part of the wall of the bulla, but it is suspended from the wall by a number of ossified struts. Suspension of the ring by struts, rather than direct fusion into the lateral wall, is a character in which *Plesiadapis* closely resembles *Necrolemur* (see Simons, 1961a).

The carotid circulation within the bulla of *Plesiadapis* has been much discussed. Initially, Russell (1959, p. 312) stated that the bony tube for the lateral branch of the internal carotid artery extended without any lateral opening to a point on the posterior side of the cochlear window. The internal carotid then crossed the ventral side of the cochlear fenestra, where it divided into a promontory and a stapedial branch. The stapedial branch passed beneath the vestibular fenestra and entered the extrapetrous portion of the Fallopian aqueduct. Russell (1959) stated that, to judge from the grooves on the surface of the promontorium, the two branches seemed to be of about equal size.

Saban (1963) noted that the grooves on the promontorium, which had been presumed to indicate the course of the stapedial and promontory branches of the internal carotid artery, were very variable in development and in course. Russell (1964, p. 97-98) subsequently noted that the presence of a stapedial artery was not certainly indicated in all specimens and suggested that this branch was, if present, reduced or vestigial.

In the Pellouin skull, the left promontorium has a bony process in a position that would apparently block any artery dividing off of the promontory branch from reaching the vestibular fenestra and stapes. It is probable that the variable, multiple grooves on the promontoria of numerous isolated petrosals are grooves for the nervous tympanic plexus, rather than for the internal carotid system of arteries.

In *Plesiadapis tricuspidens* a small internal carotid artery (.3 mm in diameter) entered the auditory bulla at its posterior margin, crossed the promontorium, and left the middle ear via the internal carotid foramen (not preserved), or via the vidian foramen (preserved in the left bulla of the Pellouin skull). It is not possible to determine with certainty if a stapedial branch of the internal carotid was present; but if it was present, the stapedial branch was apparently vestigial. The carotid circulation was thus highly reduced – another indication that the family Plesiadapidae was an aberrant and highly specialized group of early mammals.

BRAIN

Very little evidence is available on the brain anatomy of *Plesiadapis*, but a fragmentary frontal (YPM 24618, see Figure 34) does give some information on the relative size and conformation of the olfactory bulbs and assists in estimating the total volume of the brain of *Ples. tricuspidens*.

The extent of the preserved portion of the internal surface of the braincase of *Plesiadapis tricuspidens* is illustrated in Figure 35. In Figure 35, the conformation of a latex partial endocranial cast has been superimposed on an outline of the cranium. Both the endocranial cast and its relative position on the reconstruction were from YPM 24618. The outline of the remainder of the brain can be determined very approximately from the shape of the skull in dorsal view (see Plate 8). In lateral view, the ventral outline is less well defined, but it was probably not too different from that shown in Figure 35a. As Jerison (1973, p. 368) has noted, the brain of *Plesiadapis* was clearly spherical (see also Radinsky, 1976). The reconstruction of the brain of *Plesiadapis tricuspidens* in Figure 35 represents the absolute maximum brain size that could plausibly be fitted into the skull, and it is possible that the brain was actually somewhat smaller.

The external surface of the brain of *Plesiadapis* compares rather closely with that of the slightly later Eocene tarsiiform *Tetonius* (Radinsky, 1967), although it obviously occupied a relatively much smaller proportion of the skull in *Plesiadapis*. The ratio of the length of the olfactory bulbs to maximum cerebrum length is about 1:3.9 in *Plesiadapis*, which is also the ratio determined by Radinsky for *Tetonius*.

It is possible to make a very rough estimate of both the brain size and the body size of *Plesiadapis tricuspidens*, which in turn permits the relative brain size of this species to be compared with that of other mammals. Jerison's (1973, p. 50) method of graphic double integration was applied in Figure 35, yielding a brain volume of 18.7 ml. A marmot with a postcranial skeleton the size of *Plesiadapis tricuspidens* weighs about 4 kg, and this value was assumed for the weight of *Ples. tricuspidens*. Using Jerison's value k=.12 (1973, p. 61), the encephalization quotient (EQ) of *Plesiadapis tricuspidens* is:

$$\mathrm{EQ}= \frac{18.7}{(.12)(4000)^{2/3}} = \frac{18.7}{30.2} = .62$$

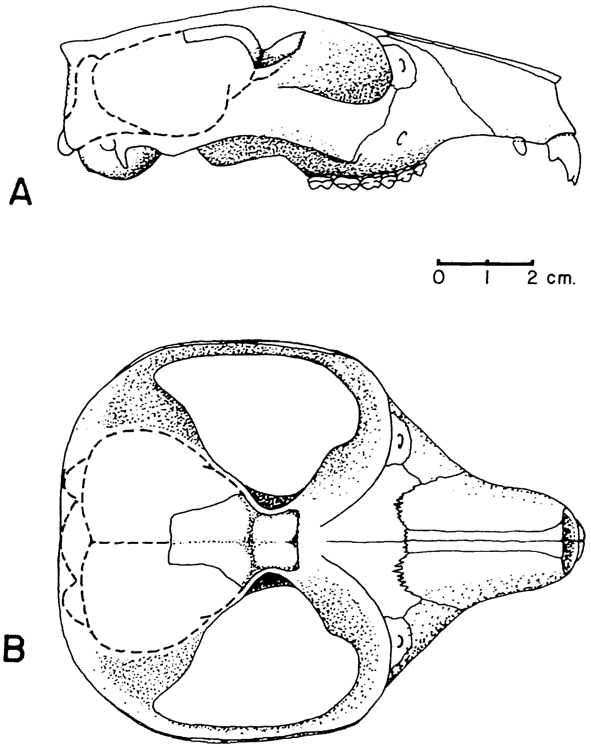


Figure 35. Conformation of the olfactory bulbs in *Plesiadapis tricuspidens*, in lateral (A) and dorsal (B) view. Outline of cerebrum and cerebellum restored to maximum size that fits within the preserved external morphology of the cranium. See also Figure 34, and text for further discussion.

Comparing this EQ with those of living prosimians (Jerison, 1973, fig. 16.7) shows *Plesiadapis* to fall at about the 5th percentile. In fact, the relative size of the brain of *Plesiadapis* is exceeded by that of all living prosimians. The EQ of *Plesiadapis* compares closely with an EQ of .68 for *Tetonius*, .55 for *Smilodectes*, and .58 for *Adapis* calculated by Jerison using this method. Comparing the EQ of *Plesiadapis* with those of other mammals (Jerison, 1973, fig. 10.6) shows that the encephalization of *Plesiadapis* is (1) much higher than that of archaic ungulates – its contemporaries in the early Tertiary, (2) among the highest 20% of living insectivores, and (3) about average for living rodents.

Radinsky (1976) has made the above calculations independently, estimating minimum and maximum possible values of the encephalization quotient by reconstructing the smallest and largest brain sizes he considered to have been possible in *Plesiadapis tricuspidens*. Radinsky thus derived a minimum EQ of .39 and a maximum EQ of .55, with the true value probably lying somewhere in between. Assuming conservatively that the EQ of *Plesiadapis* was between .40 and .50, its encephalization still far exceeded contemporary archaic ungulates, was about average for living insectivores, and was in about the 20th percentile for living rodents (following Jerison, 1973, fig. 10.6). The encephalization of *Plesiadapis* was apparently still comparable to that of the Eocene primates *Tetonius, Adapis,* and *Smilodectes*, judging from Radinsky's revised EQ estimates of .39 to .42 for the three Eocene genera (Radinsky, 1976).

VIII

NOTES ON THE PALEOBIOLOGY OF PLESIADAPIDAE

In studying any group of fossil mammals, it is desirable to reconstruct as much as possible of the life habits and habitat of the group. This must be done by comparing the extinct forms with similar living mammals. Cranial and dental morphology are important in this regard, as is postcranial anatomy. The probable habits and habitat of Plesiadapidae will be discussed following a brief consideration of the postcranial anatomy of *Plesiadapis.*

POSTCRANIAL ANATOMY AND EVOLUTION

Lemoine (1893) described the first fragmentary postcranial remains perhaps belonging to *Plesiadapis*, and Teilhard (1922, pl. 1: 33) figured the distal half of a humerus of *Plesiadapis remensis* from Cernay. Gregory (1920, p. 70, pl. 27) discussed and figured the humerus of *Nannodectes (=Nothodectes) gidleyi*. Subsequently, Simpson (1935a) discussed the postcranial anatomy of *Nannodectes (=Plesiadapis) gidleyi* in much greater detail, and Szalay et al. (1975) described additional elements preserved in *Plesiadapis tricuspidens*. Unfortunately, Gregory's comparison of the humerus of *Nannodectes* was only with that of *Notharctus*, and Simpson's comparisons of the known skeletal elements of *Nannodectes* were largely confined to *Ptilocercus, Tupaia, Lemur,* and *Tarsius*. The primary concern of Gregory, Simpson, and Szalay et al. was the systematic position of *Nannodectes*: Gregory concluded that *Nannodectes* was *not* a primate, while Simpson and Szalay et al. concluded that it *was* a primate. Russell (1964, p. 114) and Simons (1964; 1967) have also figured and briefly discussed skeletal material of *Plesiadapis tricuspidens* from Berru.

The systematic position of *Plesiadapis* and *Nannodectes* is not in question at this point, rather the problem is to determine which living mammals *Plesiadapis* most nearly resembles in its postcranial anatomy. Locomotor classification of living primates is a subject of much discussion and some disagreement. Napier and Walker (1967) recognized four main locomotor types: (1) Vertical Clinging and Leaping, (2) Quadrupedalism, (3) Brachiation, and (4) Bipedalism. They further suggested that *Plesiadapis* was rodentlike, probably quadrupedal, and possibly resembled a tree shrew or a squirrel in locomotor habit.

The basic proportions of the postcranial skeleton of *Plesiadapis insignis* are illustrated in Figure 36, based on negative impressions of two specimens preserved on four slabs of rock. The difficulty of making measurements on these specimens is, however, partially compensated by the fact that the specimens are articulated, and thus known to belong to one or the other of two individual animals.

To further pursue the suggestion of rodentlike habits for *Plesiadapis*, the limb proportions of *Ples. insignis* are compared with those of a ground squirrel (*Citellus*), a marmot (*Marmota*), and a tree squirrel (*Sciurus*) in Table 12. There is little good comparative data published on limb proportions in rodents, the recent paper by Thorington (1972) on *Sciurus carolinensis* being an exception (even here measurements on immature individuals are included in the statistics, making them unsuitable for comparison with *Plesiadapis*).

The fore and hind limbs of *Ples. insignis* are much shorter, relative to trunk length, than those of any living primate (Schultz, 1956, p. 920), and they fall within the range of the three sciurid rodents listed in Table 12. Relative proportions of the limbs and limb segments are also listed in the table. *Plesiadapis insignis*, with brachial, crural, and intermembral indices of 86, 91, and 72, respectively, resembles the three rodents listed in these proportions also. Szalay (1972b, p. 34) derived brachial, crural, and intermembral indices of 93, 93, and 81, respectively, for *Ples. tricuspidens* based on a figure published by Simons (1964, p. 56). My own measurements of casts of the limb bones of the associated partial skeleton of this species suggest indices of 95, 100, and 88, respectively.

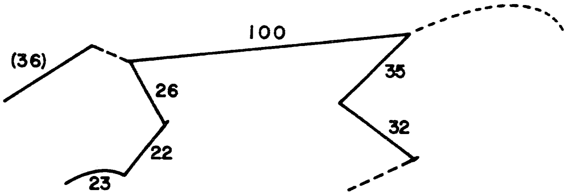


Figure 36. Limb proportions in *Plesiadapis insignis*, based on the measurements listed in Table 6. All lengths standardized to a trunk length of 100 for ease of comparison. Length of dashed segments is unknown.

Table 12. Limb lengths (mm) and proportions of *Plesiadapis insignis* compared to those of three sciurid rodents. Figures in parenthesis are standardized to a trunk length of 100. Data for *Ples. insignis* from Table 6.

Length or Index	*Plesiadapis insignis*	*Citellus tridecemlineatus* YPM 1221	*Marmota monax* YPM 111	*Sciurus carolinensis* YPM 1305
Trunk	135(100)	110(100)	250(100)	148(100)
Humerus	35(26)	24(22)	68(27)	41(28)
Radius	30(22)	22(20)	54(22)	38(26)
Femur	47(35)	33(30)	80(32)	55(37)
Tibia	43(32)	33(30)	80(32)	61(41)
Brachial Index[1]	86	92	80	93
Crural Index[2]	91	100	100	111
Intermenbral Index[3]	72	70	76	68

[1] Brachial index = radius length/humerus length

[2] Crural index = tibia length/femur length

[3] Intermembral index = humerus + radius length/femur + tibia length

All of these estimates of limb proportions in *Plesiadapis* compared with those of the sciurids listed in Table 12 suggest that the resemblance is somewhat closer to the more terrestrial forms *Citellus* and *Marmota* than to the arboreal scrambler *Sciurus*. The characters of most significance in which *Plesiadapis* differs from *Sciurus* appear to be its larger intermembral index and relatively small crural index. In other words, *Plesiadapis* lacked the elongated tibial segment of the hind leg associated with squirrel-like locomotion.

A complete description of the postcranial anatomy of *Plesiadapis tricuspidens* cannot be given here, but several points should be noted. As Simons' (1964) figure and the minimum width measurements of *Ples. insignis* in Table 6 show, the limb bones of *Plesiadapis* are more robust than is characteristic of arboreal squirrels. Certain additional morphological details of the limb bones of *Plesiadapis* and *Nannodectes* suggest a resemblance to marmots and other primarily terrestrial mammals. The humerus of *Plesiadapis* and *Nannodectes* has, as Gregory (1920, p. 70) noted, a relatively large tuberosity for the insertion of M. teres major. This tuberosity and the M. teres major are grossly enlarged in moles, with the teres major being the chief muscle used in burrowing (Campbell, 1939; Reed, 1951). This suggests a possible burrowing habit for *Plesiadapis*, although obviously more comparative evidence is needed. Fossorial gophers (*Geomys*) and prairie dogs (*Cynomys*) have little or no teres tuberosity; whereas badgers, also well known for their digging ability, have a large tuberosity for the teres major.

Similarities have been noted between the claws of *Plesiadapis* and those of the dermopteran *Cynocephalus* (Russell, 1964, p. 115), thus an alternate function of powerful retraction of the humerus by the teres major in *Plesiadapis* could possibly have been to pull the body up trees in the manner of dermopterans (see Wharton, 1950, p. 270). *Cynocephalus*, however, lacks a teres tuberosity, suggesting that its peculiar locomotion is differently powered than that of *Plesiadapis*.

The humeri of *Plesiadapis* (see Teilhard, 1922, pl. 1: 33) and *Platychoerops* (UCMP 103829) have a much more expanded supinator crest than *Nannodectes* (see Simpson, 1935a, fig. 7b). The shallow olecranon fossa of the *Platychoerops* humerus indicates that full extension of the forelimb was probably not possible and that it was habitually in a highly flexed position. The medial epicondyle is large, as one would expect in an animal having a clawed manus and requiring powerful flexor muscles. The ulna of *Nannodectes* figured by Simpson (1935a, fig. 7c) is distinctly flexed dorsally at midshaft, and the head of the radius forms a distinctly flattened oval, both of which suggest limited pronation and supination. Each of these five characters of the forelimb is shared by *Plesiadapis* and marmots of about the same size.

P. Teilhard de Chardin (1922, p. 24) was the first to speculate about the life habits of *Plesiadapis*. He concluded that the Plesiadapidae were a group of "sciuroid" adaptation, probably resembling rodents in external appearance, habitat, and habits. Furthermore, the large numbers of *Plesiadapis* found at Cernay suggested to Teilhard that *Plesiadapis* lived in bands or colonies and was not arboreal but teemed (*pullulait*) at ground level. Russell (1962) suggested that *Plesiadapis* might have climbed trees to escape danger but spent most of its time at or near ground level. Simons (1967) noted that the presence of *Plesiadapis* in Europe and western North America suggested that at least some species of the genus were able to live away from forests, reasoning that a continuous forest cover connecting the two areas was unlikely. More recently, Van Valen (1971a) noted that the near absence of *Plesiadapis* in the Paleocene forest community represented by the collection from the Bear Creek locality in Montana suggests that *Plesiadapis* was probably not arboreal. All of this evidence, together with the limb proportions and the forelimb resemblances to *Marmota*, rather strongly suggest that *Plesiadapis* was primarily a terrestrial mammal, although it is possible that some members of the family,like some Sciuridae, were partly or largely arboreal.

Several additional points need to be discussed in connection with the evolution of locomotor behavior in early primates. While *Plesiadapis* appears to have been primarily a terrestrial quadruped, this does not mean that the smaller and still less well known plesiadapiform primates close to the actual ancestry of Tarsiiformes (see next chapter) were necessarily terrestrial or even quadrupedal. The rodent family Sciuridae includes species ranging from exclusively terrestrial to exclusively arboreal, and the Plesiadapiformes may have been similarly diverse in habitat preference.

Napier and Walker (1967) and Napier (1967) have proposed Vertical Clinging and Leaping as the primary and earliest arboreal locomotor adaptation in Primates. The phylogeny of primates discussed in the following chapter suggests that *Tarsius* and the lemuriform vertical clingers and leapers are less closely related than was previously thought. Since the Plesiadapiformes now appear to represent a group broadly ancestral to the Tarsiiformes but not to the Lemuriformes, Plesiadapiformes are near, rather than antecendent to, the evolutionary pathway connecting Tarsiiformes and Lemuriformes. The absence of vertical clinging and leaping adaptations in *Plesiadapis* thus raises a serious question as to whether vertical clinging and leaping in *Tarsius* and in Lemuriformes (those that practice VCL) is a result of common inheritance or an independently acquired behavior. Stern and Oxnard (1973) recently concluded on morphological grounds that "Vertical Clinging and Leaping" is probably an artificial locomotor grouping, which suggests, as does the inferred locomotor adaptation of *Plesiadapis*, that a vertical clinging and leaping locomotor pattern was acquired independently by *Tarsius* and by lemuriform primates.

PALEOBIOLOGY

The dietary specializations, body and limb proportions, large numbers found in fossil deposits, and geographic distribution of *Plesiadapis*, suggest that the ground squirrels and marmots may represent the closest living analogues of the Plesiadapidae. Marmots (*Marmota*) and ground squirrels (*Citellus*) are omnivorous but feed largely on soft herbaceous vegetation. They are relatively short limbed and lack elongated tibial segments of the hind limb. Marmots and ground squirrels generally nest in burrows (for which there is of course no positive evidence in Plesiadapidae) and spend most of their time on the ground, although some ground squirrels are very good climbers, and marmots occasionally climb trees also (Gianini, 1925). Marmots and ground squirrels are widely distributed geographically, not being limited to forests, and are often found in large concentrations, with some species being colonial. Marmots and ground squirrels are similar to plesiadapids in having clawed extremities, and most have bushy tails.

The flora of western North America in the Paleocene was largely a temperate flora, including many of the trees still common today, such as elm, oak, hickory, and conifers. A smaller warm temperate element including palms and breadfruit was also present (Brown, 1962; Gingerich, 1968). It was noted in the systematic discussion that *Plesiadapis* is characteristic of northern faunas, while *Nannodectes* is more common in southern faunas in North America. Significantly, the northern genus *Plesiadapis* (as well as *Chiromyoides*), but apparently not *Nannodectes*, was able to inhabit the high-latitude land bridge connecting Europe and North America in the Paleocene.

Since the vegetation of North America in the Paleocene was similar to that today in general aspect, comparison of the Plesiadapidae to modern, similarly adapted North American Scuiridae is appropriate. Such a comparison is presented in Figure 37. The Plesiadapidae, like the Sciuridae (Landry, 1970), were probably omnivorous. Their evolution shows, however, several independent trends toward increasing herbivory in *Nannodectes, Plesiadapis,* and *Platychoerops. Chiromyoides*, on the other hand, shows many features of the skull and jaws suggesting a special adaptation to seed eating. Such specializations are seen in other primates (see Jolly, 1970a, b) and, interestingly, in North American squirrels and their close relatives as well. *Sciurus* has a skull approximating that of *Plesiadapis rex* in proportions, whereas some related Mexican populations more adapted to seed eating have a skull (cf. YPM 2861) more closely resembling that of *Chiromyoides*.

The Plesiadapidae became extinct in the early Eocene. The reason for this extinction is not known, but a reasonable hypothesis can be proposed. Jepsen (1949) first presented evidence that extinction of the Multituberculata may have been largely determined by the first radiation of Rodentia. Van Valen and Sloan (1966) elaborated on this proposal, noting that successive radiations of multituberculates, condylarths,

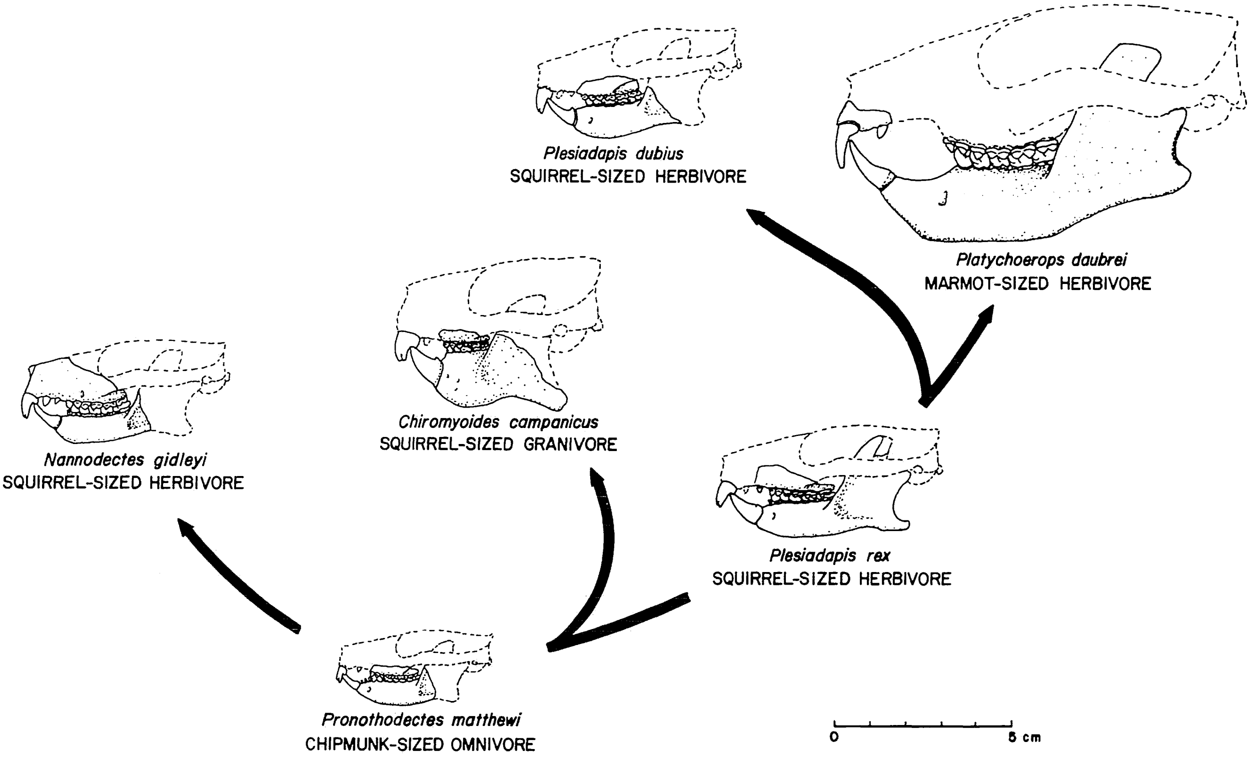


Figure 37. Cranial adaptations of Plesiadapidae, showing skulls of the major adaptive types drawn at the same scale. Stippling indicates the known parts of the species figured, although more complete skulls are known of some related species.

primates, and finally rodents, apparently competed for the same environmental resources.

The probable rodentlike habits and habitat of plesiadapids would presumably have placed them in at least partial competition with early rodents. Furthermore, the relatively rapid shift from a tricuspid incisor in *Plesiadapis* to a unicuspid, more rodentlike incisor in *Platychoerops* at precisely the time of the first appearance of rodents in the fossil record suggests that some change in the food resources available (?due to climatic warming at this time, see below) may have favored small mammals with a rodentlike anterior dentition, rather than that typical of plesiadapids. This in turn suggests that while the introduction of rodents may have prevented plesiadapids from initiating a new adaptive radiation in the Early Eocene, the actual cause of extinction of the Plesiadapidae may have been the general change in food resources.

In discussing the origin of rodents, A. Wood (1962) considered the Plesiadapidae at some length. In that paper, Wood concluded that no very close relationship of *Plesiadapis* and primitive rodents was indicated, although he has subsequently implied a direct relationship (Wood, 1972). The characteristics of rodents in which they resemble plesiadapids (enlarged incisors, large diastema, flat molars, etc) are all similarities to the later, most evolved species of Plesiadapidae, and they are all apparently independently acquired characteristics related to similar feeding behaviors. Among the plesiadapiform primates, rodents most closely resemble the Paromomyidae in dental morphology, and it is perhaps possible that they were derived from an as yet unknown early or middle Paleocene member of that family. All of the known late Paleocene paromomyids appear to have been too different from early Eocene rodents to be ancestral to them.

ORIGIN OF EARLY EOCENE MAMMALS OF MODERN ASPECT

The problem of the extinction of the Plesiadapidae is closely related to another question: the origin of the modern mammalian forms that appeared at the beginning of the Eocene to replace them. Plesiadapids underwent their broadest radiation during the late Paleocene, four lineages being known from the Tiffanian in North America. Multituberculates and some other mammalian groups similarly reached their maximum or near maximum diversity in western North America during

Table 13. Relatively sudden appearance of new modern mammals in western North America at the beginning of the Eocene. First column lists possible or probable ancestral forms for each of the major mammalian groups appearing in the early Eocene (which are listed in the third column). Intermediate late Paleocene connecting forms are as yet unknown, and probably will not be found until subtropical faunas of the late Paleocene are sampled.

Early Middle Paleocene (Puercan-Torrejonian)	Late Paleocene (Tiffanian)	Early Eocene (Clarkfork-Sand Coulee)	Reference
SUBTROPICAL CLIMATE	WARM TEMPERATE CLIMATE	SUBTROPICAL CLIMATE	Wolfe and Hopkins, 1967
?*Purgatorius*-like form	. . . .	Adapidae	
?*Palenochtha*-like form	. . . .	Omomyidae (Primates)	
Palaechthon	. . . .	*Cynodontomys*	Bown and Gingerich, 1973, p. 2
??Paromomyid primate	. . . .	*Paramys* (Rodentia)	
"Claenodon"	. . . .	*Esthonyx* (Tillodontia)	Van Valen, 1963, p. 364
?Palaeoryctid "Genus B"	. . . .	Hyaenodontidae (Creodonta)	Van Valen, 1966, p. 63
?Palaeoryctid "Genus B"	. . . .	Oxyaenidae	
?Palaeoryctid insectivore	. . . .	Miacinae (Carnivora)	See MacIntyre, 1966, p. 205 Van Valen, 1969, p. 129
Litaletes	. . . .	*Hyopsodus* (Condylarthra)	Gingerich, in prep.
Tetraclaenodon	. . . .	*Hyracotherium* (Perissodactyla)	Radinsky, 1966, p. 408
Tricentes ("Metachriacus")	. . . .	*Diacodexis* (Artiodactyla)	Van Valen, 1971, p. 526
?*Pantolambda*	. . . .	*Coryphodon* (Pantodonta)	Simons, 1960, p. 6

the Tiffanian. These typical late Paleocene mammalian genera survived for varying periods during the Eocene, being replaced in large part by ecologically similar mammals that immigrated into western North America in the earliest Eocene. Since suitable ancestral forms are not present in the immediately underlying strata, the modern early Eocene groups are usually assumed to have immigrated from Asia or some other region with an as yet unknown fossil record.

Recent studies by many authors on the origin of individual groups of early Eocene mammals of modern aspect reveal an interesting pattern. Suitable ancestral forms were not present in Tiffanian strata in western North America, but many authors have postulated derivation of one or another modern group from an ancestor in the early or middle Paleocene. Results of these studies are tabulated in Table 13. *Hyracotherium*, for example, cannot be derived from any late Paleocene ancestor yet known in western North America, but it was possibly or probably derived from a primitive middle Paleocene species of *Tetraclaenodon* (Radinsky, 1966). Similarly, most of the other groups appearing for the first time in the early Eocene can also be linked to a middle Paleocene ancestor, but late Paleocene intermediate stages are missing.

The climatic history of western North America during the late Paleocene offers a plausible explanation for the sudden appearance of mammals of modern aspect in the early Eocene. The late Paleocene (Tiffanian) was a time of climatic deterioration, with the subtropical climate of the middle Paleocene being replaced by a cooler, warm temperate climate in North America (Wolfe and Hopkins, 1967). The geographic range of mammalian groups is often controlled, directly or indirectly, by climate. Thus it is plausible that the cooler climate of the Tiffanian caused a contraction southward of the geographic ranges of many basically subtropically adapted genera. Mammals adapted to temperate climates radiated in western North America during the Paleocene. With the general warming and return of a subtropical climate in the early Eocene, the geographic ranges of subtropical mammals expanded and, in more evolved form, they reinvaded western North America. During this invasion, the mammals already present in North America either evolved rapidly (adapting to subtropical conditions), migrated north with the temperate climate belt, became isolated in temperate upland refuges, or became extinct. Some multituberculates may have survived at least until the late Eocene in upland refuges (Black, 1967), but it appears that the Plesiadapidae became extinct within a million years or so after the initial invasion of the more modern Eocene fauna.

Given this Paleocene and Eocene climatic history and the probability that many of the early Eocene immigrants into western North America evolved from North American middle Paleocene ancestors, it is probable that much of this evolution took place in southern North America and in Central America, rather than Asia or some other more distant region (see Sloan, 1969, for an earlier statement of this hypothesis). The actual ancestral forms of many of the new genera appearing in the Eocene will probably be found only when late Paleocene fossil localities are found in Central America. Some of the groups appearing in the early Eocene of North America, the adapid primates and hyaenodontid creodonts in particular, appear from later faunal evidence to be African rather than Central American in origin. Undoubtedly, the warmer climates of the early Eocene were important in making the high latitude subaerial corridors between Europe, North America, and Asia increasingly habitable and in facilitating expansion of the geographic ranges of many genera from one continent to another. Further work on the relative timing of the first appearance of each group in western North America may help to understand which immigrated from Central America and which immigrated from more distant continents.

Finally, it should be noted that the origin of the new and more modern mammalian fauna characteristic of the early Eocene parallels in many ways the origin of a still more modern mammalian fauna in the early Oligocene fossil record of the northern continents (Stehlin's "*grande coupure*"), which also followed a major climatic deterioration.

IX

PHYLOGENY AND CLASSIFICATION OF PRIMATES

As a result of critical gaps in our knowledge of the fossil record of primate evolution, the phylogeny of Primates is not well understood, and considerable disagreement exists on classification of the order. Fortunately, new fossil evidence is continually being discovered. New observations on the primate fossil record are presented here, which will hopefully contribute to future stability.

While there is little agreement about the relative ranking to give each in a classification, most authorities recognize three major groups of living primates: (1) the Simiiformes or "Anthropoidea" – including New and Old World monkeys, apes, and humans; (2) Tarsiiformes – including a single living genus *Tarsius*; and (3) Lemuriformes – including the Asian and African lemurs and lorises. Some authors would include the living treeshrews as an additional major group.

Most of the fossil primates discovered thus far clearly belong to one of these three major living groups, but the affinity of a major archaic group radiating in the Paleocene and Eocene is less clear. This archaic group includes the Plesiadapidae, and Romer (1966) provisionally placed the group in a distinct suborder Plesiadapoidea. Simons (1972) subsequently formally recognized this assemblage as the infraorder Plesiadapiformes.

In this chapter the relationships of groupings within Plesiadapiformes will be reviewed. The relationship of Plesiadapiformes to the three major surviving groups of primates, and the question of whether the Plesiadapiformes are in fact primates will be discussed. Finally, this evidence is integrated in a general discussion of the phylogeny and classification of Primates.

RELATIONSHIPS WITHIN PLESIADAPIFORMES

In addition to the Plesiadapidae, Simons (1972) included the families Carpolestidae, Paromomyidae, and Picrodontidae in Plesiadapiformes. Szalay (1973), apparently unaware of the book by Simons (1972), has recently proposed a new ordinal-level taxon Paromomyiformes to include the same four families. Paromomyiformes Szalay, 1973 is evidently synonymous with Plesiadapiformes Simons, 1972, and the former name is used here. Subsequent research has shown that the Microsyopidae should also be included in Plesiadapiformes (Bown and Gingerich, 1973).

All of the known Plesiadapiformes have relatively enlarged lower central incisors. The upper central incisors of Microsyopidae (including *Palaechthon, Cynodontomys*, etc.) are bicuspid, with a large anterocone and a large posterocone (see Fig. 38). The upper central incisors of Plesiadapidae (see Fig. 26), Carpolestidae (Rose, 1973, has shown that the tooth identified by Szalay, 1972b, as an upper incisor of *Carpolestes* is probably a lower incisor of the dermopteran *Planetotherium*), and Paromomyidae (including *Phenacolemur*, see Fig. 38) have, in addition, a large apical laterocone. The latter three families all share the important derived character of tricuspate upper incisors, and placement together in the superfamily Plesiadapoidea is justified. The Microsyopidae, and possibly the Picrodontidae, constitute a generally more primitive superfamily Microsyopoidea.

Saxonella was first described by Russell (1964) as a European carpolestid. Van Valen (1969b) and others have suggested that *Saxonella* is a plesiadapid. Considering the morphology of the lower incisor (see Russell, 1964, pl. 8: 7d), relationship to the paromomyid *Phenacolemur* seems more likely. Alternatively, *Saxonella* might be placed in a family of its own (Rose, 1975, p. 51). *Saxonella* clearly was not derived from *Pronothodectes*, but a common origin of *Saxonella, Pronothodectes*, the primitive carpolestid *Elphidotarsius*, and the primitive paromomyid *Paromomys* in the Early Paleocene is likely.

In view of the close relationship of the Paromomyidae and the Plesiadapidae, it is not surprising that *Phenacolemur* (see Szalay, 1972a) shares with *Plesiadapis* an enlarged ectotympanic forming the lateral wall

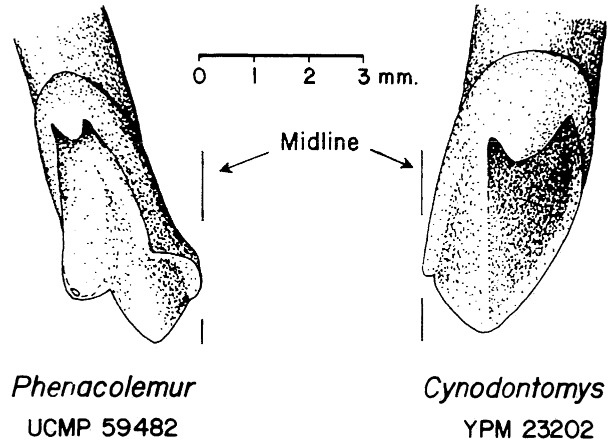


Figure 38. Comparison of upper central incisors of *Phenacolemur* and *Cynodontomys*. Left incisor of the plesiadapoid *Phenacolemur praecox* is from the early Eocene Four Mile fauna (Timberlake Quarry). Right incisor of the microsyopoid *Cynodontomys latidens* is from the early Eocene of the Big Horn Basin (Yale-Michigan Loc. 45). Both figured in posterior-occlusal view.

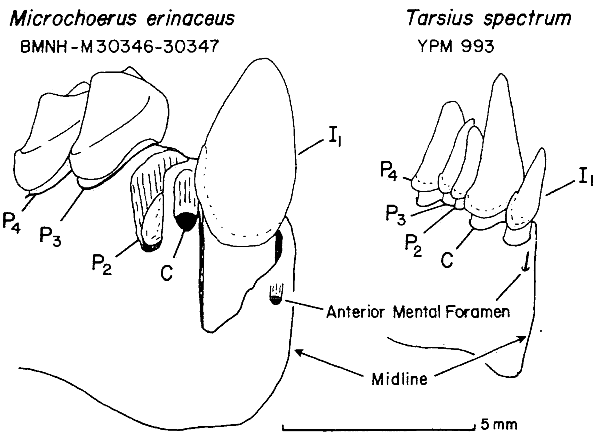


Figure 39. Comparison of the anterior dentition of *Microchoerus* with that of *Tarsius*. Note the pointed incisor in each, and the position of the anterior mental foramen (with bristle in *Tarsius*). Both figures in anterior view, and drawn at the same scale.

of the auditory bulla. This bulla construction, like the tricuspid upper incisor, is presumably a shared derived character of Plesiadapoidea, which are more advanced in these characters than the Microsyopoidea.

PLESIADAPIFORMES AND OTHER PRIMATES

As was noted in the introductory chapter, one of the central goals in undertaking this study of the Plesiadapidae was to clarify the relationship of the Plesiadapiformes to Primates. Most paleontologists include Plesiadapiformes in Primates, whereas the zoologists Martin (1972) and Cartmill (1972) recently concluded that the Plesiadapiformes should be excluded from the order. This problem is complicated by the apparently accidental way *Plesiadapis* first came to be considered a primate.

The first of Lemoine's specimens of *Plesiadapis* were described by Gervais (1877), who noted their resemblance to *Adapis*. However, the two specimens Gervais described are not very similar to *Adapis*, and it is probable that his statement of resemblance was based on specimens first described the following year by Lemoine (1878) as several new species of "*Plesiadapis*." The latter *Adapis*-like specimens Lemoine subsequently correctly placed in a new genus *Protoadapis*. Delfortrie (1873) and Gervais (1873) had only a few years earlier recognized the affinities of *Adapis* with the living lemurs; thus it is natural that *Plesiadapis*, once given a name compounded from *Adapis*, should be compared with lemurs. The real *Adapis*-like fossils were, however, those subsequently placed in *Protoadapis* — species of which probably were related to the ancestry of *Adapis*.

Having correctly distinguished *Protoadapis* from *Plesiadapis*, Lemoine saw in *Plesiadapis* "des caractères lémuriens avec un facies marsupial" [!] (Lemoine, 1887, p. 192). Stehlin (1916), and subsequently Teilhard (1922, 1927), attempted to reconcile the marsupial aspect of *Plesiadapis* with its supposed lemur affinity by suggesting possible relationship with the peculiar lemur *Daubentonia (=Chiromys)*.

With his discovery of primitive middle Paleocene Plesiadapiformes, including the first species of *Pronothodectes, Paromomys, Palaechthon,* and *Elphidotarsius*, Gidley (1923) recognized that these forms shared the molar morphology (in particular, having a postprotocingulum, elongated M3, constricted trigonid and expanded talonid) characteristic of certain Eocene genera then recognized beyond question as primates. Gidley's discoveries provided important new evidence of the relationship of the Paleocene Plesiadapiformes to Primates, independent of that put forward by Lemoine, Stehlin, and Teilhard.

Simpson's study of *"Plesiadapis" [Nannodectes] gidleyi* (Simpson, 1935a) subsequently showed that the resemblance of *Nannodectes* to *Daubentonia* was superficial and convergent, but he emphasized that the close resemblance of the cheek teeth of plesiadapids to those of the Eocene adapid *Pelycodus* leaves little question that they are related. The more recent discovery of a skull of *Plesiadapis* (Russell, 1959) with an auditory bulla virtually identical to that of certain undoubted primates (albeit Tarsiiformes) further supports the inclusion of Plesiadapiformes in Primates.

In discussing Martin's (1972) and Cartmill's (1972) suggestion that the Plesiadapiformes be removed from Primates, emphasis was placed on the similarity of the dentition of early Eocene primates to that of the Paleocene Plesiadapiformes ("Plesiadapoidea" of Romer, 1966), and on the proximity in geological time of Plesiadapiformes and the early Eocene undoubted primates (Gingerich, 1973a). As a result of a more recent study of the European Eocene primates, some additional comments can be made on these two points.

The dental formula of *Necrolemur* and *Microchoerus* (European Eocene primates placed in Tarsiidae) has been variously interpreted. Most authors agree that the upper formula is 2.1.3.3. The lower formula of the microchoerines has been interpreted as 0.1.4.3 by Stehlin (1916), Simons (1961a), Cray (1973), and others. Simons (1961a, p. 61) noted the presence of an "alveolus" in front of the enlarged "canine" in *Microchoerus edwardsi*. This "alveolus" is also clearly shown in a very complete mandible (BMNH M30346) of *Microchoerus erinaceus* (Fig. 39). Development of an anterior mental foramen in *Tarsius* is variable. The foramen sometimes occupies precisely the position of the "alveolus" in *Microchoerus*, and the latter is, with little doubt, an anterior mental foramen as well.

The enlarged anterior tooth of *Microchoerus* illustrated in Figure 39 has usually been identified as a canine, but well-developed interstitial wear facets on its medial edge indicate that the tooth is an incisor (since the left and right lower canines do not contact in any mammal, see discussion of tooth homologies in Chapter 7). The occlusal relationships of the anterior teeth of *Microchoerus* are clearly shown by Simons (1961a, fig. 2). The two posterior premolars ($P_{2\text{-}3}$) are correctly identified in his figure (as shown by their occlusal relationships with the upper premolars), but it seems most likely that the tooth identified as P_1 is in fact the lower canine. Since there are three upper premolars in all of the known Microchoerinae (except *Nannopithex raabi*, where there are only two), the probability is small that there were ever more than three lower premolars in this subfamily. The full dental formula of Microchoerinae is thus the same as that of *Tarsius*, $\frac{2}{1}\ \frac{1}{1}\ \frac{3}{3}\ \frac{3}{3}$, although the anterior teeth of *Tarsius* are differently specialized (Simpson, 1937b, p. 145, came to the same conclusion regarding the dental formula of *Necrolemur*).

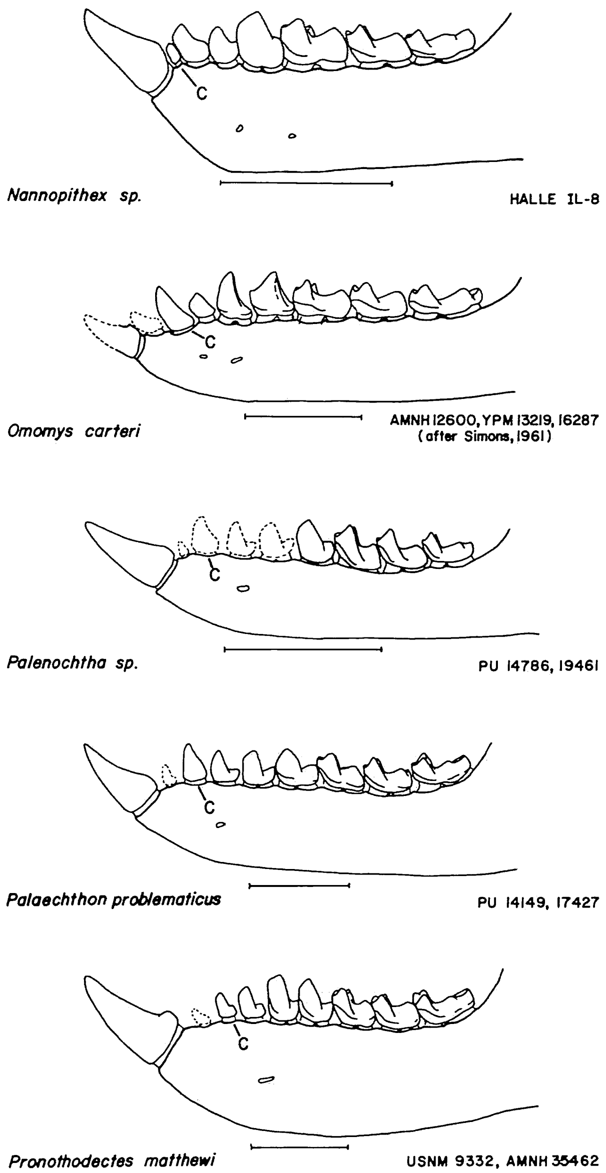


Figure 40. Comparison of the lower dentition of representative Eocene Tarsiiformes (*Nannopithex, Omomys*) with that of middle Paleocene Plesiadapiformes (*Palenochtha, Palaechthon*, and *Pronothodectes*). Lower canine (C) indicated in each. All figures in lateral view and brought to same general size for comparison; scale line represents 5 mm in each figure.

Teilhardina belgica from the Early Eocene of Belgium has often been interpreted as having had four lower premolars, but the number of alveoli following the lower canine is variable – some specimens clearly had only three premolars, the most anterior having a single root. Other specimens have one additional alveolus, indicating that some specimens had a double-rooted P_2, or possibly that in some specimens P_1 was variably present. The possibility that the type (Teilhard, 1927, p. 13, fig. 9c) and additional specimens of *"Plesiadapis orsmaelensis"* (microsyopid-type upper incisors similar to that illustrated in Fig. 38 and of the correct size to belong to *T. belgica*) belong to *Teilhardina* suggests that the anterior lower incisor in this genus may have been moderately enlarged as in the other Eocene tarsioids. A more detailed study of the anterior dentition of *Teilhardina belgica* will be published elsewhere (Gingerich, in prep.).

With the possible exception of *Teilhardina*, no Eocene tarsioid is known to have had more than three premolars in the upper or lower dentition. This, together with recognition that the enlarged anterior lower tooth of microchoerines is an incisor, suggests that some or all of the Eocene microchoerines may well be derived directly from Paleocene Plesiadapiformes. Mandibles of the European microchoerine *Nannopithex* and the North American omomyine *Omomys*, both of Middle Eocene age, are compared with representative Middle Paleocene Plesiadapiformes in Figure 40. The resemblance in anterior dentition is striking in the figure, and even more remarkable when comparing original specimens.

Early North American workers (for example Gidley, 1923; Simpson, 1940, 1945) generally classified many of the Paleocene Plesiadapiformes (especially *Palenochtha, Palaechthon, Paromomys*) as "tarsioid" because of their resemblances to North American *Tetonius* and to the European microchoerine genera. The Plesiadapidae were classified by Simpson (1945) and others as "lemuroid." The established distinctions between Eocene lemuroid and tarsioid primates were discredited by Hürzeler's (1948) assertion that the archetype of Eocene tarsioids, *Necrolemur*, had a free ectotympanic within the auditory bulla and was thus in fact lemuroid. In his study of *Phenacolemur*, Simpson (1955) was unable to place it in either of the two categories, lemuroid or tarsioid, and concluded that a lemuroid-tarsioid dichotomy probably did not exist in the early evolution of Primates.

Simons' (1961a) study of the tympanic construction of *Necrolemur* was of great importance in establishing beyond doubt the tarsioid, not lemuroid (as Hürzeler had proposed), character of the middle ear in this genus. Of equal importance was Simons' demonstration that a tarsioid-lemuroid dichotomy does in fact exist in the Eocene Primates. Following Simpson's (1955) study of *Phenacolemur*, it has increasingly been recognized that the Paleocene forms are best classified as a separate group, finally formalized by Simons (1972) as the infraorder Plesiadapiformes.

The purpose of this brief review of a complicated history has been to outline the most important studies leading to the firm establishment of a major distinction between the Eocene Tarsiiformes (including *Necrolemur*, etc.) and the Eocene Lemuriformes (including *Pelycodus, Adapis*, etc.), and to the recognition of Plesiadapiformes (including *Plesiadapis, Phenacolemur*, etc.) as a unified stock of earlier mammals.

The comparison of *primitive* Plesiadapiformes with representative Tarsiiformes presented in Figure 40 is of particular importance to this discussion. With our present knowledge of primitive Plesiadapiformes, including *Purgatorius*, there is only one characteristic that distinguishes them from the Eocene Tarsiiformes: the postorbital bar. Other distinctions that have been made in the past are the result of comparing derived, highly evolved Plesiadapiformes with Eocene Lemuriformes and Tarsiiformes. This led Simpson (1935a) to overestimate the significance of the dental resemblance of *Plesiadapis* to the lemuroid *Pelycodus* (probably largely due to parallel or convergent evolution in related stocks, enhanced by their being of similar large size and, possibly, dietary adaptation).

More recently, the discovery and description of skulls of highly specialized species of *Plesiadapis* (Plates 8 and 9), *Cynodontomys* (Plate 10 C), *Microsyops*, and *Phenacolemur* (Plate 10 D) has led to the characterization of Plesiadapiformes as archaic, aberrant mammals too specialized to have given rise to any primates of modern aspect. This is certainly true of the late Paleocene and Eocene species for which adequate skulls are known, but it is probably not true of the more primitive ancestors of *Plesiadapis, Microsyops*, and *Phenacolemur*. All that is known to date of the primitive Middle Paleocene Plesiadapiformes, and some of the smaller Late Paleocene and Early Eocene species such as *Berruvias lasseroni*, is that they closely resemble Eocene Tarsiiformes in dental formula and in dental configuration (with enlarged anterior incisors, similarly constructed premolars, constricted trigonids, and expanded molar talonids).

The close resemblance of primitive Plesiadapiformes to Eocene Tarsiiformes suggests that inclusion of *Tarsius* in a monophyletic order Primates requires the inclusion of the Plesiadapiformes as well. This does not mean that Plesiadapiformes possessed all of the morphological features characteristic of modern primates. For example, the most primitive group, the Microsyopoidea, almost certainly did not have an auditory bulla formed from the petrosal bone. Rugosity on the ventromedial side of the petrosal of *Cynodontomys* (Plate 10 C), first described by McKenna (1966), suggests that this genus and its ancestors had an entotympanic auditory bulla like that of *Leptictis* illustrated in Figure 41.

In *Leptictis*, as apparently in *Cynodontomys*, the entotympanic bulla was continuous with the petrosal and contacted it medially along a rugose suture. Thus microsyopids, like tree shrews and leptictid insectivores, retained a primitive bullar construction. Possibly the auditory bulla of *Plesiadapis* included an entotympanic element also, but the only skulls preserving this region

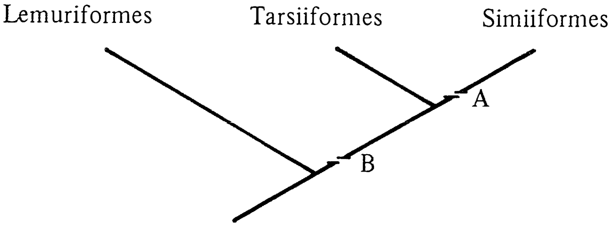
(Plates 8 and 9) are of old individuals with all sutures obliterated, as happens with age in tree shrews. In spite of the presence of an entotympanic auditory bulla, the close resemblance of *Palaechthon (=Plesiolestes)* to other middle Paleocene primates (Bown and Gingerich, 1973), and their resemblance in turn to Eocene tarsioids (Figure 40), leaves little doubt that the microsyopids, like the plesiadapids, are closely related phyletically to primates and should be included in that order.

PHYLOGENY AND CLASSIFICATION OF PRIMATES

The living and fossil primates can be divided into four natural groups (if treeshrews are excluded): Simiiformes, Lemuriformes, Tarsiiformes, and Plesiadapiformes (Simiiformes was introduced to replace "Anthropoidea" by Hoffstetter, 1974). Evolutionary lineages and phylogenetic relationships are understood within each of these groups to the extent that the fossil record of each is known. The purpose of this concluding section is to review the relationships between each of the four major groups.

Gregory (1910) and Hill (1953, p. 20-25) have reviewed the history of primate classification in detail. Two arrangements of the major living groups of primates have been proposed. In the traditional arrangement, the Lemuriformes and Tarsiiformes are included in the suborder Prosimii, which is of equal rank with Simiiformes (=Anthropoidea) – this is in essence the arrangement advocated by most early primatologists and more recently by Simpson (1945), Le Gros Clark (1962), McKenna (1967), and Simons (1972). The alternative arrangement, whereby Tarsiiformes and Simiiformes are united (usually as Haplorhini) and given a rank equal to that of Lemuriformes (usually referred to in this arrangement as Strepsirhini) has been advocated by Wortman (1903), Pocock (1918), Hill (1953), and more recently by Martin (1972), Szalay (1973), and others. The Plesiadapiformes have been integrated into the Prosimii (Simons, 1972) or given a rank equal to Haplorhini and Strepsirhini (Szalay, 1973).

The two classifications described above reflect an emphasis on, respectively, grades or clades within essentially the same phylogeny. This can be illustrated diagrammatically as follows:



Subordinal division at A leads to a graded classification (with Prosimii-Simiiformes), while division at B leads to a cladistic grouping (with Strepsirhini-Haplorhini).

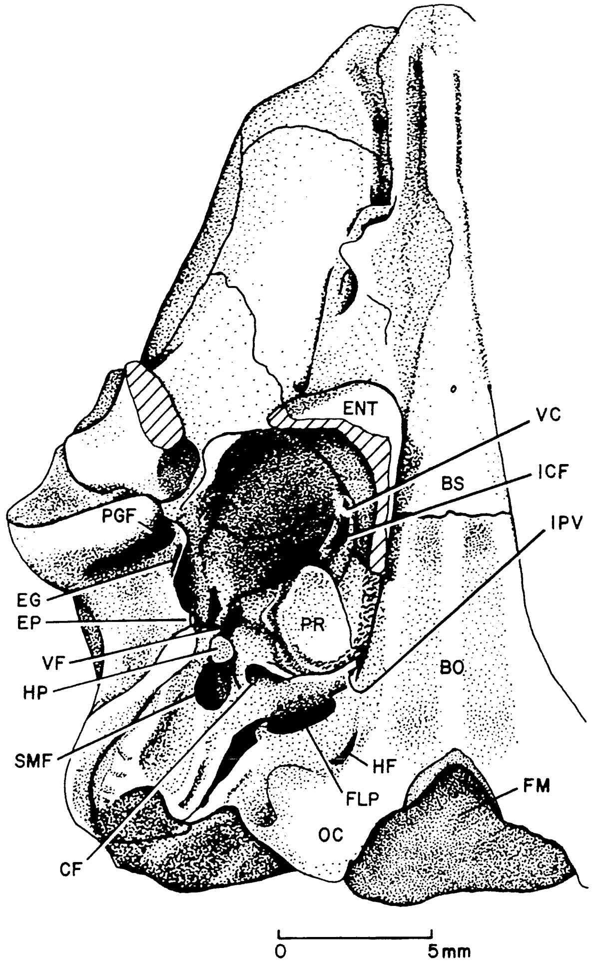
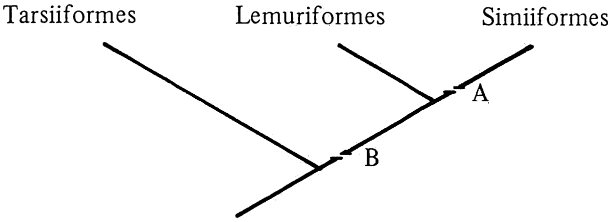


Figure 41. Right auditory region of the Oligocene leptictid insectivore *Leptictis* (UM 15437), in ventral view. Only a portion of the entotympanic part of the bulla remains, and the ectotympanic anulus is also missing. Rugosity along the medial edge of the petrosal indicates continuity of the auditory bulla with the petrosal and not with the basioccipital or basisphenoid. Compare with Plate 10 A & B, and see text for discussion. See also Butler (1956) and McDowell (1958) for discussion of the auditory region of *Leptictis*. Abbreviations: BO, Basioccipital; BS, Basisphenoid; CF, Cochlear fenestra; EG, Ectotympanic groove; ENT, Entotympanic; EP, Ectotympanic process; FLP, Foramen lacerum posterius; FM, Foramen magnum; HG, Hypoglossal foramen; HP, Hyoid process (tympanohyal); ICF, Internal carotid foramen; IPV, Canal for inferior petrous vein; OC, Occipital condyle; PGF, Postglenoid foramen; PR, Promontorium of petrosal; SMF, Stylomastoid foramen; VC, Vidian canal; VF, Vestibular fenestra. Drawn by Ms. Krystyna Swirydczuk, University of Michigan.

The question raised here is not which of these classifications is best, but rather the validity of the phylogenetic relationships underlying both. Evidence that the Simiiformes are derived from lemuriform and not tarsiiform ancestors includes: (1) the apparent presence of an *Adapis* or *Lemur*-like "free" ectotympanic in the primitive anthropoid *Apidium* (Gingerich, 1973c), (2) similarity of the anterior dental configuration of Eocene lemuroids to that of anthropoids (presence of vertical, spatulate incisors, and projecting, interlocking canines in both), (3) the biogeographic distribution of Eocene Adapidae in both the Old and New World, and (4) the difficulty of distinguishing Eocene Adapidae such as *Hoanghonius* from primitive Oligocene anthropoids such as *Oligopithecus* (see Gingerich, 1975e).

Considering this evidence, the more probable phylogenetic relationships of living Primates can be illustrated diagrammatically as follows:



Subordinal division can again be made at A, resulting in the standard Prosimii-Simiiformes dichotomy; or at B, yielding the revised classification advocated here. This phylogeny cannot, however, be interpreted to yield a Haplorhini-Strepsirhini dichotomy.

The phylogeny of Primates that best conforms to the fossil record is presented in Figure 42. It illustrates clearly the relationships of the four major groups of living and extinct primates. The most important morphological changes documented by the fossil record are noted in the figure.

Of fundamental importance is the dichotomy in incisor morphology apparent in the earliest Eocene primates. Plesiadapiformes and Tarsiiformes both have enlarged, pointed, procumbent incisors; whereas the earliest Lemuriformes have anthropoidlike incisors, which are small, vertical, and spatulate. The close similarity and probable relationship of Plesiadapiformes and Tarsiiformes discussed above justifies placing them together as infraorders in the suborder Plesitarsiiformes (Gingerich, 1975b). Similarly, the close resemblance of Simiiformes and Lemuriformes justifies placing them together as infraorders in the suborder Simiolemuriformes (Gingerich, 1975b). The content of each of the four infraorders is apparent from Figure 42. The possible evolution of Lemuroidea and Lorisoidea from an adapoid ancestor has been discussed in detail elsewhere (Gingerich, 1975d).

A fundamental division is recognized between Plesitarsiiformes on one hand and Simiolemuriformes on the other because this seems to be the major natural separation within Primates when fossil as well as living members of the order are considered. When the ancestry of the living primates is traced back in time, the major dichotomy that emerges in the dental remains (all that is yet available for many genera and species) is between early tarsioid primates having enlarged, procumbent, pointed, central incisors, and early lemuroid primates with relatively small, vertical, spatulate central incisors. Virtually all of the early genera of primates can be identified as "tarsioid" or "lemuroid" (*sensu* Adapoidea) on the basis of their anterior dentition alone.

This clear difference between early Plesitarsiiformes and Simiolemuriformes contrasts with the present difficulty of defining the boundary between Simiiformes and Prosimii. Largely as a result of Simons' important new collections from the Oligocene of Egypt (the first significant collections of *primitive* Simiiformes), the distinction between primitive anthropoids and advanced adapoids has become blurred. A fused ectotympanic, a premolar-canine tooth hone, vertical spatulate incisors, and a deep mandible with a fused symphysis are all features at one time thought to characterize Old World anthropoids and distinguish them from prosimians, but the first was apparently absent in some early anthropoids and the remainder are commonly found in Eocene adapoids. When both fossil and living primates are considered, the Simiiformes-Prosimii dichotomy appears less profound than that between Plesitarsiiformes and Simiolemuriformes.

Simpson and others have often stressed the fact that for any given phylogeny, two or more classifications may be equally appropriate. In one context one classification may be preferable, in another context an alternate may be preferred. Formalization of a Plesitarsiiformes-Simiolemuriformes dichotomy in the classification of Primates is proposed in this spirit. This classification emphasizes the similarity of Simiiformes to other primates, particularly the early Lemuriformes, whereas a Simiiformes-Prosimii dichotomy emphasizes the advancement of higher primates over their prosimian ancestors. While the two classifications are mutually incompatible, both can be used to describe the same phylogeny, and either may be justified, depending on the particular application. The prosimian genera included in Plesitarsiiformes and Simiolemuriformes are listed in Table 14.

It is desirable that characters of the soft anatomy of Primates be compared in light of the phylogeny proposed in Figure 42. Soft anatomical characters

Table 14. Classification of prosimian primates. Results of a recent review of all adapid taxa are included (Gingerich, in prep.), but the classifications of Omomyidae and Microchoerinae are tentative pending publication of revisions by Szalay and by Sudre.

- Order **PRIMATES**
  - Suborder **PLESITARSIIFORMES**
    - Infraorder **PLESIADAPIFORMES**
      - Superfamily Microsyopoidea
        - Family Microsyopidae
          - Subfamily Purgatoriinae
            - *Purgatorius*
          - Subfamily Microsyopinae
            - *Palaechthon (=Plesiolestes)*
            - *Torrejonia*
            - *Cynodontomys*
            - *Microsyops*
            - *Craseops*
          - Subfamily Uintasoricinae
            - *Palenochtha*
            - *Berruvius*
            - *Navajovius*
            - *Niptomomys*
            - *Uintasorex*
      - Superfamily Plesiadapoidea
        - Family Plesiadapidae
          - *Pronothodectes*
          - *Nannodectes*
          - *Chiromyoides*
          - *Plesiadapis*
          - *Platychoerops*
        - Family Carpolestidae
          - *Elphidotarsius*
          - *Carpodaptes*
          - *Carpolestes*
        - Family Paromomyidae
          - Subfamily Paromomyinae
            - *Paromomys*
            - *Phenacolemur*
            - *Ignacius*
            - *?Micromomys*
            - *?Tinimomys*
          - Subfamily Saxonellinae
            - *Saxonella*
        - Family Picrodontidae
          - *Picrodus*
          - *Zanycterus*
    - Infraorder **TARSIIFORMES**
      - Superfamily Tarsioidea
        - Family Omomyidae
          - Subfamily Omomyinae
            - *Loveina*
            - *Shoshonius*
            - *Washakius*
            - *Omomys*
            - *Hemiacodon*
            - *Ourayia*
            - *Stockia*
            - *Utahia*
            - *Macrotarsius*
            - *Rooneyia*
            - *Ekgmowechashala*
            - *?Lushius*
          - Subfamily Anaptomorphinae
            - *Teilhardina*
            - *Anemorhysis*
            - *Tetonius*
            - *Absarokius*
            - *Anaptomorphus*
            - *Trogolemur*
            - *Uintanius*
            - *Uintalacus*
            - *Pseudotetonius*
        - Family Tarsiidae
          - Subfamily Microchoerinae
            - *Nannopithex*
            - *Necrolemur*
            - *Microchoerus*
            - *Pseudoloris*
          - Subfamily Tarsiinae
            - *Tarsius*
  - Suborder **SIMIOLEMURIFORMES**
    - Infraorder **LEMURIFORMES**
      - Superfamily Adapoidea
        - Family Adapidae
          - Subfamily Notharctinae
            - *Pelycodus*
            - *Notharctus*
            - *Smilodectes*
          - Subfamily Cercamoniinae
            - *Cercamonius*
          - Subfamily Adapinae
            - *Cantius*
            - *Protoadapis*
            - *Adapis*
            - *Microadapis*
            - *Leptadapis*
            - *Pronycticebus*
            - *Caenopithecus*
            - *Anchomomys*
            - *Periconodon (=Agerina)*
            - *Hoanghonius*
            - *?Indraloris*
          - Subfamily Azibiinae*
            - *Azibius*
      - Superfamily Lemuroidea
        - Family Lemuridae
          - Subfamily Lemurinae
            - *Lemur*
            - *Varecia*
          - Subfamily Lepilemurinae
            - *Lepilemur*
            - *Hapalemur*
          - Subfamily Megaladapinae
            - *Megaladapis*
          - Subfamily Cheirogaleinae
            - *Chirogaleus*
            - *Microcebus*
            - *Phaner*
            - *Allocebus*
        - Family Indriidae
          - Subfamily Indriinae
            - *Indri*
            - *Propithecus*
            - *Avahi*
            - *Mesopropithecus*
          - Subfamily Palaeopropithecinae
            - *Palaeopropithecus*
            - *Archaeoindris*

Subfamily Archaeolemurinae
        Archaeolemur
        Hadropithecus
    Family Daubentoniidae
        Daubentonia
Superfamily Lorisoidea
    Family Lorisidae
        Loris
        Nycticebus
        Allocebus
        Perodicticus
        Mioeuoticus
    Family Galagidae
        Galago
        Progalago
        Komba

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* *Azibius trerki* Sudre resembles other Adapidae in the structure of its molars, but differs from them in having a specialized enlarged P_4. For this reason it is here placed in a new subfamily Azibiinae of the family Adapidae. A more complete discussion is in preparation.

often have little value for reconstructing a phylogeny because of the near impossibility of establishing the primitive condition of characters not represented in the fossil record or of detecting parallel evolution. The nature of the primate placenta is a good case in point. Le Gros Clark (1962, p. 309) presents a concise review of placental evolutionary pathways in primates and their relatives.

Simiiformes have a haemochorial placenta, in which the fetal and maternal circulation is intimately related. This is presumed (by the anthropocentric investigator?) to be the most functionally efficient type of placenta. Lemurs, on the other hand, have a "primitive" epitheliochorial placenta with no intimate merging of chorionic tissues with those of the uterus. The fact that *Tarsius* has a placenta of the "advanced" haemochorial type would seem on functional evidence to ally it with Simiiformes. However, this overlooks the fact that most insectivores and many rodents have an "advanced" haemochorial placenta also. On functional evidence *Tarsius* and Simiiformes appear to share an advanced derived character, but on strict comparative evidence they appear only to retain the primitive placental condition in primates. Even if the haemochorial placenta shared by *Tarsius* and Anthropoidea is an advanced condition in primates, its wide distribution in other mammalian orders suggests that it could easily have evolved independently in these two groups.

This example is important in illustrating the difficulty of determining which character states are primitive and which are derived for characters not preserved in the fossil record, and the difficulty of determining which states postulated to be derived are shared due to common inheritance and which have evolved independently. Placental type may not favor any particular relationship of the three infraorders of living primates – which pattern of evolutionary pathways is most parsimonious in this case is apparently in part a function of the range of taxonomic comparisons included. This is not to detract from the recent studies of Luckett (1974) on placentation in primates, Goodman (1973), Sarich and Cronin (1976), and others on biochemical systems in primates, etc., but to point out that comparative methods of phylogeny reconstruction based on the study of characters seen only in living animals assume that the evolution of the character being studied was parsimonious (i.e., included an insignificant amount of parallel evolution and a minimum of evolutionary reversal). Assumptions such as these minimize the importance attached to adaptation, when in fact adaptation is central to modern evolutionary theory. Since in each case the phylogeny itself is based on these assumptions, it cannot be used to test them. The value of paleontology is in providing a continuous series of specimens from successive geological time periods, which document the morphology of species actually living in each period. Studying the pattern of linking in these fossil forms, as discussed in Chapter 2, yields a phylogeny that requires no *a priori* assumptions about the direction or tempo of evolution of any anatomical characters. Linking the primate fossils that are presently known yields the phylogeny outlined in Figure 42, which potentially provides an independent framework for testing the amount of parallelism and reversal in the evolution of many anatomical systems. For example, it appears from Figure 42 that the ectotympanic became fused into the lateral wall of the auditory bulla independently at least three times during the course of evolution: in Plesiadapiformes, in lorisoids, and in primitive Simiiformes. This relatively large amount of parallelism is consistent with the view that there was an important adaptive reason for fusing the ectotympanic into the wall of the auditory bulla, and it is consistent with the amount of parallelism seen in the evolution of such dental characters as enamel crenulation in independent lineages within the family Plesiadapidae.

The phylogeny presented in Figure 42 is an hypothesis derived from stratophenetic linking of the known fossil and living primates. The linking is relatively well documented in some parts of the phylogeny (between Tarsiiformes and Plesiadapiformes, and between Simiiformes and Adapoidea, for example), but it is weaker in other areas (particularly between Lemuroidea-Lorisoidea and Adapoidea). Like any other stratophenetic hypothesis of phylogeny, the adequacy of this particular phylogeny will be tested continually by each new discovery of additional fossil primates.

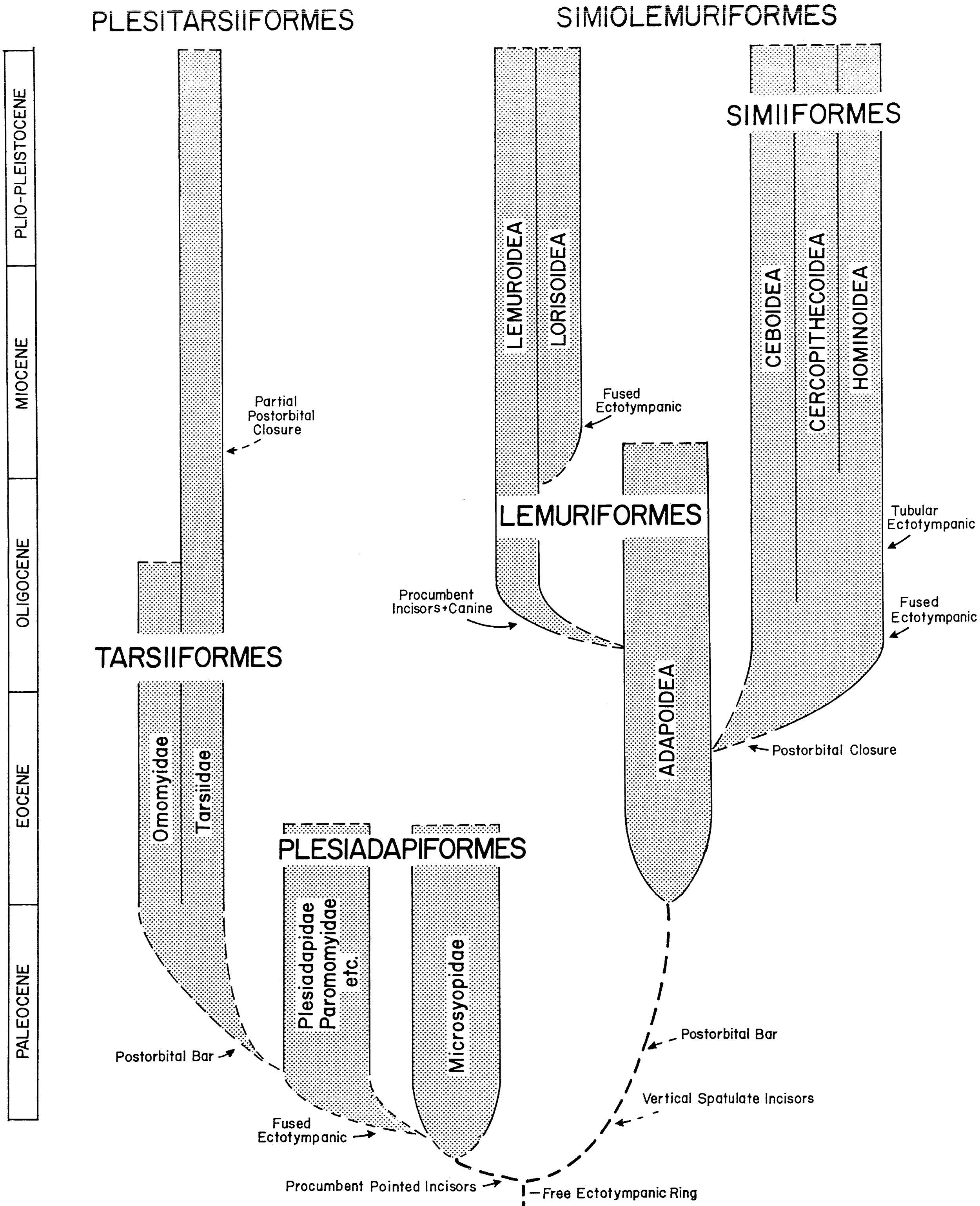

Figure 42. Phylogeny of the order Primates, showing suggested relationships of the four major groups Plesiadapiformes, Tarsiiformes, Lemuriformes, and Simiiformes (=Anthropoidea) based on stratophenetic linking of fossil forms. Approximate times of divergence and approximate times of acquisition of distinguishing characters (arrows) are also indicated.

X

CONCLUSIONS

Three general questions were posed at the beginning of this study: (1) To what extent is it possible to reconstruct the phylogenetic history of a well-known group of extinct early Tertiary mammals from the fossil record? (2) How closely related are the Paleocene and early Eocene faunas of North America and Europe, and what are their relative temporal relationships? (3) What is the relationship of *Plesiadapis* to other primates, and what is its significance for understanding the history of Primates? Each of these questions is now considered in turn.

PHYLOGENY RECONSTRUCTION FROM THE FOSSIL RECORD

Plesiadapis and its allies are among the most important and interesting of all primates because of their abundant fossil record spanning some 12 million years of geological time. By studying the variation within population samples and the stratigraphic distribution of these samples, it has been possible to reconstruct in considerable detail the phylogenetic relationships of the North American species of Plesiadapidae. The *stratophenetic* approach to phylogeny reconstruction employed in this study can be outlined in three steps:

1. *Stratigraphic organization* of all fossil samples. This includes first an analysis of each sample to determine the number of distinct biological species populations present in each (the names of the species are not important at this stage). Secondly, all samples within one stratigraphic column are arranged in proper sequence from oldest to youngest. Thirdly, these columns are integrated by correlating stratigraphic intervals containing very similar or identical species populations. This yields a composite stratigraphic column with all recognizably distinct species populations in proper stratigraphic and temporal order.
2. *Phenetic linking* of similar species populations in adjacent stratigraphic intervals, forming a branching pattern of lineages, each population being connected to another above and below on the basis of their overall similarity. At this stage lineages that change significantly through the stratigraphic column may be divided arbitrarily into segments to express the major stages of morphological change in each lineage – these segments are paleontological species (with biological characteristics in each time plane and a significant time dimension).
3. *Critical testing* involves asking if the density and continuity of the given fossil record is sufficient to support the proposed phylogenetic pattern of relationships between species. Would other arrangements be possible in parts of the pattern where there are significant discontinuities? The entire phylogenetic hypothesis is, of course, continually tested by the extent to which fossils discovered subsequently fit into the proposed pattern.

Application of this stratophenetic approach to North American Plesiadapidae yielded a dense and continuous pattern of phylogenetic relationships linking 18 species into four related lineages (see Fig. 17). When individual morphological characters are studied in this phylogenetic context, it is possible to trace their gradual change through geological time (Figs. 24-28). The resulting pattern shows lineages both increasing and decreasing in overall size, with strong character divergence in tooth size (and undoubtedly body size as well) following each cladogenetic speciation event. The evolution of some characters involved considerable parallel but independent acquisition of new character states, or evolutionary reversals where a new derived character state was gained and then lost.

In the examples studied here it was possible to reconstruct the phylogenetic relationships of all North American species thus far discovered. Each of the species appears to have been derived from one known from a lower stratigraphic interval in western North America. The evolution of these species was both gradual and continuous, supporting the Darwinian model of gradual phyletic evolution. No evidence was found to suggest a "punctuated equilibrium" pattern of phylogeny. Since one goal of the study was to discover trends in the evolution of dental characters in *Plesiadapis* through a significant period of geological time, no *a priori* assumptions could be made about these trends, and the stratigraphic distribution of the fossils was critical to understanding their temporal and phylogenetic relationship. With an adequate stratigraphic record it *is* possible to study the evolution of fossil mammals at the *species* level, and these studies promise to considerably improve our understanding of speciation in natural populations of mammals.

NORTH AMERICAN AND EUROPEAN BIOSTRATIGRAPHY AND CORRELATION

The stratophenetic method of phylogeny reconstruction requires that a composite stratigraphic column be constructed from all stratigraphic sections containing two or more of the species populations under study. One important result of careful study of stratigraphic distribution and phylogeny like that outlined above is a good understanding of the stratigraphic range of each fossil species. The ranges of species in the best known lineages can be used for detailed biostratigraphic zonation. A well-established system of correlation with successive biostratigraphic range zones based on one group of animals provides a biostratigraphic and temporal context for the study of other animal groups. Figure 16 shows the stratigraphic position of all of the major North American middle Paleocene through early Eocene localities that yield plesiadapid fossils. The system of eight biostratigraphic range zones obtained by subdividing the lineage from *Pronothodectes matthewi* to *Plesiadapis cookei* should be valuable in understanding the evolution of individual Paleocene genera or whole mammalian faunas.

The stratigraphic record of plesiadapid evolution is not as complete in Europe as it is in North America, but six superposed biostratigraphic range zones can be recognized in the late Paleocene and early Eocene of Europe (Fig. 19). By comparing the European species of *Plesiadapis* with their counterparts in North America, it is possible to make a more detailed correlation of European and North American deposits than has been possible previously (Fig. 20). On a North American scale, the important German locality of Walbeck appears on this basis to be approximately middle Tiffanian in age. On a North American scale the French Sparnacian locality of Meudon appears to be equivalent to the Clarkforkian mammal age, or stated the other way around, the Clarkforkian mammal age in North America is correlative with the Sparnacian in the Paris Basin and should be considered earliest Eocene in age rather than latest Paleocene as it conventionally is.

The fact that the evolution of Thanetian species of *Plesiadapis* in Europe so closely parallels the evolution of Tiffanian species in North America suggests that the European and North American species may possibly have been widely separated parts of a single continuous or nearly continuous pangeographic distribution evolving through the late Paleocene. The European species differ slightly from their North American counterparts in each case, but when a better European fossil record is known, each pair may prove to be simply two geographic subspecies of the same biological species. This very close similarity of European and North American *species* of *Plesiadapis* is a strong indication that a continuous land connection linked the two during the late Paleocene. With the onset of rifting in the North Atlantic Ocean, the two continents separated. This final separation in the Sparnacian postdated only very slightly the dispersal of characteristically Eocene mammals from North America to Europe and vice versa, since these stocks began to show significant differences very shortly after they appeared on each continent.

PLESIADAPIS AND THE PHYLOGENY OF PRIMATES

The first described and best known plesiadapid species, *Plesiadapis tricuspidens*, had a large, rodentlike skull with enlarged central incisors, a large diastema, only two lower premolars, and no postorbital bar. Postcranially, *Plesiadapis* also resembled rodents in general proportions and in having terminal phalanges. Judging from its abundance in the late Paleocene and its morphological characteristics, *Plesiadapis* was probably basically a terrestrial animal that thrived at high population densities in warm temperate climatic zones. None of these attributes of *Plesiadapis* are found consistently in any primates living today, and it is not surprising that its primate status is disputed by neontologists.

Plesiadapis and its allies are included in the order Primates by paleontologists for the following reason. While the later species of the Plesiadapidae, Microsyopidae, and Paromomyidae are forms highly specialized in ways not characteristic of more modern primates, the primitive middle Paleocene ancestors giving rise to each of these specialized families were much more generalized. Primates of modern aspect can be traced back in the fossil record to the beginning of the Eocene when they appeared suddenly, probably due to northward migration with the subtropical climatic belt expanding at that time. The only mammals known before the Eocene that were very similar to the first primates of modern aspect (Adapidae and Omomyidae) are the early and middle Paleocene generalized Plesiadapiformes, which were present in western North America during the previous period of subtropical climates. During the intervening late Paleocene warm temperate period, most of the known plesiadapiform primates became aberrantly specialized, but those that moved southward and stayed in the subtropical belt were presumably the ones that advanced toward early Eocene primates of modern aspect.

Primitive Tarsiiformes, in particular, are very similar to early Plesiadapiformes in molar structure, in having enlarged procumbent pointed central incisors, and in having an ossified tubular ectotympanic. The close stratophenetic linking between Tarsiiformes and Plesiadapiformes contrasts with the origin of adapid Lemuriformes. The only possible plesiadapiform ancestor from which the Lemuriformes could be derived is the earliest one known, *Purgatorius*, from the early Paleocene. Early Oligocene simian primates link very closely stratophenetically with adapid Lemuriformes, and there appears to be a fundamental dichotomy between the Plesiadapiformes and Tarsiiformes on the one hand, and the Lemuriformes and Simiiformes on the other.

The significance of *Plesiadapis* and its allies for our understanding of the phylogenetic history and relationships of the living primates lies in their extension of the fossil record of tarsierlike primates back to the middle Paleocene. Thus the living *Tarsius* would appear to have had a very long history of evolution independent of the other living primates. This in turn suggests that many of the anatomical characteristics shared by *Tarsius* and anthropoid primates are a result of convergent evolution, or they are parallel retentions of characteristics present in the early Paleocene common ancestor of the two groups. Parallelism and convergence have clearly been very important in the origin of osteological characters preserved in the primate fossil record, and the central importance of adaptation in evolution makes it very likely that convergence was present in characters of soft anatomy as well.

The amount of parallel and convergent evolution in the fossil record suggests that species behaved independently and opportunistically through the course of their evolution: they consistently adopted the optimal available adaptation, regardless of whether or not some other close or distant species had previously acquired the same adaptation. This makes it especially important that phylogenetic relationships be based on characters preserved in the fossil record.

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APPENDIX

Sufficiently large samples are available of most plesiadapid species to warrant statistical treatment. In the following tables a series of standard measurements (defined in Figure 6 in the text) are summarized for each of the largest samples of a species from a single quarry or a restricted geographic area (in the case of *Ples. cookei*). These statistics will be of use in identifying samples discovered in the future, and they are important in showing the variability in size of each population. Additional raw measurements are listed in the tables incorporated in the text.

All measurements are in millimeters. The following standard abbreviations are employed:

H	incisor height
L	tooth length
n	sample size (number of specimens)
OR	observed range
s	standard deviation
SE	standard error of mean
V	coefficient of variation $[V=100(s/\bar{x})]$
W	tooth width
$\bar{x}$	mean
depth	mandibular depth below M_2

Table A-1. Summary of measurements of the upper and lower dentition of *Pronothodectes matthewi* from the Gidley Quarry. All measurements in millimeters.

	n	OR	$\bar{x} \pm$ SE	s	V
MANDIBLES					
P_3 L	2	1.6-1.8	1.70 ± .10	.14	8.3
W	2	1.5-1.7	1.60 ± .10	.14	8.8
P_4 L	5	1.7-1.9	1.80 ± .03	.07	3.9
W	5	1.6-1.9	1.74 ± .06	.13	7.7
M_1 L	9	2.0-2.3	2.13 ± .03	.09	4.1
W	9	1.9-2.2	2.03 ± .03	.09	4.3
M_2 L	7	2.2-2.3	2.21 ± .01	.04	1.7
W	7	2.1-2.4	2.30 ± .04	.12	5.0
M_3 L	8	3.1-3.3	3.19 ± .03	.08	2.6
W	8	1.8-2.3	2.10 ± .05	.15	7.2
Depth	6	4.8-5.9	5.28 ± .17	.42	7.9
I_1 W	1	1.8	–	–	–
H	2	2.7-2.8	2.75 ± .05	.07	2.6
MAXILLAE					
P^3 L	1	1.5	–	–	–
W	1	2.1	–	–	–
P^4 L	4	1.8-2.0	1.95 ± .05	.10	5.1
W	4	2.6-3.1	2.85 ± .10	.21	7.4
M^1 L	3	2.1-2.2	2.17 ± .03	.06	2.8
W	3	3.2-3.5	3.37 ± .09	.15	4.5
M^2 L	3	2.2	–	–	–
W	3	3.5	–	–	–
M^3 L	1	2.1	–	–	–
W	1	3.0	–	–	–

Table A-2. Summary of measurements of the upper and lower dentition of *Pronothodectes jepi* from the Rock Bench quarry.

	n	OR	$\bar{x} \pm$ SE	s	V
MANDIBLES					
P_3 L	6	1.7-1.8	1.75 ± .02	.05	3.1
W	6	1.4-1.8	1.60 ± .06	.14	8.8
P_4 L	9	1.8-2.1	1.93 ± .03	.10	5.2
W	9	1.8-2.1	1.93 ± .03	.10	5.2
M_1 L	11	2.2-2.4	2.35 ± .02	.07	2.9
W	11	2.0-2.4	2.22 ± .03	.11	4.9
M_2 L	11	2.2-2.6	2.47 ± .03	.10	4.1
W	11	2.3-2.8	2.58 ± .05	.17	6.7
M_3 L	3	3.3-3.8	3.60 ± .15	.26	7.4
W	3	2.2-2.4	2.33 ± .07	.12	4.9
Depth	9	5.4-6.5	5.91 ± .14	.43	7.3
I_1 W	5	1.6-1.9	1.76 ± .06	.13	7.6
H	5	2.8-3.4	3.02 ± .12	.27	8.9
MAXILLAE					
P^3 L	–	–	–	–	–
W	–	–	–	–	–
P^4 L	1	2.1	–	–	–
W	1	3.2	–	–	–
M^1 L	4	2.4-2.6	2.45 ± .05	.10	4.1
W	4	3.8-4.4	4.03 ± .13	.26	6.5
M^2 L	4	2.4-2.5	2.42 ± .03	.05	2.1
W	4	3.9-4.4	4.17 ± .11	.22	5.3
M^3 L	1	2.3	–	–	–
W	1	3.2	–	–	–

Table A-3. Summary of measurements of the lower dentition of *Nannodectes intermedius* from Keefer Hill.

	n	OR	$\bar{x} \pm$ SE	s	V
MANDIBLES					
P_3 L	4	1.8-1.9	1.82 ± .03	.05	2.7
W	4	1.4-1.7	1.55 ± .06	.13	8.4
P_4 L	16	1.9-2.1	1.99 ± .01	.05	2.5
W	16	1.7-2.0	1.88 ± .03	.10	5.3
M_1 L	49	2.2-2.6	2.42 ± .01	.08	3.3
W	49	2.0-2.5	2.24 ± .02	.14	5.6
M_2 L	42	2.4-2.7	2.52 ± .02	.10	4.0
W	42	2.3-2.8	2.52 ± .02	.14	5.5
M_3 L	42	3.0-4.0	3.63 ± .03	.22	6.1
W	42	2.0-2.6	2.32 ± .02	.14	6.0
Depth	4	6.2-6.9	6.47 ± .15	.30	4.6

Table A-4. Summary of measurements of the upper and lower dentition of *Nannodectes gazini* from the Bison Basin Saddle locality.

	n	OR	$\bar{x} \pm$ SE	s	V
MANDIBLES					
P_3 L	5	1.7-1.8	1.78 ± .02	.04	2.2
W	5	1.3-1.5	1.40 ± .04	.10	7.1
P_4 L	13	1.8-2.2	1.95 ± .03	.11	5.6
W	13	1.5-2.0	1.73 ± .04	.14	8.1
M_1 L	22	2.1-2.5	2.35 ± .02	.11	4.7
W	22	1.9-2.3	2.09 ± .02	.11	5.3
M_2 L	25	2.2-2.6	2.46 ± .02	.12	4.9
W	25	2.0-2.7	2.36 ± .03	.15	6.4
M_3 L	17	2.7-4.3	3.60 ± .08	.34	9.4
W	17	1.9-2.5	2.16 ± .04	.15	6.9
Depth	13	5.5-7.0	6.23 ± .10	.36	5.8
I_1 W	2	1.7	–	–	–
H	2	2.8-2.9	–	–	–
MAXILLAE					
P^3 L	4	1.7-1.8	1.75 ± .03	.06	3.4
W	4	2.0-2.2	2.05 ± .05	.10	4.9
P^4 L	4	1.8-2.0	1.90 ± .06	.12	6.3
W	4	2.6-2.9	2.75 ± .06	.13	4.7
M^1 L	11	2.3-2.5	2.41 ± .03	.08	3.3
W	11	3.3-3.7	3.47 ± .04	.15	4.3
M^2 L	10	2.3-2.6	2.48 ± .03	.09	3.6
W	9	3.4-3.9	3.64 ± .06	.19	5.2
M^3 L	4	2.0-2.7	2.37 ± .15	.30	12.6
W	4	2.7-3.4	3.02 ± .15	.30	9.9

Table A-5. Summary of measurements of the upper and lower dentition of *Nannodectes simpsoni* from the Bison Basin Ledge locality.

	n	OR	$\bar{x} \pm$ SE	s	V
MANDIBLES					
P_3 L	2	2.1-2.3	2.20 ± .10	.14	6.4
W	2	1.4-1.7	1.55 ± .15	.21	13.5
P_4 L	7	2.0-2.4	2.27 ± .05	.14	6.2
W	7	1.8-2.2	1.96 ± .05	.14	7.1
M_1 L	11	2.5-2.8	2.69 ± .03	.09	3.3
W	11	2.3-2.8	2.58 ± .05	.17	6.6
M_2 L	9	2.7-3.1	2.97 ± .05	.14	4.7
W	9	2.6-3.2	2.89 ± .06	.18	6.2
M_3 L	6	3.5-4.3	4.00 ± .12	.30	7.5
W	6	2.3-2.7	2.55 ± .07	.18	7.1
Depth	6	5.7-6.7	6.32 ± .14	.35	5.5
MAXILLAE					
P^3 L	2	1.9-2.1	2.00 ± .10	.14	7.0
W	2	2.2-2.5	2.35 ± .15	.21	8.9
P^4 L	3	2.2-2.3	2.27 ± .03	.06	2.6
W	3	3.1	3.10 –	–	–
M^1 L	3	2.7-2.9	2.80 ± .06	.10	3.6
W	3	4.1-4.2	4.13 ± .03	.06	1.5
M^2 L	5	2.9-3.0	2.96 ± .02	.05	1.7
W	5	4.5-4.8	4.64 ± .06	.13	2.8
M^3 L	3	2.8-2.9	2.87 ± .03	.06	2.1
W	3	3.4-3.6	3.50 ± .06	.10	2.9

Table A-6. Summary of measurements of the upper and lower dentition of *Nannodectes gidleyi* from the Tiffany Mason Pocket locality.

		n	OR	$\bar{x} \pm$ SE	s	V
MANDIBLES						
P_3	L	9	2.1-2.3	2.24 ± .02	.07	3.1
	W	9	1.7-2.0	1.82 ± .03	.10	5.5
P_4	L	9	2.2-2.4	2.31 ± .03	.08	3.5
	W	9	1.9-2.5	2.17 ± .06	.17	7.8
M_1	L	12	2.7-3.1	2.88 ± .03	.11	3.8
	W	12	2.5-3.1	2.70 ± .05	.18	6.7
M_2	L	9	3.0-3.3	3.14 ± .03	.09	2.9
	W	9	2.9-3.3	3.04 ± .04	.13	4.3
M_3	L	7	4.4-5.0	4.66 ± .08	.20	4.3
	W	7	2.7-3.2	2.90 ± .07	.18	6.2
Depth		9	5.8-8.1	7.12 ± .23	.69	9.7
I_1	W	5	2.1-2.3	2.24 ± .04	.09	4.0
	H	5	3.5-3.8	3.70 ± .06	.14	3.8
MAXILLAE						
P^3	L	7	2.2-2.4	2.24 ± .03	.08	3.6
	W	7	2.4-2.9	2.64 ± .06	.15	5.7
P^4	L	8	2.3-2.5	2.37 ± .03	.09	3.8
	W	8	3.0-3.7	3.44 ± .07	.22	6.4
M^1	L	9	2.7-3.1	2.96 ± .05	.14	4.7
	W	9	3.9-4.5	4.23 ± .07	.21	5.0
M^2	L	7	3.0-3.2	3.13 ± .04	.10	3.2
	W	7	4.4-5.0	4.71 ± .07	.19	4.0
M^3	L	7	2.7-3.2	2.87 ± .07	.18	6.3
	W	7	3.6-4.1	3.93 ± .06	.16	4.1

Table A-7. Summary of measurements of the lower dentition of *Plesiadapis anceps* from the Bison Basin Saddle locality.

		n	OR	$\bar{x} \pm$ SE	s	V
MANDIBLES						
P_3	L	4	2.1-2.2	2.17 ± .03	.05	2.3
	W	4	1.8-2.0	1.92 ± .05	.10	5.2
P_4	L	6	2.2-2.5	2.30 ± .04	.11	4.8
	W	6	2.2-2.6	2.42 ± .07	.17	7.0
M_1	L	11	2.6-3.0	2.87 ± .04	.13	4.5
	W	11	2.7-3.0	2.84 ± .03	.09	3.2
M_2	L	10	2.8-3.1	2.97 ± .03	.11	3.7
	W	11	3.0-3.3	3.12 ± .03	.11	3.5
M_3	L	6	4.2-4.5	4.37 ± .05	.12	2.7
	W	6	2.8-3.0	2.89 ± .03	.08	2.8
Depth		8	5.9-8.6	7.50 ± .29	.83	11.1

Table A-8. Summary of measurements of the upper and lower dentition of *Plesiadapis rex* from the Cedar Point Quarry.

		n	OR	$\bar{x} \pm$ SE	s	V
MANDIBLES						
P_3	L	57	2.0-2.4	2.20 ± .01	.11	5.0
	W	56	1.6-2.3	2.00 ± .02	.13	6.5
P_4	L	103	2.1-2.7	2.37 ± .01	.13	5.5
	W	104	2.1-2.8	2.47 ± .01	.15	6.1
M_1	L	130	2.7-3.4	3.07 ± .01	.14	4.6
	W	126	2.6-3.4	2.95 ± .01	.15	5.1
M_2	L	148	2.9-3.6	3.33 ± .01	.16	4.8
	W	149	2.9-3.8	3.35 ± .01	.16	4.8
M_3	L	98	4.2-5.5	4.95 ± .03	.25	5.1
	W	102	2.7-3.5	3.13 ± .02	.17	5.4
Depth		118	5.5-9.5	7.97 ± .07	.74	9.3
I_1	W	113	2.1-2.9	2.54 ± .01	.15	5.9
	H	109	3.5-4.8	4.18 ± .03	.30	7.2
MAXILLAE						
P^3	L	8	2.0-2.6	2.29 ± .07	.19	8.3
	W	8	3.0-3.5	3.19 ± .07	.20	6.3
P^4	L	10	2.3-2.6	2.43 ± .03	.11	4.5
	W	10	3.9-4.5	4.11 ± .07	.21	5.1
M^1	L	14	2.9-3.4	3.11 ± .05	.17	5.5
	W	14	4.3-5.2	4.66 ± .07	.28	6.0
M^2	L	14	3.0-3.9	3.29 ± .06	.24	7.3
	W	14	4.7-5.9	5.19 ± .10	.37	7.1
M^3	L	12	2.9-3.9	3.25 ± .08	.29	8.9
	W	13	3.8-4.8	4.33 ± .09	.31	7.2
I^1	W	62	2.5-3.3	2.83 ± .02	.16	5.7
	H	62	3.8-5.2	4.57 ± .04	.37	8.1

Table A-9. Summary of measurements of the upper and lower dentition of *Plesiadapis churchilli* from the Long Draw quarry.

	n	OR	$\bar{x} \pm SE$	s	V
MANDIBLES					
P_3 L	4	2.2-2.6	2.40 ± .09	.18	7.5
W	4	2.0-2.3	2.12 ± .08	.15	7.1
P_4 L	3	2.4-2.6	2.53 ± .07	.12	4.7
W	3	2.5-2.8	2.60 ± .10	.17	6.5
M_1 L	4	3.4-3.6	3.47 ± .05	.10	2.9
W	4	3.2-3.5	3.27 ± .08	.15	4.6
M_2 L	4	3.6-4.0	3.75 ± .10	.19	5.1
W	4	3.4-3.8	3.52 ± .09	.19	5.4
M_3 L	2	4.7-5.1	4.90 ± .20	.28	5.7
W	2	3.0-3.2	3.10 ± .10	.14	4.5
Depth	2	8.4-8.7	8.55 ± .15	.21	2.5
I_1 W	2	2.5	2.50 –	–	–
H	2	3.5-4.1	3.80 ± .30	.42	11.0
MAXILLAE					
P^3 L	1	2.3	–	–	–
W	1	3.5	–	–	–
P^4 L	4	2.5-2.8	2.60 ± .07	.14	5.4
W	4	4.1-4.6	4.30 ± .11	.22	5.1
M^1 L	2	3.3-3.4	3.35 ± .05	.07	2.1
W	2	4.2-5.1	4.65 ± .45	.64	13.8
M^2 L	1	3.9	–	–	–
W	1	5.9	–	–	–
M^3 L	5	3.2-3.7	3.48 ± .10	.23	6.6
W	5	4.9-5.5	5.10 ± .10	.23	4.5

Table A-10. Summary of measurements of the upper and lower dentition of *Plesiadapis fodinatus* from the Princeton Quarry.

	n	OR	$\bar{x} \pm SE$	s	V
MANDIBLES					
P_3 L	23	2.2-2.9	2.57 ± .03	.16	6.2
W	23	1.8-2.4	2.08 ± .03	.12	5.8
P_4 L	26	2.4-2.8	2.67 ± .02	.10	3.7
W	26	2.2-2.8	2.40 ± .03	.14	5.8
M_1 L	34	2.8-3.5	3.22 ± .02	.12	3.7
W	34	2.7-3.2	2.93 ± .03	.15	5.1
M_2 L	33	3.1-3.7	3.45 ± .03	.16	4.6
W	33	3.1-3.5	3.27 ± .02	.13	4.0
M_3 L	26	4.8-5.6	5.21 ± .05	.24	4.6
W	27	3.0-3.5	3.24 ± .02	.13	4.0
Depth	20	6.5-8.3	7.45 ± .11	.49	6.6
I_1 W	7	2.1-2.5	2.37 ± .05	.13	5.5
H	7	3.2-4.0	3.66 ± .10	.26	7.1
MAXILLAE					
P^2 L	2	1.7-2.0	1.85 ± .15	.21	11.4
W	2	1.2-1.9	1.55 ± .35	.49	31.6
P^3 L	11	2.1-2.6	2.46 ± .04	.14	5.7
W	11	3.1-3.6	3.39 ± .06	.19	5.6
P^4 L	13	2.4-2.9	2.59 ± .04	.14	5.2
W	13	3.8-4.4	4.08 ± .06	.22	5.4
M^1 L	18	3.0-3.5	3.24 ± .03	.11	3.4
W	18	4.3-4.8	4.61 ± .04	.16	3.5
M^2 L	22	3.3-3.7	3.50 ± .02	.10	2.9
W	21	4.8-5.7	5.18 ± .06	.28	5.4
M^3 L	20	2.9-3.7	3.31 ± .05	.21	6.3
W	20	4.4-5.4	4.80 ± .07	.31	6.5
I^1 H	6	3.3-4.0	3.70 ± .09	.23	6.2
W	6	2.3-2.6	2.47 ± .06	.14	5.7

Table A-11. Summary of measurements of the upper and lower dentition of *Plesiadapis fodinatus* from the Schaff Quarry.

	n	OR	$\bar{x}$ ± SE	s	V
MANDIBLES					
P_3 L	15	2.4-2.9	2.59 ± .04	.16	6.2
W	15	1.9-2.2	1.99 ± .02	.09	4.5
P_4 L	23	2.3-2.8	2.59 ± .03	.13	5.0
W	23	2.0-2.6	2.33 ± .03	.14	6.0
M_1 L	23	2.9-3.5	3.17 ± .03	.16	5.0
W	23	2.5-3.1	2.92 ± .03	.16	5.5
M_2 L	21	3.2-3.8	3.39 ± .03	.14	4.1
W	21	2.8-3.6	3.20 ± .05	.21	6.6
M_3 L	14	4.7-5.6	5.11 ± .07	.28	5.5
W	14	2.9-3.6	3.21 ± .05	.20	6.2
Depth	16	6.6-8.4	7.51 ± .12	.49	6.5
I_1 W	5	2.2-2.7	2.32 ± .10	.22	9.5
H	5	3.2-3.8	3.42 ± .11	.25	7.3
MAXILLAE					
P^2 L	3	1.5-2.0	1.77 ± .15	.25	14.1
W	3	1.2-1.5	1.33 ± .09	.15	11.4
P^3 L	6	2.2-2.5	2.40 ± .04	.11	4.6
W	6	3.1-3.4	3.25 ± .06	.14	4.3
P^4 L	6	2.4-2.7	2.52 ± .05	.12	4.8
W	7	3.7-4.0	3.94 ± .04	.11	2.8
M^1 L	7	3.2-3.3	3.27 ± .02	.05	1.5
W	7	4.3-4.8	4.56 ± .07	.18	3.9
M^2 L	12	3.3-3.7	3.42 ± .04	.13	3.8
W	12	4.6-5.3	5.03 ± .06	.20	4.0
M^3 L	7	3.1-3.5	3.34 ± .06	.15	4.5
W	7	4.6-5.0	4.79 ± .06	.17	3.5
I^1 W	4	3.3-3.9	3.60 ± .12	.24	6.7
H	4	2.3-2.5	2.40 ± .04	.08	3.3

Table A-12. Summary of measurements of the upper and lower dentition of *Plesiadapis dubius* from the Paint Creek locality.

	n	OR	$\bar{x}$ ± SE	s	V
MANDIBLES					
P_3 L	1	2.5	–	–	–
W	1	2.0	–	–	–
P_4 L	2	2.6-2.9	2.75 ± .15	.21	7.6
W	2	2.2-2.3	2.25 ± .05	.07	3.1
M_1 L	3	2.7-3.1	2.90 ± .12	.20	6.9
W	3	2.5-2.7	2.60 ± .06	.10	3.8
M_2 L	4	3.0-3.2	3.07 ± .05	.10	3.3
W	4	2.8-2.9	2.85 ± .03	.06	2.1
M_3 L	2	4.7-5.1	4.90 ± .20	.28	5.7
W	2	3.1	–	–	–
Depth	1	8.2	–	–	–
I_1 W	3	2.0-2.2	2.07 ± .07	.12	5.8
H	2	3.0-3.3	3.15 ± .15	.21	6.7
MAXILLAE					
P^3 L	1	2.4	–	–	–
W	1	3.4	–	–	–
P^4 L	3	2.6	–	–	–
W	3	3.8-4.1	3.97 ± .09	.15	3.8
M^1 L	5	2.8-3.2	3.06 ± .07	.17	5.6
W	5	4.0-4.4	4.20 ± .09	.20	4.8
M^2 L	5	3.0-3.4	3.22 ± .07	.16	5.0
W	5	4.3-5.0	4.64 ± .13	.29	6.2
M^3 L	4	3.0-3.3	3.10 ± .07	.14	4.5
W	4	4.3-4.7	4.45 ± .10	.19	4.3
I^1 W	1	2.6	–	–	–
H	1	3.4	–	–	–

Table A-13. Summary of measurements of the upper and lower dentition of *Plesiadapis cookei* from the Little Sand Coulee area.

	n	OR	$\bar{x} \pm SE$	s	V
MANDIBLES					
P_3 L	4	4.5-5.3	5.07 ± .19	.39	7.7
W	4	3.7-4.1	3.92 ± .10	.21	5.4
P_4 L	5	4.3-5.1	4.72 ± .15	.33	7.0
W	5	4.3-4.7	4.54 ± .07	.17	3.7
M_1 L	7	5.1-5.7	5.41 ± .08	.21	3.9
W	7	4.8-5.4	5.10 ± .07	.19	3.7
M_2 L	8	5.4-6.1	5.82 ± .08	.23	4.0
W	8	5.1-5.7	5.47 ± .08	.21	3.8
M_3 L	3	8.4-9.1	8.83 ± .22	.38	4.3
W	3	5.5-5.6	5.53 ± .03	.06	1.1
Depth	5	15.6-19.3	17.46 ± .59	1.32	7.6
I_1 W	4	4.2-4.3	4.25 ± .03	.06	1.4
H	3	5.9-6.8	6.33 ± .29	.50	7.9
MAXILLAE					
P^4 L	2	4.1-4.3	4.20 ± .10	.14	3.3
W	2	5.7-6.2	5.95 ± .25	.35	5.9
M^1 L	4	5.4-5.9	5.67 ± .11	.22	3.9
W	4	7.3-7.8	7.60 ± .12	.24	3.2
M^2 L	4	5.8-6.0	5.87 ± .05	.10	1.7
W	3	8.5-8.9	8.67 ± .12	.21	2.4
M^3 L	1	5.7	–	–	–
W	1	7.5	–	–	–
I^1 W	3	4.1-5.1	4.57 ± .29	.50	11.1
H	2	6.8-6.9	6.85 ± .05	.07	1.0

Table A-14. Summary of measurements of the upper and lower dentition of *Plesiadapis walbeckensis* from the Walbeck fissure-filling.

	n	OR	$\bar{x} \pm SE$	s	V
MANDIBLES					
P_3 L	1	2.0	–	–	–
W	1	2.0	–	–	–
P_4 L	8	1.9-2.2	2.09 ± .04	.10	4.8
W	8	2.1-2.4	2.25 ± .04	.11	4.9
M_1 L	21	2.6-3.0	2.85 ± .02	.11	3.9
W	21	2.5-2.9	2.70 ± .02	.11	4.1
M_2 L	29	2.9-3.4	3.18 ± .02	.13	4.1
W	29	2.9-3.3	3.12 ± .02	.13	4.2
M_3 L	25	4.2-5.0	4.72 ± .04	.20	4.2
W	25	2.5-3.1	2.91 ± .03	.16	5.5
Depth	9	7.6-9.9	8.33 ± .25	.74	8.9
I_1 W	5	2.3-2.7	2.52 ± .07	.15	5.9
H	5	4.1-4.9	4.48 ± .14	.32	7.1
MAXILLAE*					
P^3 L	15	1.8-2.2	1.97 ± .03	.12	6.2
W	15	2.7-3.0	2.77 ± .04	.14	5.2
P^4 L	15	1.8-2.5	2.06 ± .04	.54	7.5
W	15	3.0-3.8	3.26 ± .06	.22	6.9
M^1 L	15	2.7-3.0	2.89 ± .03	.13	4.5
W	15	4.0-4.4	4.20 ± .04	.15	3.7
M^2 L	15	2.9-3.2	3.12 ± .04	.14	4.5
W	15	4.4-5.0	4.72 ± .04	.16	3.3
M^3 L	15	2.5-3.1	2.81 ± .05	.18	6.4
W	15	3.9-4.4	4.31 ± .05	.18	4.2

* Data for maxillae from Russell (1964, p. 296).

Table A-15. Summary of measurements of the upper and lower dentition of *Plesiadapis remensis* from the Conglomerat de Cernay.*

		n	OR	$\bar{x} \pm SE$	s	V
MANDIBLES						
P_3	L	1	2.6	–	–	–
	W	–	–	–	–	–
P_4	L	3	2.7-2.9	2.83 ± .07	.12	4.2
	W	2	3.0	–	–	–
M_1	L	5	3.4-3.7	3.56 ± .05	.11	3.1
	W	4	3.1-3.4	3.27 ± .06	.13	4.0
M_2	L	10	3.7-4.3	4.00 ± .06	.18	4.5
	W	10	3.5-4.0	3.73 ± .05	.16	4.3
M_3	L	9	5.5-6.2	5.90 ± .09	.28	4.7
	W	9	3.3-3.9	3.60 ± .07	.21	5.8
Depth		9	8.8-12.5	10.82 ± .47	1.42	13.1
**I_1	W	3	2.7-3.0	2.87 ± .09	.15	5.2
	H	3	4.0-4.6	4.33 ± .18	.31	7.2
MAXILLAE						
P^3	L	1	2.9	–	–	–
	W	1	4.0	–	–	–
P^4	L	3	2.8-3.2	3.00 ± .12	.20	6.7
	W	3	4.7-4.9	4.83 ± .07	.12	2.5
M^1	L	8	3.5-3.9	3.65 ± .05	.14	3.8
	W	8	4.5-5.3	5.04 ± .09	.26	5.2
M^2	L	11	3.8-4.2	4.10 ± .04	.13	3.2
	W	10	5.5-6.5	6.12 ± .11	.36	5.9
M^3	L	5	3.8-4.5	4.14 ± .13	.30	7.2
	W	5	5.3-5.7	5.54 ± .07	.15	2.7
I^1	W	1	3.1	–	–	–
	H	1	4.4	–	–	–

* To avoid any confusion with *Ples. tricuspidens*, only teeth in jaw fragments are included in this table.

** Data for I_1 from Lentille, Pellouin collection.

Table A-16. Summary of measurements of the upper and lower dentition of *Plesiadapis tricuspidens* from Berru (Carrière Mouras, not Lentille).

		n	OR	$\bar{x} \pm SE$	s	V
MANDIBLES*						
P_3	L	25	2.9-3.8	3.43 ± .05	.24	7.0
	W	25	2.5-3.5	3.06 ± .05	.24	7.8
P_4	L	38	3.0-4.0	3.45 ± .04	.24	7.0
	W	38	3.0-4.0	3.50 ± .04	.26	7.4
M_1	L	40	3.7-4.6	4.22 ± .03	.19	4.5
	W	40	3.5-4.4	3.81 ± .03	.20	5.2
M_2	L	52	4.3-5.3	4.87 ± .03	.23	4.7
	W	52	4.0-4.9	4.39 ± .03	.22	5.0
M_3	L	63	6.8-8.7	7.63 ± .05	.41	5.4
	W	63	4.0-5.0	4.46 ± .03	.25	5.6
Depth		42	11.3-20.0	15.41 ± .33	2.13	13.8
I_1	W	10	3.3-3.8	3.60 ± .05	.16	4.4
	H	10	4.6-5.8	5.04 ± .12	.37	7.3
MAXILLAE*						
P^3	L	6	3.0-3.9	3.37 ± .12	.30	8.9
	W	6	4.5-5.5	4.85 ± .16	.40	8.2
P^4	L	4	3.1-3.8	3.35 ± .17	.33	9.8
	W	4	5.3-6.4	5.67 ± .25	.50	8.8
M^1	L	5	4.2-4.7	4.40 ± .09	.20	4.5
	W	5	5.7-6.3	6.04 ± .11	.24	4.0
M^2	L	10	4.6-5.1	4.83 ± .06	.18	3.7
	W	10	6.8-7.8	7.34 ± .12	.39	5.3
M^3	L	8	4.4-5.4	4.82 ± .12	.35	7.3
	W	8	6.6-7.2	6.99 ± .08	.23	3.3
I^1	W	1	4.0	–	–	–
	H	1	5.7	–	–	–

* Data given for mandibular dentition includes isolated teeth, that for the maxillary dentition does not.

Table A-17. Summary of measurements of the upper and lower dentition of *Platychoerops daubrei* from the Mutigny locality.

	n	OR	$\bar{x} \pm$ SE	s	V
MANDIBLES					
P_3 L	14	4.2-5.1	4.66 ± .07	.25	5.4
W	14	3.1-4.2	3.67 ± .08	.30	8.2
P_4 L	14	4.4-5.1	4.79 ± .06	.21	4.4
W	15	3.8-4.8	4.20 ± .07	.26	6.2
M_1 L	12	4.6-5.3	5.03 ± .06	.20	4.0
W	12	3.7-4.4	4.07 ± .06	.21	5.2
M_2 L	18	4.9-5.9	5.39 ± .07	.28	5.2
W	18	4.1-4.8	4.39 ± .05	.23	5.2
M_3 L	21	7.0-8.4	7.73 ± .08	.35	4.5
W	22	4.2-5.2	4.59 ± .06	.27	5.9
Depth	6	13.7-18.1	15.00 ± .66	1.63	10.1
MAXILLAE					
P^2 L	6	3.0-3.8	3.33 ± .12	.29	8.7
W	6	2.5-3.2	2.77 ± .13	.31	11.2
P^3 L	11	3.2-4.7	4.02 ± .13	.44	10.9
W	11	4.4-6.2	5.59 ± .16	.52	9.3
P^4 L	13	3.9-4.8	4.30 ± .08	.29	6.7
W	13	5.6-7.0	6.22 ± .12	.44	7.1
M^1 L	6	4.7-5.3	4.97 ± .08	.21	4.2
W	5	5.7-6.5	6.12 ± .15	.33	5.4
M^2 L	14	4.7-5.5	5.06 ± .07	.27	5.3
W	14	6.1-7.5	6.56 ± .10	.39	5.9
M^3 L	15	4.7-5.6	5.13 ± .07	.27	5.3
W	14	5.9-7.2	6.71 ± .09	.35	5.2

PLATES

PLATE 1

Pronothodectes

(All figures 3 times natural size)

A. Left mandible of *Pronothodectes matthewi* with $I_1P_{3\text{-}4}M_{1\text{-}3}$ (AMNH 35462) from the Gidley Quarry, lateral view.
B. Left mandible of *Pronothodectes jepi* with $I_1P_{3\text{-}4}M_{1\text{-}3}$ (PU 14783) from the Rock Bench quarry, lateral view.
C. Left mandible of *Pronothodectes jepi* with $P_{3\text{-}4}M_{1\text{-}3}$ (type specimen, PU 14782) from the Rock Bench quarry, lateral view.
D. Same as (A), occlusal stereophotograph.
E. Same as (B), occlusal stereophotograph.
F. Same as (C), occlusal stereophotograph.
G. Left maxilla of *Pronothodectes matthewi* with $P^{2\text{-}4}M^{1\text{-}2}$ (AMNH 35470) from the Gidley Quarry, occlusal stereophotograph.
H. Left maxilla of *Pronothodectes jepi* with $P^4M^{1\text{-}2}$ (PU 17500) from the Rock Bench quarry, occlusal stereophotograph.


0
1cm
A
B
C
D
E
F
G
H
PU17500

PLATE 2

Nannodectes

(All figures 3 times natural size)

A. Left mandible of *Nannodectes intermedius* with $P_4M_{1\text{-}3}$ (type specimen, UW 3223) from the Keefer Hill locality, lateral view.

B. Right mandible of *Nannodectes gazini* with $P_{3\text{-}4}M_1$ (type specimen, AMNH 92008) from the Saddle locality, lateral view.

C. Right mandible of *Nannodectes simpsoni* with $P_4M_{1\text{-}3}$ (type specimen, USNM 20754) from the Ledge locality, lateral view.

D. Left mandible of *Nannodectes gidleyi* with $I_1P_{3\text{-}4}M_{1\text{-}3}$ (AMNH 17389) from the Mason Pocket locality, lateral view.

E. Same as (A), occlusal stereophotograph.

F. Same as (B), occlusal stereophotograph.

G. Same as (C), occlusal stereophotograph.

H. Same as (D), occlusal stereophotograph.

I. Left maxilla of *Nannodectes intermedius* with $M^{1\text{-}3}$ (AMNH 88308) from the Keefer Hill locality, occlusal stereophotograph.

J. Left maxilla of *Nannodectes gazini* with $P^{3\text{-}4}M^{1\text{-}3}$ (CM 20956) from the Saddle locality, occlusal stereophotograph.

K. Left maxilla of *Nannodectes simpsoni* with $P^{3\text{-}4}M^{1\text{-}3}$ (USNM 20781) from the Ledge locality, occlusal stereophotograph.

L. Right maxilla of *Nannodectes gidleyi* with $P^4M^{1\text{-}3}$ (AMNH 17200) from the Mason Pocket locality, occlusal stereophotograph.

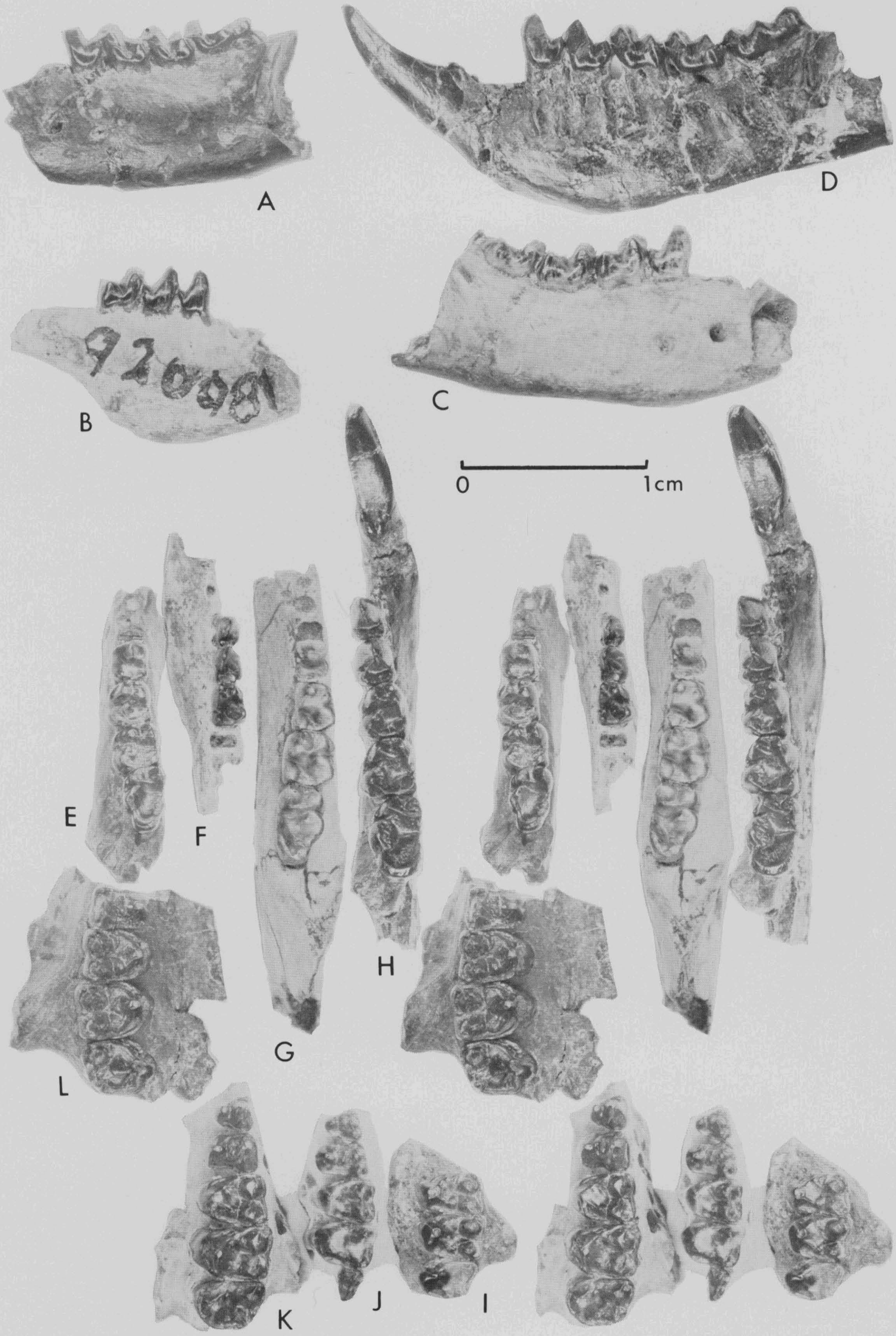

A
D
B
C
0
1cm
E
F
G
H
L
K
J
I

PLATE 3

Plesiadapis

(All figures twice natural size)

A. Left mandible of *Plesiadapis praecursor* with P_4M_{1-2} (type specimen, PU 14512) from the Douglass Quarry, lateral view.
B. Left mandible of *Plesiadapis anceps* with $I_1P_{3-4}M_{1-3}$ (PU 18738) from the Highway Blowout locality, lateral view.
C. Right mandible of *Plesiadapis rex* with $I_1P_{3-4}M_{1-3}$ (PU 21246) from the Cedar Point quarry, lateral view.
D. Same as (C), medial view.
E. Right mandible of *Plesiadapis walbeckensis* with $I_1P_4M_{1-3}$ (type specimen, GH Wa-287) from the Walbeck fissure-filling, lateral view.
F. Left mandible of *Plesiadapis churchilli* with $I_1P_{3-4}M_{1-3}$ (type specimen, PU 21234) from the Long Draw quarry, lateral view.
G. Right mandible of *Plesiadapis churchilli* with $I_1P_{3-4}M_{1-2}$ (PU 20846) from the Long Draw quarry, lateral view.
H. Left mandible of *Plesiadapis fodinatus* with $I_1P_{3-4}M_{1-3}$ (PU 13930) from the Princeton Quarry, lateral view.
I. Right mandible of *Plesiadapis dubius* with P_4M_{1-3} (AMNH 16073) from the south side of Polecat Bench, lateral view.

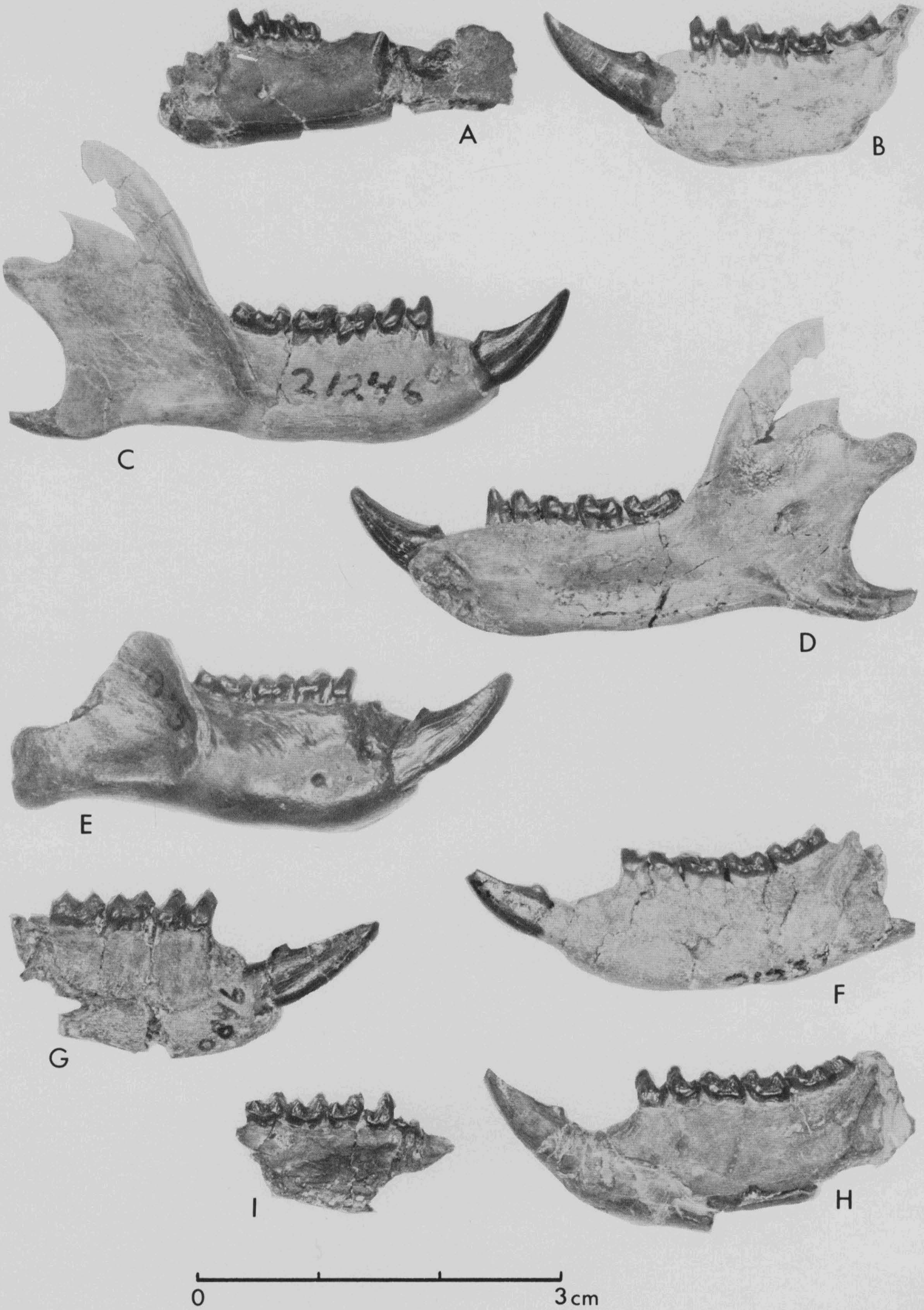

A
B
21246
C
D
E
F
G
I
H
0
3cm

PLATE 4

Plesiadapis

(All figures twice natural size)

A. Left mandible of *Plesiadapis praecursor* with P_4M_{1-2} (type specimen, PU 14512) from the Douglass Quarry, occlusal stereophotograph.
B. Left mandible of *Plesiadapis anceps* with $I_1P_{3-4}M_{1-3}$ (PU 18738) from the Highway Blowout locality, occlusal stereophotograph.
C. Right mandible of *Plesiadapis walbeckensis* with $I_1P_4M_{1-3}$ (type specimen, GH Wa-287) from the Walbeck fissure-filling, occlusal stereophotograph.
D. Right mandible of *Plesiadapis rex* with $I_1P_{3-4}M_{1-3}$ (PU 21246) from the Cedar Point quarry, occlusal stereophotograph.
E. Left mandible of *Plesiadapis churchilli* with $I_1P_{3-4}M_{1-3}$ (type specimen, PU 21234) from the Long Draw quarry, occlusal stereophotograph.
F. Left mandible of *Plesiadapis fodinatus* with $I_1P_{3-4}M_{1-3}$ (PU 13930) from the Princeton Quarry, occlusal stereophotograph.
G. Right mandible of *Plesiadapis dubius* with P_4M_{1-3} (type specimen, AMNH 16073) from the south side of Polecat Bench, occlusal stereophotograph.
H. Left maxilla of *Plesiadapis rex* with $P^{3-4}M^{1-3}$ (PU 20703) from the Cedar Point quarry, occlusal stereophotograph.
I. Left maxilla of *Plesiadapis fodinatus* with $I^2P^{3-4}M^{1-3}$ (PU 13393) from the Princeton Quarry, occlusal stereophotograph.

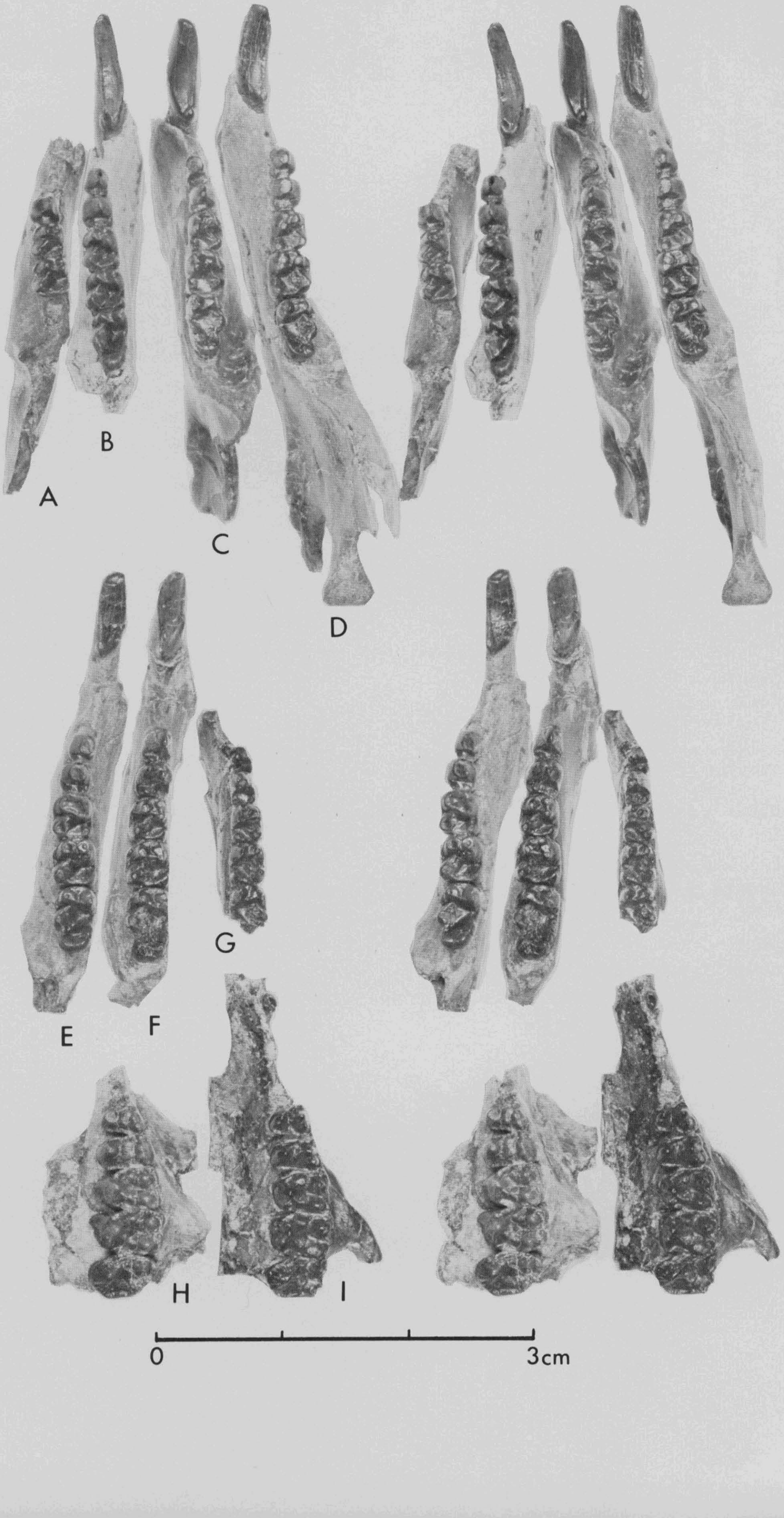

B
A
C
D
G
E
F
H
I
0
3cm

PLATE 5

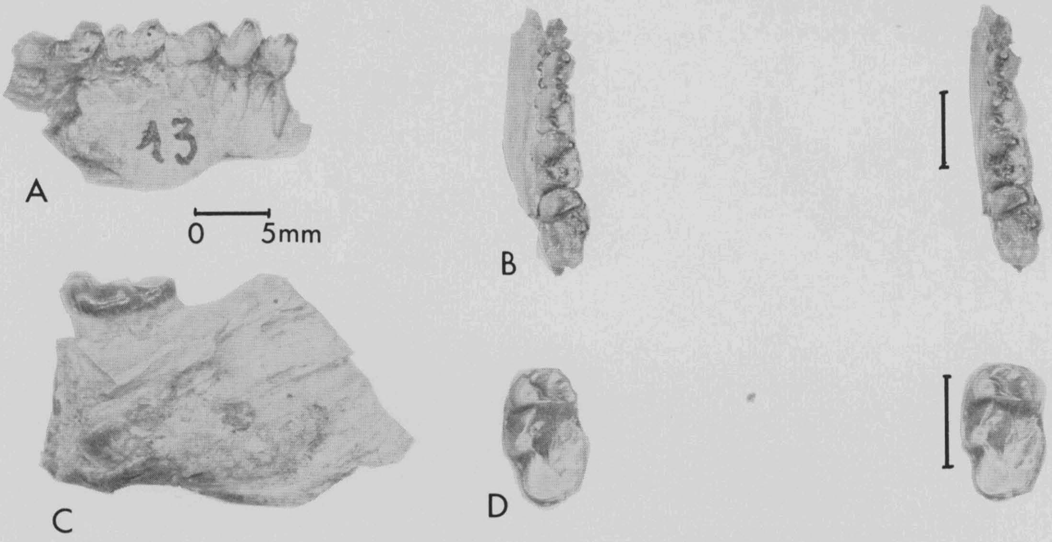
Plesiadapis

(Scale bar equals 5 mm in figures A-D)

A. Right mandible of *Plesiadapis remensis* with $P_{3-4}M_{1-3}$ (type specimen, MNHN Crl-13) from Cernay, lateral view.
B. Same as (A), occlusal stereophotograph.
C. Left mandible of *Plesiadapis tricuspidens* with M_3 (type specimen, MNHN Crl-16) from Calcaires de Rilly near Reims, lateral view.
D. Same as (C), tooth only, occlusal stereophotograph.

(Figures E-K, natural size)

E. Right mandible of *Plesiadapis simonsi* with M_{1-2} (type specimen, PU 17814) from the Sand Draw area, lateral view.
F. Same as (E), occlusal stereophotograph.
G. Left mandible of *Plesiadapis tricuspidens* with $I_1P_{3-4}M_{1-3}$ (Louis collection) from Berru, occlusal stereophotograph.
H. Left mandible of *Plesiadapis cookei* with $P_{3-4}M_{1-2}$ (type specimen, PU 13293) from the Little Sand Coulee area, occlusal stereophotograph.
I. Right mandible of *Plesiadapis remensis* with M_3 (Pellouin collection) from the Lentille de Berru locality, lateral view.
J. Same as (G), lateral view.
K. Same as (H), lateral view.


A
13
0
5mm
B
C
D

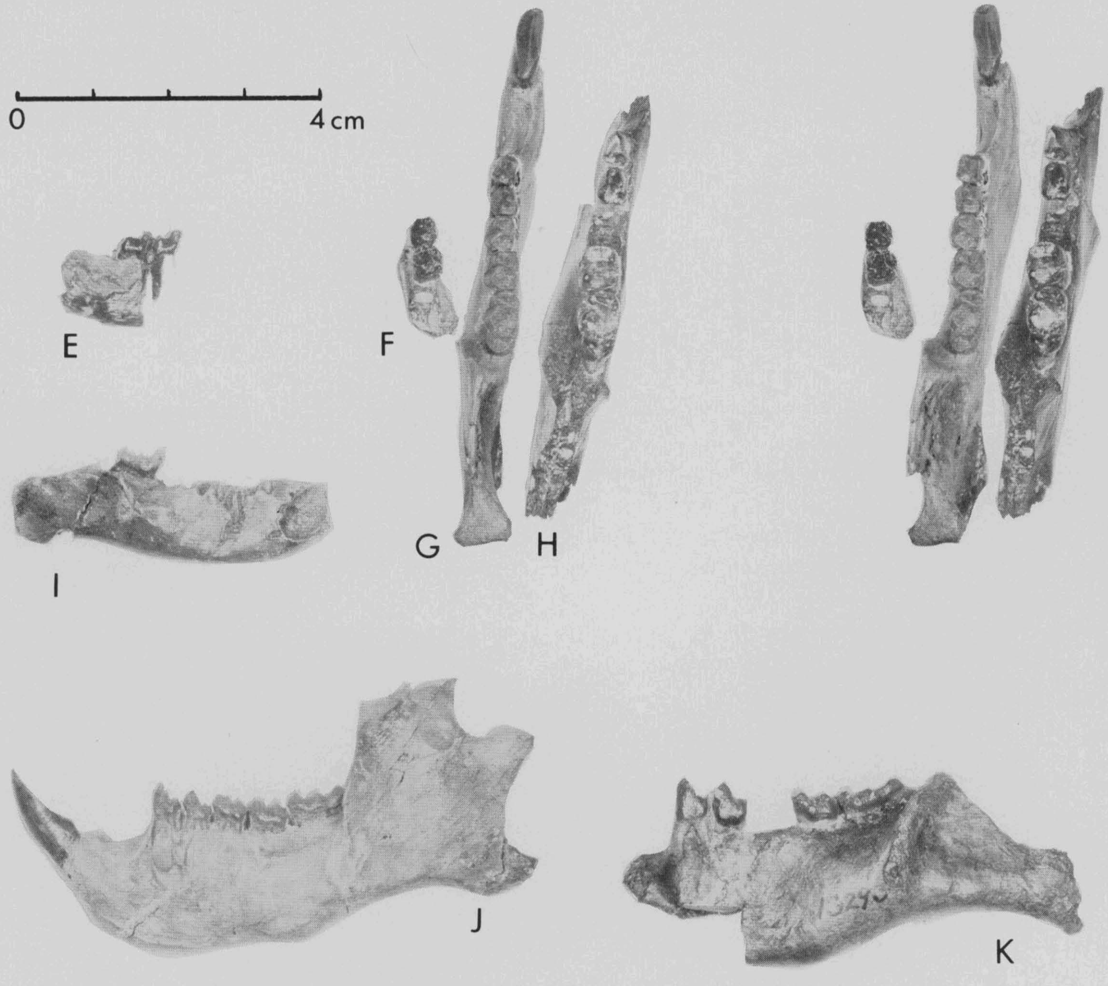

0
4 cm
E
F
G
H
I
J
K

PLATE 6

Plesiadapis and **Platychoerops**

(Figures A-F, twice natural size)

A. Left upper central incisor of *Plesiadapis tricuspidens* (Louis collection) from Berru, occlusal stereophotograph.
B. Left upper central incisor of *Plesiadapis cookei* (PU 18118) from the Little Sand Coulee area, occlusal stereophotograph.
C. Left upper central incisor of *Platychoerops daubrei* (Louis collection) from Mutigny, occlusal stereophotograph.
D. Right upper central incisor of *Plesiadapis russelli* (type specimen, LGM collection) from Meudon, occlusal stereophotograph. Arrow indicates vestigial laterocone.
E. Same as (D), lateral view. Arrow indicates vestigial laterocone. Note strong posterocone.
F. Right mandible of *Platychoerops ?richardsonii* with M_{1-3} (MNHN Al-5170) from Lemoine's Ageian collection, occlusal stereophotograph. Note straight crest connecting the protoconid with the paraconid on M_{2-3}.

(Figures G-K, natural size)

G. Right mandible of *Platychoerops daubrei* with $I_1P_{3-4}M_{1-3}$ (UCMP 71477) from Mutigny, lateral view.
H. Same as (G), occlusal stereophotograph.
I. Right maxilla of *Plesiadapis cookei* with P^4M^{1-3} (type specimen, PU 13293) from the Little Sand Coulee area, occlusal stereophotograph.
J. Left maxilla of *Plesiadapis tricuspidens* with P^3M^{1-3} (Louis collection) from Berru, occlusal stereophotograph.
K. Palate of *Platychoerops richardsonii* with P^4M^{2-3} (type specimen, YM 520) from Herne Bay, occlusal stereophotograph.

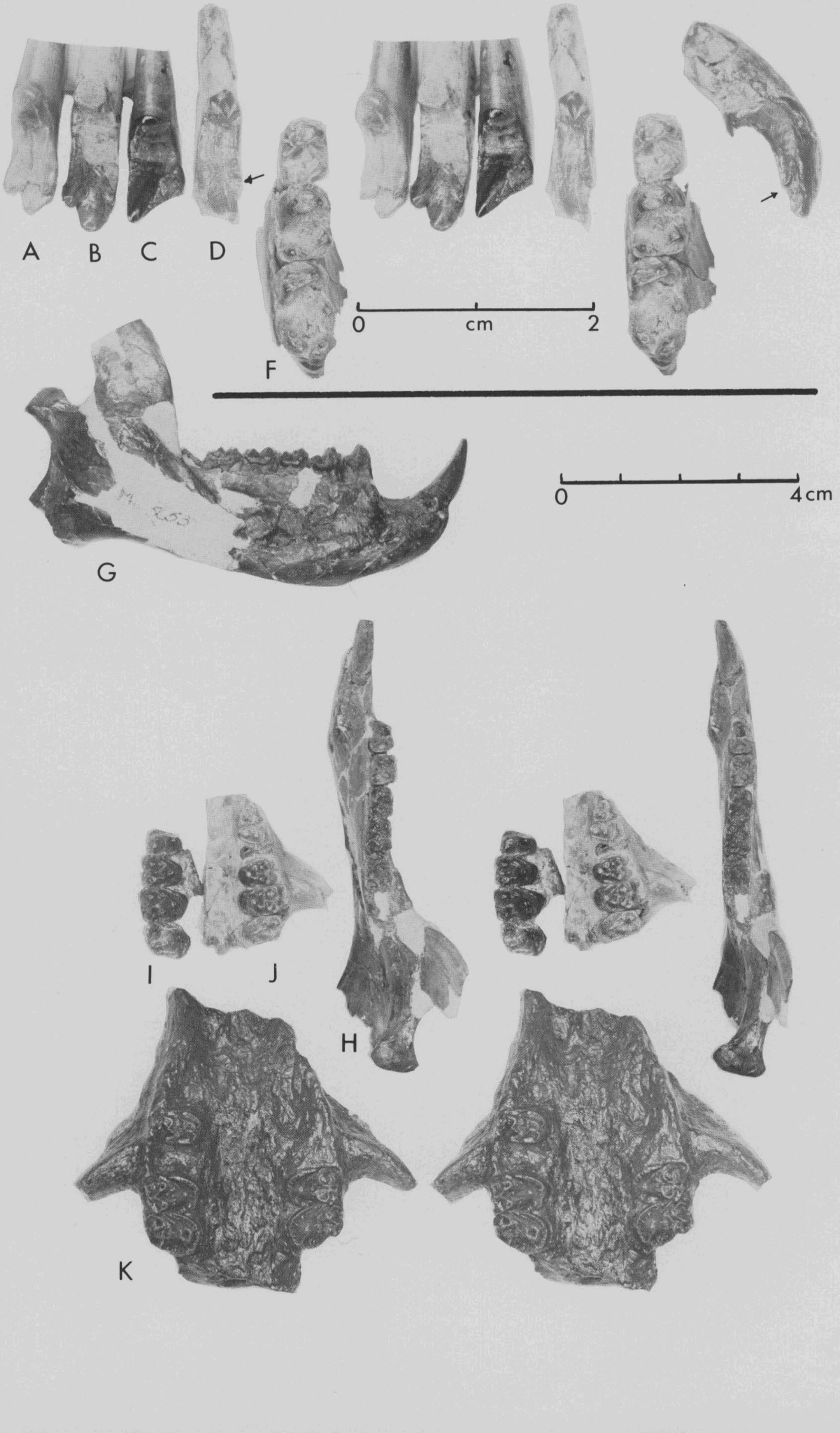

A
B
C
D
F
0
cm
2
G
0
4cm
I
J
H
K

PLATE 7

Chiromyoides

(All figures twice natural size)

A. Right upper central incisor of *Chiromyoides minor* (type specimen, USNM field no. 35-63) from Chappo-17, occlusal stereophotograph.
B. Left upper central incisor of *Chiromyoides caesor* (type specimen, PU 21575) from the Croc Tooth quarry, occlusal stereophotograph.
C. Left upper central incisor of *Chiromyoides potior* (type specimen, USNM 10639) from Bayfield area, occlusal stereophotograph.
D. Left upper central incisor of *Chiromyoides major* (type specimen, PU 21150) from the Paint Creek locality, occlusal stereophotograph. Medial portion of tooth is broken away.
E. Right upper central incisor of *Chiromyoides campanicus* (Louis collection) from Berru, occlusal stereophotograph.
F. Same as (A), lateral view.
G. Same as (B), lateral view.
H. Same as (C), lateral view.
I. Same as (D), lateral view.
J. Same as (E), lateral view.
K. Right lower central incisor of *Chiromyoides major* (PU 21587) from the Paint Creek locality, lateral view.
L. Left mandible of *Chiromyoides campanicus* with $I_1P_{3\text{-}4}M_{1\text{-}3}$ (type specimen, NMB Cy-153) from Cernay, medial view.
M. Same as (L), lateral view.
N. Same as (L), occlusal stereophotograph.
O. Left maxilla of *Chiromyoides campanicus* with $P^4M^{1\text{-}2}$ (MNHN Cr-858) from Berru, occlusal stereophotograph.

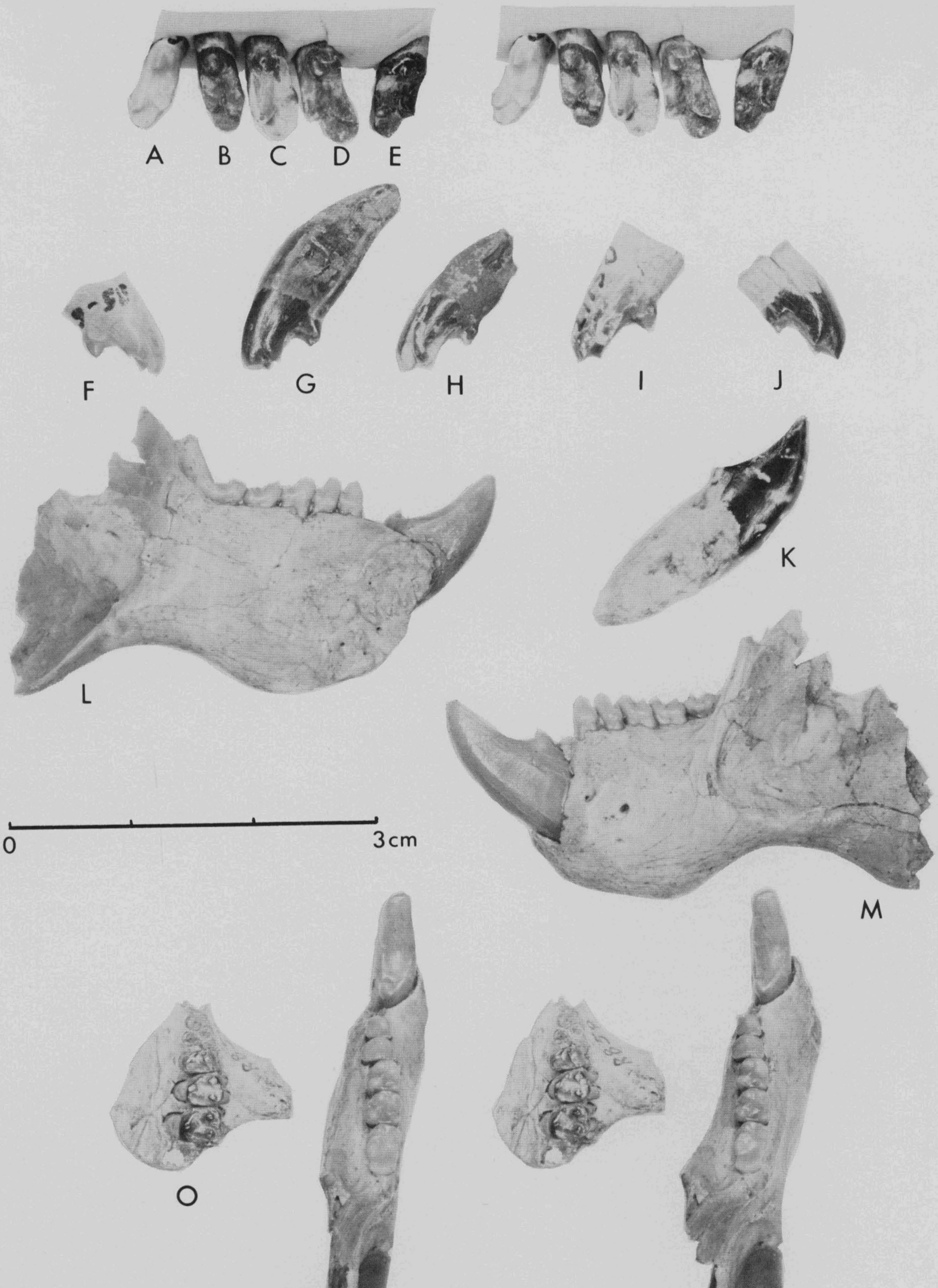

A
B
C
D
E
F
G
H
I
J
K
L
M
0
3cm
O
N

PLATE 8

Cranium of **Plesiadapis tricuspidens**

A. Dorsal aspect of frontal region of flattened cranium MNHN Cr-125 from Berru. Arrows indicate most posterior extension of premaxillae. Stereophotograph.

B. Dorsal aspect of flattened cranium MNHN Cr-125 from Berru, stereophotograph. Approximately 4/5 natural size.

C. Same as (B), ventral aspect, stereophotograph. Approximately 4/5 natural size.

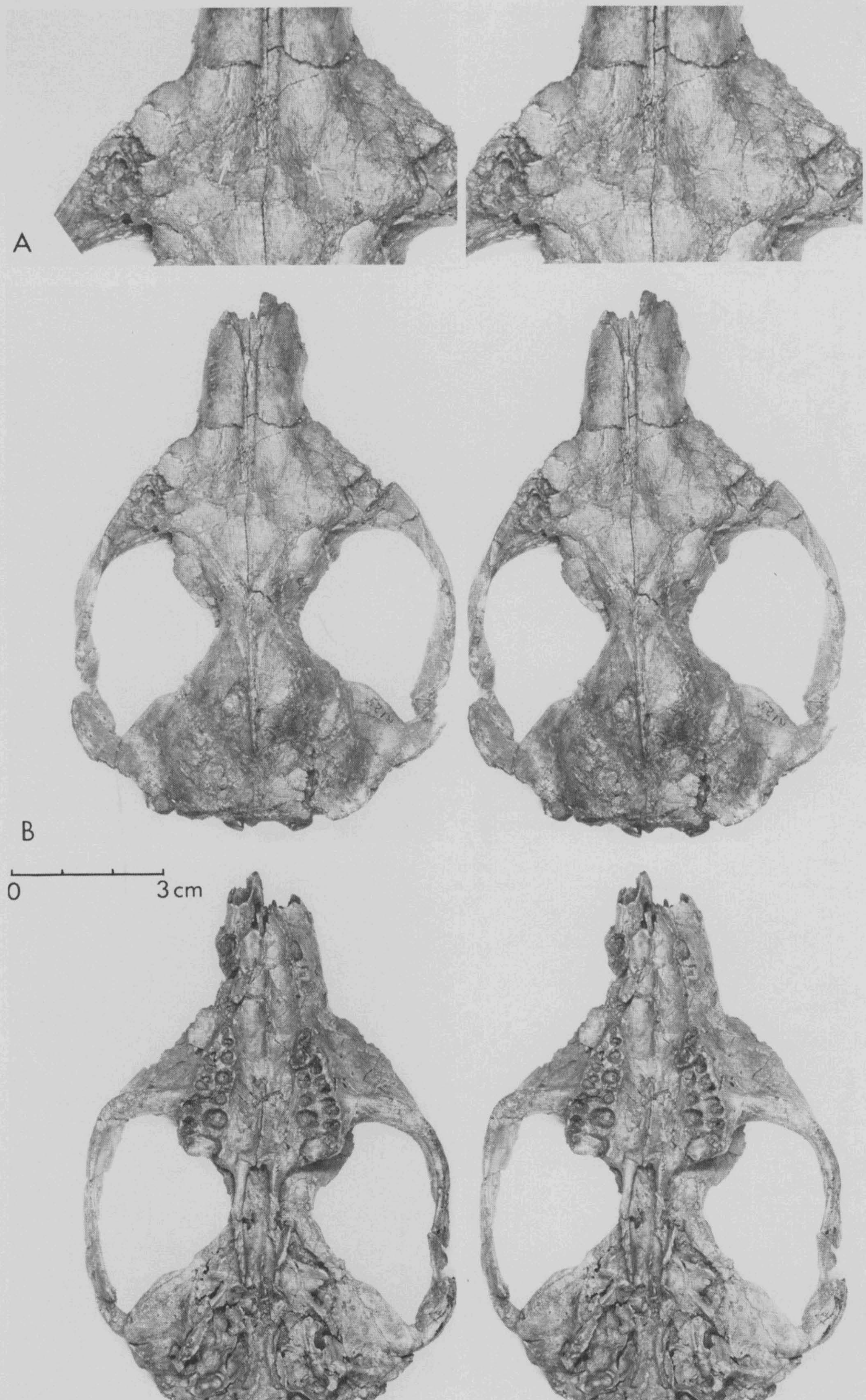

A
B
0
3 cm
C

PLATE 9

Cranium of **Plesiadapis tricuspidens**

A. Pellouin skull of *Plesiadapis tricuspidens* from Berru, natural size, stereophotograph of ventral aspect. Photographed by Mr. Karoly Kutasi, University of Michigan.

B. Right auditory bulla of Pellouin skull from Berru, 2.2 times natural size, stereophotograph of ventral aspect. Several fragments of bulla removed to show interior. A.t., anulus tympanicus; C.c., canalis caroticus; M.a.e., meatus acousticus externus.

C. Left middle ear of Pellouin skull from Berru, 2.2 times natural size, stereophotograph of ventral aspect. Inferred course of internal carotid artery shown with dashed line, stapedial artery may have been lost in this species. A.c.i., arteria carotis interna; C.f., canalis facialis; F.v., fenestra vestibuli; M.a.e., meatus acousticus externus; P.t., plexus tympanicus.

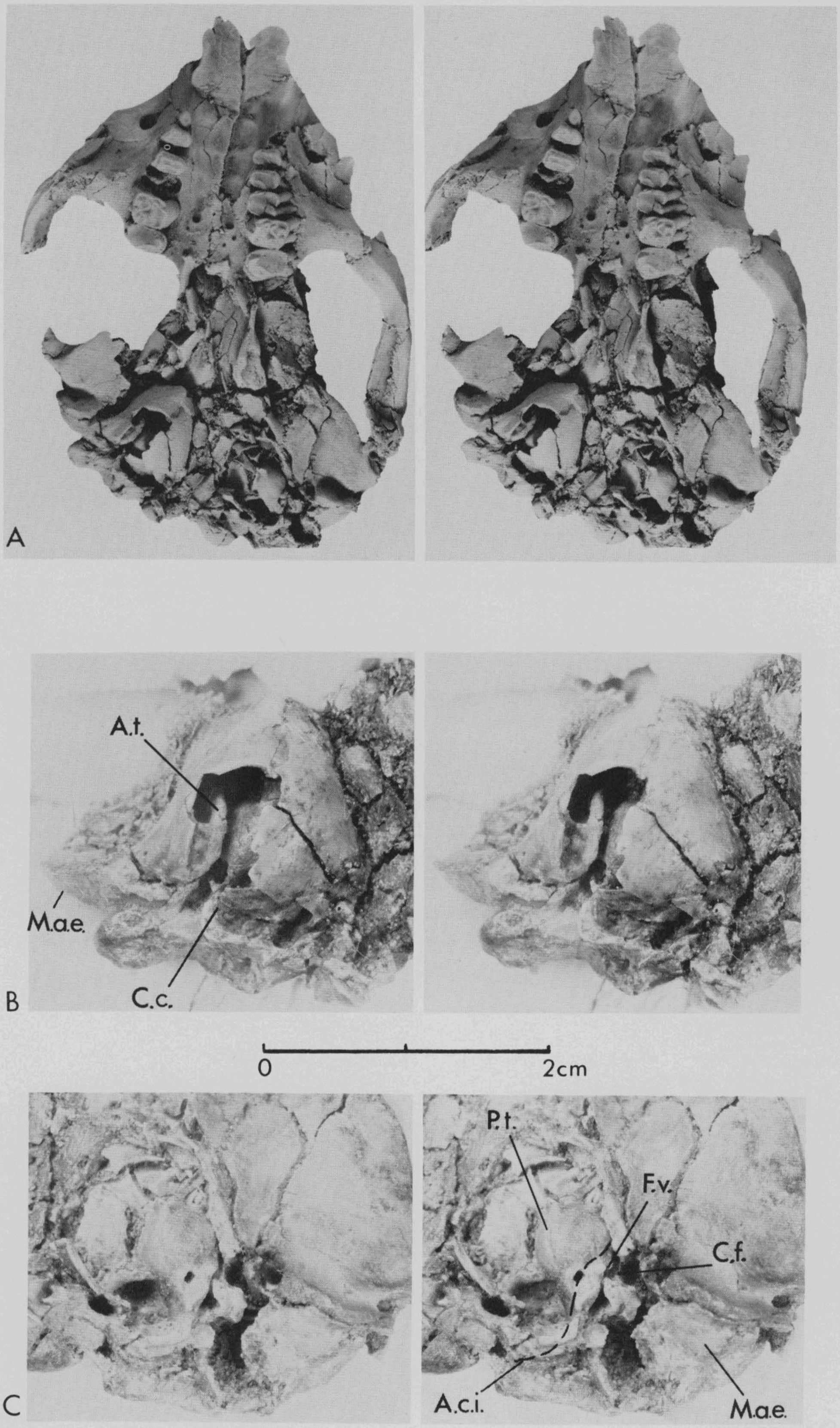

A
A.t.
M.a.e.
C.c.
B
0
2cm
P.t.
F.v.
C.f.
A.c.i.
M.a.e.
C

PLATE 10

Basicranium of **Leptictis**, **Cynodontomys**, and **Phenacolemur**

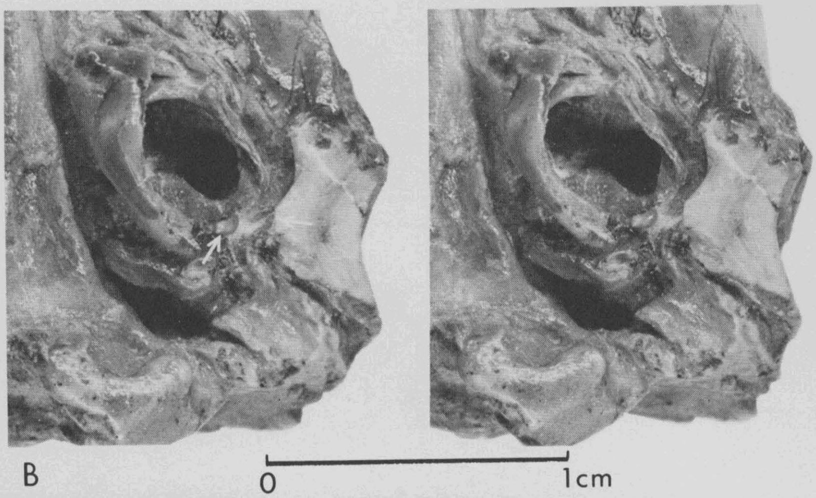
A. Left auditory region of skull of Oligocene leptictid insectivore *Leptictis* from Slim Buttes, South Dakota (FMNH - HM14), ventral view. Arrow points to free ectotympanic anulus, which was enclosed within the auditory bulla. See also (B) and Text-figure 41 for further explanation.

B. Same as (A), ventral view of auditory region of *Leptictis*. Stereophotograph, 4 times natural size. Arrows point to proximal end of ectotympanic anulus and to its articulation with the ectotympanic process of the squamosal. Distal end of ectotympanic articulated with groove on medial part of squamosal anterior to the ectotympanic process. See Text-figure 41 for further explanation.

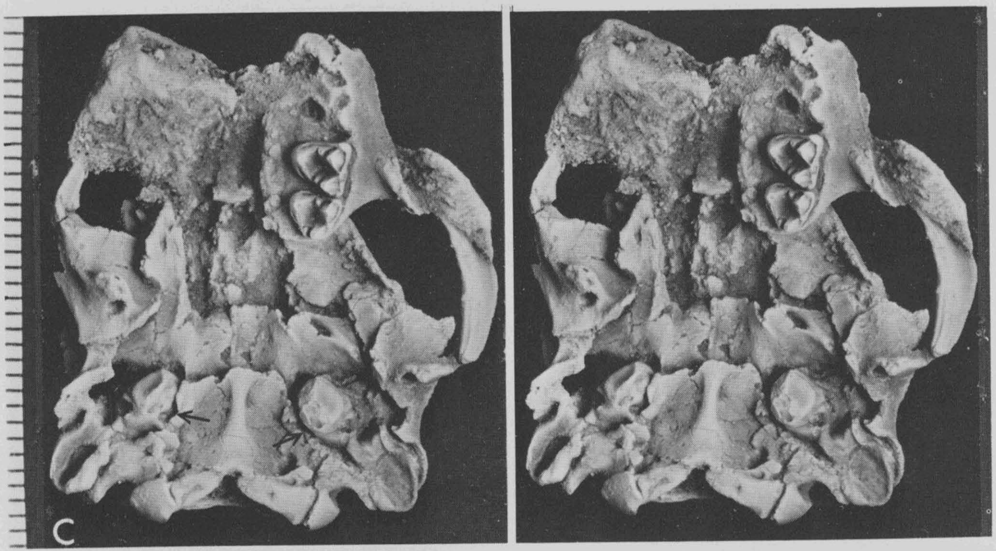
C. Basicranium of skull of Eocene microsyopid primate *Cynodontomys latidens* from Locality II, Huerfano Formation, Fossil Creek, Colorado (AMNH 55286). Stereophotograph, 2 times natural size. Arrows point to internal acoustic meatus of left and right petrosals, incorrectly identified by Szalay (1969, fig. 17) as grooves for a large medial entocarotid artery. Photographed by Mr. Karoly Kutasi, University of Michigan.

D. Basicranium of skull of Eocene paromomyid primate *Phenacolemur jepseni* from head of Arroyo Blanco, Almagre facies of San José Formation, New Mexico. Stereophotograph, 2 times natural size. Arrow points to *Plesiadapis*-like ectotympanic which formed the lateral wall of the auditory bulla and extended laterally into an external auditory meatus. An annular crest is preserved on the medial side of the ectotympanic for attachment of the tympanic membrane. Photographed by Mr. Karoly Kutasi, University of Michigan.

A



B



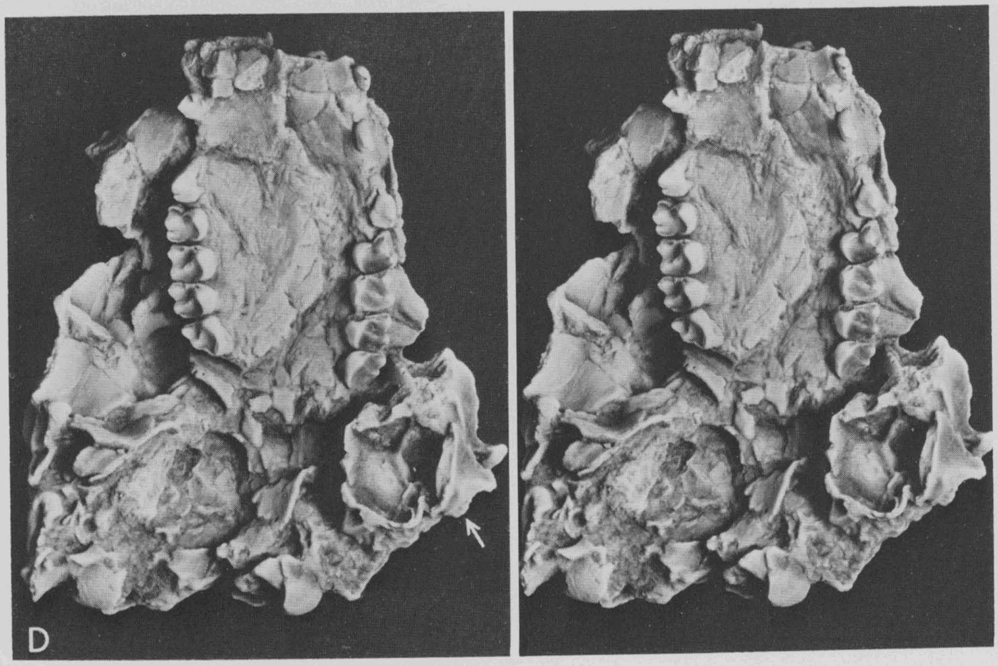


PLATE 11

Skull and skeleton of **Plesiadapis insignis**

A. Lateral view of impression of skull of *Plesiadapis insignis* (type specimen, MNHN collection). Reproduced 1.5 times natural size. Left and right stereophotographs have been reversed to give a positive image.

B. Reversed stereophotographs of skull and skeleton of *Plesiadapis insignis* (type specimen, MNHN collection), reproduced 3/5 natural size.

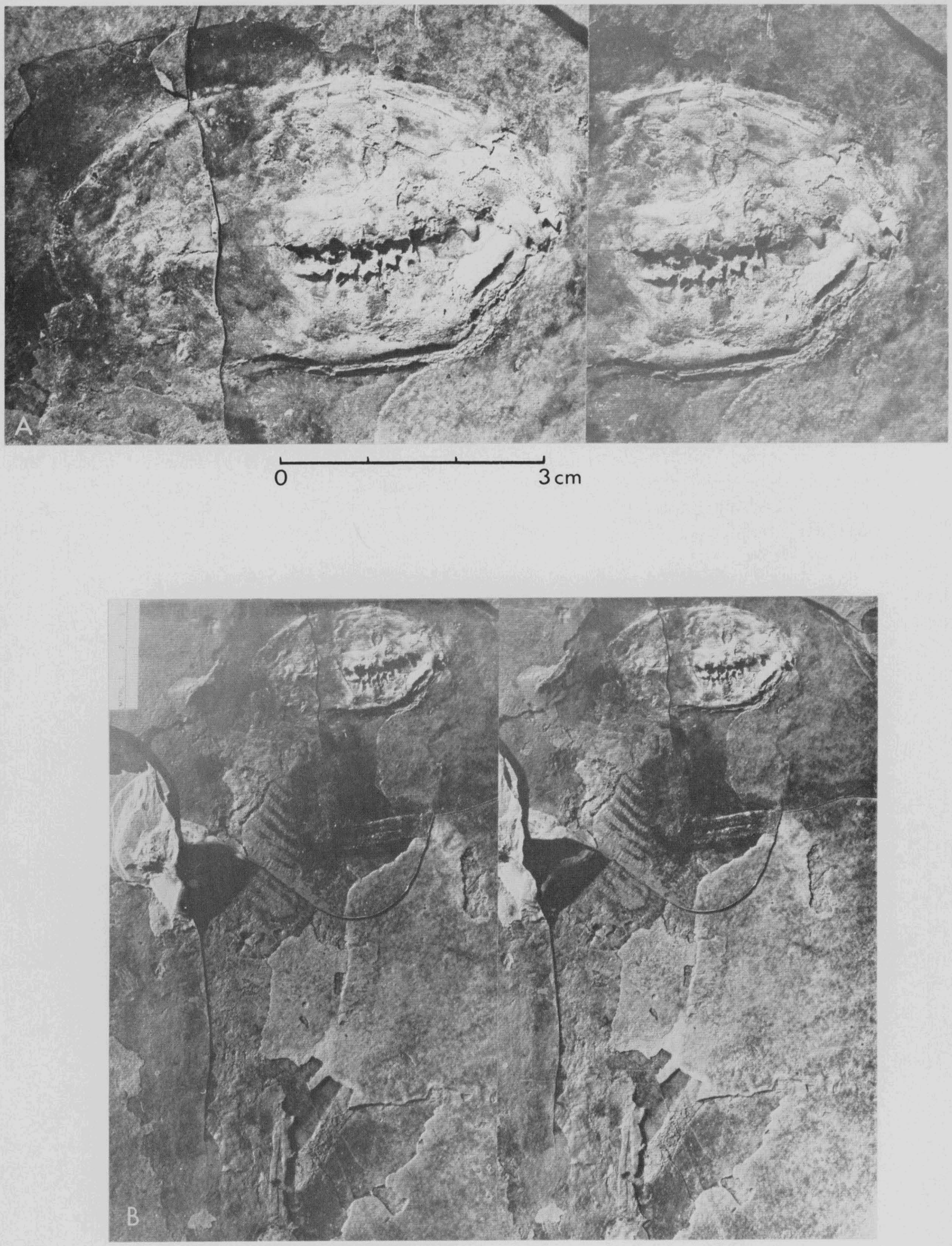

A
0
3 cm
B

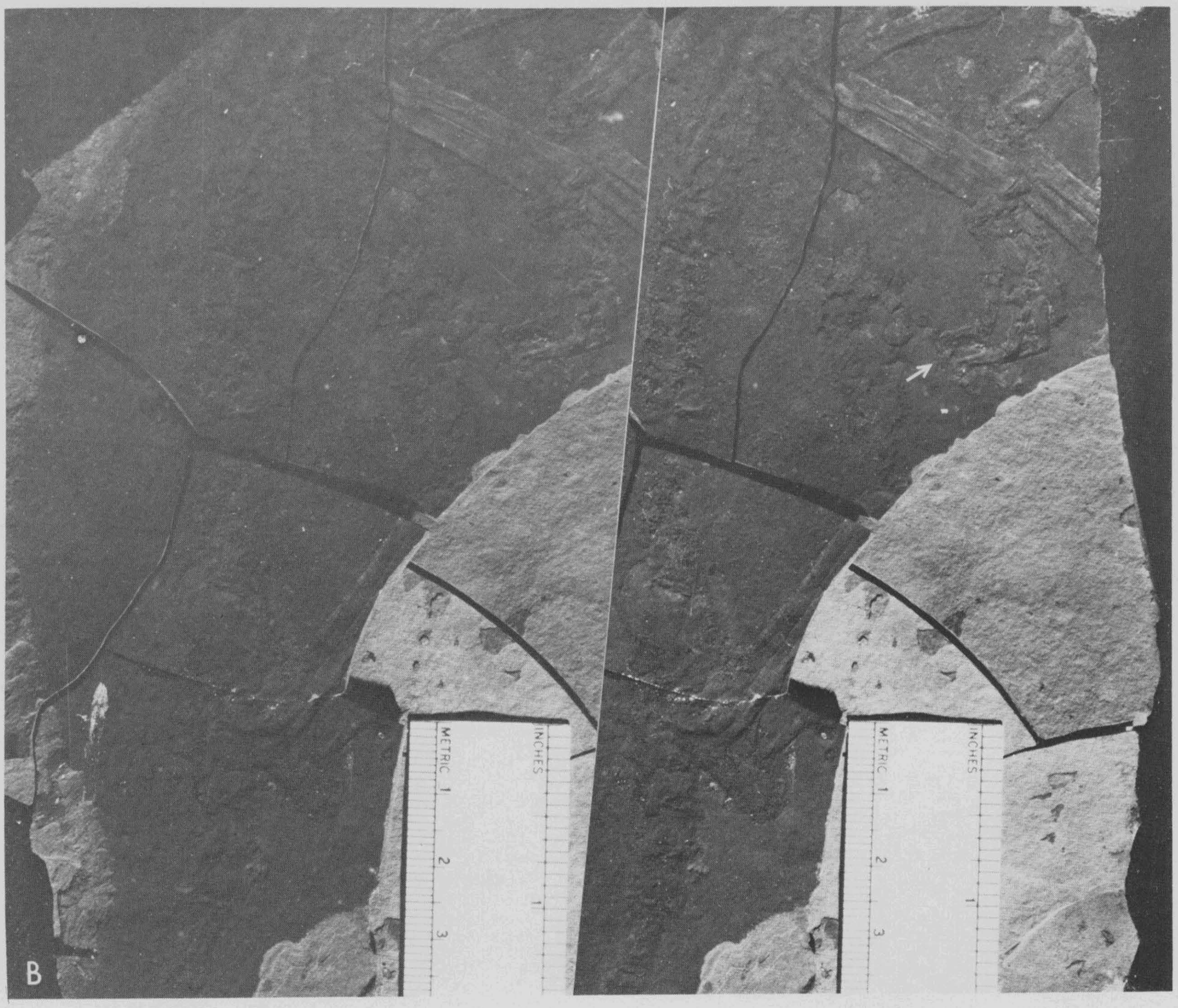
PLATE 12

Skeleton of **Plesiadapis insignis**

A. Reversed stereophotographs of posterior limb of *Plesiadapis insignis* (referred specimen, main slab, MNHN collection), showing femur, tibia-fibula, and pes. Note preserved impression of bushy tail, clawed pedal unguals. Figure reproduced natural size.

B. Reversed stereophotographs of skeleton of *Plesiadapis insignis* (referred specimen, counterpart slab, MNHN collection), showing humerus, ulna-radius, and manus. Note claws on manus. Figure reproduced natural size.


A


B

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