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NEW NORTH AMERICAN PLESIADAPIDAE (MAMMALIA, PRIMATES) AND A BIOSTRATIGRAPHIC ZONATION OF THE MIDDLE AND UPPER PALEOCENE

BY
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NEW NORTH AMERICAN PLESIADAPIDAE (MAMMALIA, PRIMATES) AND A BIOSTRATIGRAPHIC ZONATION OF THE MIDDLE AND UPPER PALEOCENE

BY PHILIP D. GINGERICH

ABSTRACT — Eight new species of Plesiadapidae are described, bringing to eighteen the total number of valid North American species. A new genus, *Nannodectes*, is proposed for a lineage of four relatively small species with very narrow cheek teeth. The remaining species belong to the genera *Pronothodectes* (2 sp.), *Plesiadapis* (8 sp.), and *Chiromyoides* (4 sp.). Plesitarsiiformes and Simiolemuriformes are proposed as suborders of Primates, replacing Plesitarsioidea and Anthrolemuroidea respectively.

The stratigraphic and phylogenetic relationships of the species of North American Plesiadapidae are outlined, and the Middle and Late Paleocene are divided into seven superposed biostratigraphic zones based on the evolution of *Pronothodectes* and *Plesiadapis*. The result is a detailed stratigraphic framework for the study of evolutionary change in Paleocene mammals. The Clarkforkian mammal age is discussed briefly— on the basis of its correlation with European faunas, the Clarkforkian appears to be earliest Eocene in age, rather than late Paleocene.

INTRODUCTION

Species of *Plesiadapis* and its allies are among the most common mammalian fossils found in the Middle and Upper Paleocene continental deposits of North America and Europe. Estimates of the relative ages of Paleocene mammalian faunas have in the past often been based implicitly on the stage of evolution of the *Plesiadapis* they contained, though the evolution of this genus was never studied in detail. Large samples of *Pronothodectes* and *Plesiadapis* are now known from numerous localities widely distributed geographically and stratigraphically in North America. Thus it appeared that a careful study of the Plesiadapidae might yield results of general importance to the stratigraphy of the Middle and Upper Paleocene.

A study of virtually all of the European and North American Plesiadapidae has been completed (Gingerich, 1974a), and a systematic revision of the family will eventually be published. In the meantime it seems advisable to make both the new taxa and the major stratigraphic conclusions available in this preliminary publication. One new genus and eight new species of Plesiadapidae are described here, followed by an outline of the phylogenetic relationships of the North American species and a discussion of a new biostratigraphic zonation of the Middle and Late Paleocene. Complete descriptions of the taxa, detailed stratigraphic documentation, a discussion of plesiadapid evolution, and a discussion of the systematic position of the Plesiadapidae are included in the longer monograph.

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York (AMNH). Important comparative material was made available in many additional museums. Valuable guidance and assistance during the course of this study were provided by E. L. Simons, J. H. Ostrom, D. R. Pilbeam, and J. A. W. Kirsch of Yale University. Financial assistance was provided by a Dana Fellowship of Yale University and a Shadle Fellowship of the American Society of Mammalogists.

SYSTEMATIC PALEONTOLOGY

Since living species consist of variable populations of individuals, one's concept of a given fossil species is properly based, not on a type specimen, but on the entire sample available from the type locality. Where more than a single specimen is known, the descriptions and measurements of species given below summarize available information for the entire sample of that species at its type locality. Measurements of the length and width of M_1 are summarized in Table 1 for the North American species of *Pronothodectes*, Nannodectes, and Plesiadapis, since that tooth is generally the least variable in the tooth row and thus the best tooth to characterize the size of closely related species (Gingerich, 1974c). Cheek teeth of North American Chiromyoides are very rare, and the incisors are the most diagnostic element of its dentition. Table 2 gives relevant measurements of the incisors of the North American species of Chiromyoides.

Order PRIMATES Suborder PLESITARSIIFORMES

The name Plesitarsioidea was originally proposed for this suborder (Gingerich, 1974a) but, to avoid confusion with the superfamilies of Primates, it seems advisable to amend the termination. Thus Plesitarsiiformes, including the primate infraorders Plesiadapiformes and Tarsiiformes, is proposed to replace Plesitarsioidea. Similarly, the suborder Simiolemuriformes, including Hoffstetter's Simiiformes (= Anthropoidea; Hoffstetter, 1974) and Lemuriformes as infraorders, is here proposed to replace Anthrolemuroidea (Gingerich, 1974a).

Infraorder PLESIADAPIFORMES

Plesiadapiformes Simons (1972) includes the same four families as Paromomyiformes Szalay (1973) and the former name, having priority, is used here.

Family PLESIADAPIDAE

The commonly used family name Plesiadapidae Trouessart, 1897, is predated by the *nomen oblitum* Platychoeropidae Lydekker, 1887, and a proposal that Platychoeropidae be suppressed in favor of Plesiadapidae has been submitted to the International Commission on Zoological Nomenclature (Gingerich, 1974b).

Pronothodectes Gidley, 1923

Genotype. - Pronothodectes matthewi Gidley, 1923.

Included species. - Genotype and Pronothodectes jepi n. sp.

Diagnosis. — The species of *Pronothodectes* differ from those of the other plesiadapid genera in retaining the primitive plesiadapid dental formula of $\frac{2}{2}$, $\frac{1}{1}$, $\frac{3}{3}$, $\frac{3}{3}$.

TABLE 1 — Measurements (in millimeters) and relevant statistics for the length and width of M_1 in the type or largest sample of each valid North American species of *Pronothodectes*, *Nannodectes*, and *Plesiadapis*.

Species	Sample		N	OR	$\bar{x} \pm SE$	S	v
Pro. matthewi	Gidley Quarry	L	9	2.0 - 2.3	2.13 ± .03	.09	4.1
	(type)	W	9	1.9 - 2.2	$2.03 \pm .03$.09	4.3
Pro. jepi	Rock Bench Q.	L	11	2.2 - 2.4	$2.35 \pm .02$.07	2.9
	(type)	W	11	2.0 - 2.4	$2.22 \pm .03$.11	4.9
N. intermedius	Keefer Hill L.	L	49	2.2 - 2.6	$2.42 \pm .01$.08	3.3
	(type)	W	49	2.0 - 2.5	$2.24 \pm .02$.14	5.6
N. gazini	Saddle Locality	L	22	2.1 - 2.5	$2.35 \pm .02$.11	4.7
	(type)	W	22	1.9 - 2.3	$2.09 \pm .02$.11	5.3
N. simpsoni	Ledge Locality	${f L}$	11	2.5 - 2.8	$2.69 \pm .03$.09	3.3
	(type)	W	11	2.3 - 2.8	$2.58 \pm .05$.17	6.6
N. gidleyi	Mason Pocket Q.	${f L}$	12	2.7 - 3.1	$2.88 \pm .03$.11	3.8
	(type)	W	12	2.5 - 3.1	$2.70 \pm .05$.18	6.7
Ples. praecursor	Douglass Q.	L	3	2.6 - 2.7	$2.63 \pm .03$.06	2.3
	(type)	W	3	2.5 - 2.6	$2.57 \pm .03$.06	2.3
Ples. anceps	Saddle Locality	L	11	2.6 - 3.0	$2.87 \pm .04$.13	4.5
	(largest)	W	11	2.7 - 3.0	$2.84 \pm .03$.09	3.2
Ples. rex	Cedar Point Q.	L	130	2.7 - 3.4	$3.07 \pm .01$.14	4.6
	(largest)	W	126	2.6 - 3.4	$2.95 \pm .01$.15	5.1
Ples. churchilli	Long Draw Q.	${f L}$	4	3.4 - 3.6	$3.47 \pm .05$.10	2.9
	(type)	W	4	3.2 - 3.5	$3.27 \pm .08$.15	4.6
Ples. fodinatus	Princeton Q.	${f L}$	34	2.8 - 3.5	$3.22 \pm .02$.12	3.7
	(type)	W	34	2.7 - 3.2	$2.93 \pm .03$.15	5.1
Ples. dubius	Paint Creek L.	L	3	2.7 - 3.1	$2.90 \pm .12$.20	6.9
	(largest)	W	3	2.5 - 2.7	$2.60 \pm .06$.10	3.8
Ples. simonsi	M. Sand Draw	L	1		4.0* -	-	-
	(type)	W	1		3.9 -	-	-
Ples. cookei	L. Sand Coulee	L	7	5.1 - 5.7	$5.41 \pm .08$.21	3.9
	(type)	W	7	4.8 - 5.4	$5.10 \pm .07$.19	3.7

Abbreviations: N, number; OR, observed range; \bar{x} , mean; SE, standard error; S, standard deviation; V, coefficient of variation; L, anteroposterior length; W, maximum transverse width. Measurements followed by an asterisk were estimated from specimens that are nearly complete.

Pronothodectes jepi n. sp. Pl. 1, figs. 1, 3

Type. — PU 14782, a left mandible with alveolifor I_{1-2} C P_2 , and the crowns of P_{3-4} M_{1-3} preserved intact.

Type locality. — The type and 19 additional specimens were collected at the Rock Bench Quarry, Polecat Bench Formation, in the Big Horn Basin, Wyoming.

Diagnosis. — Pronothodectes jepi is a significantly larger species than Pro. matthewi (see Table 1 for comparative measurements).

Etymology. — Named for the late Prof. G. L. Jepsen ("Jep", as he preferred to be called by students and friends) of Princeton University, in recognition of his important contributions to the study of Paleocene mammals. (Note: Pronothodectes jepi is not to be confused with Plesiadapis jepseni Gazin, a junior synonym of Ples. anceps Simpson.)

Nannodectes n. gen.

Genotype. - Nannodectes gazini n. sp.

Included species. — Genotype, N. intermedius (Gazin), N. simpsoni (Gazin), and N. gidleyi (Matthew).

Diagnosis. — Species of Nannodectes differ from those of Pronothodectes in consistently lacking I_2 . They differ from contemporaneous species of Plesiadapis in being smaller, retaining P_2 and in most species the lower canine, having much narrower central incisors and cheek teeth (especially noticeable in the lower premolars), having a more triangular P^3 which usually lacks a paraconule, and lacking a centroconule on I^1 .

Etymology. — Nannos (Gr.) dwarf, and dektes (Gr., masc.) biter, in reference to the relatively small size of species of this lineage compared to contemporaneous species of Plesiadapis.

Nannodectes gazini n. sp. Pl. 1, figs. 2, 4

Pronothodectes cf. matthewi, Gazin, 1956, p. 20, Pl. 2, fig. 1, 2. Pronothodectes cf. simpsoni, Gazin, 1956, p. 21, Pl. 3, fig. 2. Cf. Pronothodectes matthewi, Gazin, 1969, p. 7, Pl. 2, fig. 9.

EXPLANATION OF PLATE 1

All figures x 3

- FIGS. 1,3-Pronothodectes jepi n. sp., type specimen PU 14782, left mandible with alveoli for $I_{1-2} \subset P_2$ and the crowns of P_{3-4} M_{1-3} intact; 1, stereophotograph of occlusal view; 3, lateral view.
 - 2,4- Nannodectes gazini n. gen., n. sp., type specimen AMNH 92008, right mandible with alveoli for I_1 C P_2 and the crowns of P_{3-4} M_1 intact; 2, stereophotograph of occlusal view; 4, lateral view.
 - 5,9—Chiromyoides minor n. sp., type specimen USNM 209876, right upper central incisor (11); 5, stereophotograph of occlusal view; 9, lateral view.
 - 6,10- Chiromyoides caesor Gingerich, type specimen PU 21575, left upper central incisor (1^{1}); 6, stereophotograph of occlusal view; 10, lateral view.
 - $7,11 Chiromyoides\ potior\ n.\ sp.\ ,$ type specimen USNM 10639, left upper central incisor (1); 7, stereophotograph of occlusal view; 11, lateral view.
 - 8,12 Chiromyoides major n. sp., type specimen PU 21150, left upper central incisor (I¹); 8, stereophotograph of occlusal view; 12, lateral view.

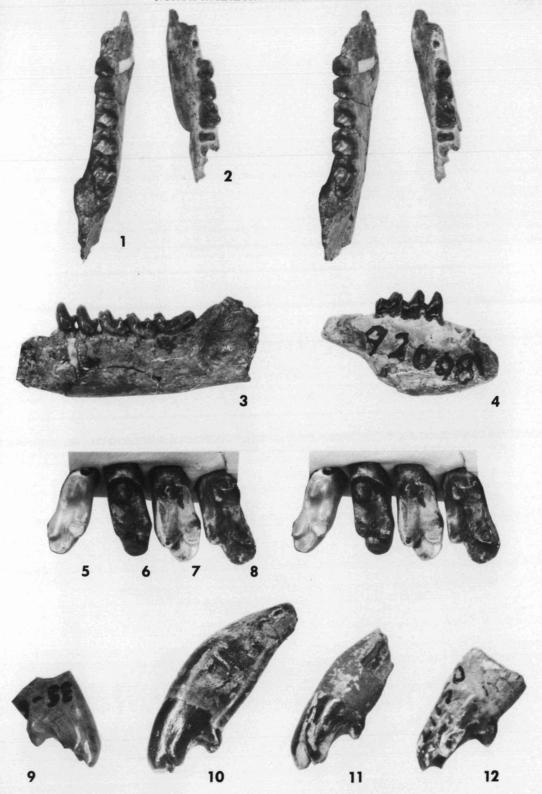


PLATE 1



PLATE 2

Type. - AMNH 92008, a right mandible with alveoli for $I_1 \subset P_2$, with the crowns of $P_{3-4} M_1$ intact.

Type locality. — The type and numerous additional upper and lower jaws were collected at the Saddle Locality, Fort Union Formation, in the Bison Basin, Wyoming.

Diagnosis. — The smallest species of Nannodectes (see Table 1 for comparative measurements).

Etymology. — Named for Dr. C. L. Gazin of the Smithsonian Institution, in recognition of his important contributions to the study of North American Plesiadapidae.

Plesiadapis Gervais, 1877

Genotype. - Plesiadapis tricuspidens Gervais, 1877.

Synonyms. — Tricuspidens Lemoine, 1887, p. 192 (subgenus, type: Plesiadapis (T.) gervaisi Lemoine). Nothodectes Matthew, 1915, p. 482 (type: Nothodectes dubius Matthew). Menatotherium Piton, 1940, p. 290 (type: Menatotherium insigne Piton). Ancepsoides Russell, 1964, p. 115 (subgenus, type: Plesiadapis (A.) anceps Simpson).

North American species. — Ples. praecursor n. sp., Ples. anceps Simpson, Ples. rex (Gidley), Ples. churchilli n. sp., Ples. fodinatus Jepsen, Ples. dubius (Matthew), Ples. simonsi n. sp., Ples. cookei Jepsen.

Diagnosis.—Species of Plesiadapis differ from those of Pronothodectes and most species of Nannodectes in lacking the lower canine. They differ from advanced species of Nannodectes in generally having centroconules on the upper central incisors, broader cheek teeth, and more squared, fissured heels on M_3 . They differ from species of Chiromyoides in having less robust incisors, and from Platychoerops in retaining a tricuspid upper incisor.

Plesiadapis praecursor n. sp.

Pl. 2, figs. 1, 5

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

Type. — PU 14512, a left mandible with alveoli for I_1 P_{2-3} M_3 , and the crowns of P_4 M_{1-2} preserved intact.

Type locality. — The type and three additional specimens were found in the Douglass Quarry, Melville member of the Fort Union Formation, in the Crazy Mountain field, Montana.

Diagnosis. — The smallest species of Plesiadapis which retains P_2 .

Etymology. - praecursor, L., refers to the early appearance of this species.

EXPLANATION OF PLATE 2

All figures x 3

- FIGS. 1,5—Plesiadapis praecursor n. sp., type specimen PU 14512, left mandible with alveoli for I_1 P_{2-3} M_3 and the crowns of P_4 M_{1-2} intact; 1, stereophotograph of occlusal view; 5, lateral view.
 - 2,6—Plesiadapis churchilli n. sp., type specimen PU 21234, left mandible with $\rm I_1$ $\rm P_{3-4}$ $\rm M_{1-3}$; 2, stereophotograph of occlusal view; 6, lateral view.
 - 3,4—Plesiadapis simonsi n. sp., type specimen PU 17814, right partial mandible with M_{1-2} ; 3, stereophotograph of occlusal view; 4, lateral view.

Plesiadapis churchilli n. sp. Pl. 2, figs. 2, 6

Type. - PU 21234, a left mandible with I_1 P_{3-4} M_{1-3} .

Type locality. — The type and four additional specimens were found in the Long Draw Quarry, Polecat Bench Formation, in the northern Big Horn Basin, Montana.

Diagnosis. - Differs from Plesiadapis rex and earlier species inbeing larger and in having P₂ variably present, a significant diastema between I₁ and P₃, 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.

Etymology. - Named for the Churchill family of Powell, Wyoming, in recognition of their generous assistance to three generations of paleontologists working in the Big Horn Basin.

> Plesiadapis simonsi n. sp. Pl. 2, figs. 3, 4

Type. — PU 17814, a right mandible with M_{1-2} .

Type locality. - The type specimen was found in the middle level of Sand Draw (southern part of Section 24, T 55 N, R 97 W, Big Horn County), Polecat Bench Formation, in the Big Horn Basin, Wyoming.

Diagnosis. - Plesiadapis simonsi differs from all other North American species of Plesiadapis (except Ples. cookei) in being significantly larger. It resembles Ples. cookei in known details, but is significantly smaller than that species.

Etymology. - Named for Prof. E. L. Simons, Yale University, in recognition of his contributions to the study of Paleocene mammals, including the first description of fossils from the general provenance of the type specimen of this species.

Chiromyoides Stehlin, 1916

Genotype. - Chiromyoides campanicus Stehlin, 1916.

North American species. - Chiromyoides minorn. sp., C. caesor Gingerich, C. potior n. sp., C. major n. sp.

Diagnosis. - Species of Chiromyoides differ from those of the other plesiadapid genera in having extraordinarily robust central incisors and a very deep mandible, with relatively small but broad cheek teeth.

Specimens of Chiromyoides have only recently been discovered in the North American fauna (Gingerich, 1973). Four distinct forms are now known from beds spanning most of the Late Paleocene.

Chiromyoides minor n. sp.

Pl. 1, figs. 5, 9

Type. - USNM 208976, a right upper central incisor.

Type locality. - The type and a lower incisor of this species come from Section 17, T 26 N, R 113 W, Lincoln County, where they were found in the Chappo member of the Wasatch Formation (hence designation of the locality as "Chappo-17") in the La Barge area of Wyoming.

Diagnosis. - C. minor differs from the other species of Chiromyoides in being significantly smaller (see Table 2 for comparative measurements). It has a relatively more narrow crown than either C. potior or C. major.

Etymology. - minor, L., in reference to the relatively small size of this species.

TABLE 2 — Measurements of the type specimens of the North American species of *Chiromyoides*. Type specimens are all upper central incisors, and the measurements (in millimeters) are anteroposterior and transverse diameters (measured at the base of the crown), and crown width (measured half way between posterocone and laterocone).

	Anteroposterior Diameter	Transverse Diameter	Crown Width
C. minor	5.6	2.7	3.3
C. caesor	6.0	3.2	3.4
C. potior	5.3	3.2	4.0
C. major	6.0	3.9*	4.3*

^{*}Based on two additional specimens from the type locality.

Chiromyoides potior n. sp. Pl. 1, figs. 7, 11

Nothodectes gidleyi (in part), Gidley, 1923, Pl. 3, fig. 16. Plesiadapis gidleyi (in part), Simpson, 1937, Pl. 9, fig. 16.

Type. - USNM 10639, a left upper central incisor.

Type locality. — Tiffany? beds, $5 \frac{1}{2}$ miles east of Bayfield, Colorado.

Diagnosis. — Chiromyoides potior differs from C. minor, C. caesor, and C. campanicus in having an upper central incisor with a less elongated cross section anteroposteriorly, a relatively broader crown, and a smaller posterocone. C. potior is similar to C. major, but it is significantly smaller and differs in having the mediocone on I¹ only approximately equal in size to the laterocone.

Etymology. - potior, L., in reference to the stouter, stronger upper incisors of this species, compared to those of the earlier species.

Chiromyoides major n. sp. Pl. 1, figs. 8, 12

Type. - PU 21150, most of the crown of a left upper central incisor.

 $Type\ locality.$ — The type and three additional incisors were found at the Paint Creek locality, Willwood Formation, in the Big Horn Basin, Wyoming.

 $Diagnosis. - Chiromyoides \ major$ differs from $C.\ potior$ and the other species of Chiromyoides in being significantly larger, and in having a relatively larger mediocone on I^1 .

Etymology. - major, L., in reference to the larger size of the incisors in this species compared to the earlier species.

STRATIGRAPHIC AND PHYLOGENETIC RELATIONSHIPS

The next problem of interest is determining the phylogenetic relationships of the eighteen valid species of Plesiadapidae now known from North America. Though several paleontologists have recently advocated ignoring stratigraphy when solving phylogenetic problems (e.g. Schaeffer, Hecht, and Eldredge, 1972; Cracraft, 1974), in this

study the stratigraphic distribution of the species proved critical to understanding their relationships, and I doubt that a unique, reliable solution could have been achieved without detailed stratigraphic documentation.

The methodology involved is relatively simple, and it is based on the application of two classic principles of stratigraphy: Steno's principle of superposition, whereby the strata at the bottom of a normal sequence are recognized as older than those above; and William Smith's law of faunal succession, which recognizes the value of guide fossils in correlating rocks of equivalent age. Stratigraphic columns including two or more plesiadapid species were established in as many local areas as possible. Four new columns (including a measured column with six species in sequence in the type section of the Polecat Bench Formation) were combined with five columns already available in the literature (e.g. Simpson, 1937, p. 43). Stratigraphic levels containing the same species were correlated in all columns. Thus the relative ages of almost all species (all except *Pronothodectes matthewi* vis-à-vis *Pro. jepi*) were firmly established on stratigraphic evidence.

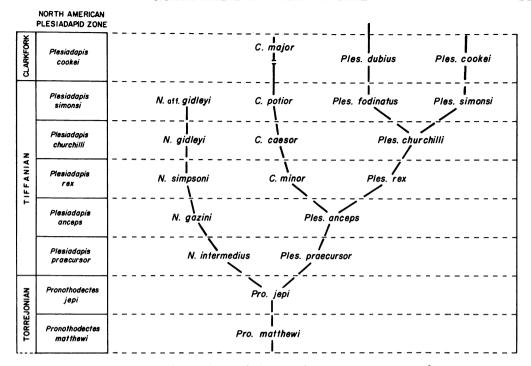
Plesiadapid species are known from eight stratigraphic levels in the Torrejonian, Tiffanian, and Clarkforkian (Middle Paleocene to Early Eocene, see below) of North America. The species which are found in each successive level are listed in rows in Text-fig. 1. It is clear that the species of Nannodectes form a single evolutionary lineage, as do the successive species of Chiromyoides. The main lineage of Plesiadapis divides in the upper levels into two, with a lineage of small species (Ples. fodinatus — Ples. dubius) coexisting with a lineage of larger species. On the basis of their close resemblance, it is almost certain that Nannodectes intermedius is derived from Pronothodectes jepi, and Chiromyoides minor appears similarly to be derived from Plesiadapis anceps. Plesiadapis fodinatus and Ples. simonsi both appear to be derived from Ples. churchilli.

BIOSTRATIGRAPHIC ZONATION

Each of the stratigraphic levels listed in Text-fig. 1 is a distinctive biostratigraphic zone, with a characteristic assemblage of plesiadapid species. For convenience, the largest species in each zone has been chosen to bear the name of the zone and its stratigraphic range defines the limits of the zone. The sequence of North American plesiadapid zones is listed in a column at the left of text-fig. 1. In the absence of evidence to the contrary, the zones have been represented as approximately equal in time duration (with the exception of the *Ples. cookei* zone, which may span a longer period than the others).

Whereas previously the age of a Middle or Late Paleocene fossil deposit was tentatively estimated to be Torrejonian, early Tiffanian, late Tiffanian, or Clarkforkian (note, for example, the clustering of localities in these categories in Van Valen and Sloan, 1966, fig. 1), it is now possible to be more precise -- if the deposit contains plesiadapid fossils it can confidently be placed in one of eight biostratigraphic zones, depending on the identity of the species involved.

The fact that *Plesiadapis cookei* is known only from a restricted time period between the Tiffanian and the Graybullian has an important bearing on the validity of the Clarkforkian age. H. F. Wood, et al. (1941) first proposed the Clarkforkian as a latest Paleocene provincial age, based on the Clark Fork beds of northwestern Wyoming. *Plesiadapis cookei* was listed in this proposal as the only index fossil of the Clarkforkian. More recently, R. Wood (1967) completed a general review of the fauna from the Clark Fork beds and concluded that any recognition of a Clark Fork stratigraphic, faunal, or time unit was unwarranted by the available evidence. He disqualified *Plesiadapis cookei* and other important species as members of the Clark Fork fauna since the specimens



TEXT-FIG. 1—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, though additional study of other lineages will be necessary to confirm this.

representing the species could not be unequivocally assigned to the Paleocene or to the Eocene. However, which epoch the fossils are assigned to is not really relevant to the question of faunal distinctness. The present study has shown that specimens of *Plesiadapis cookei* are limited to a definite biostratigraphic zone intermediate between the Tiffanian and Graybullian, lending considerable support to recognition of a distinct Clark Fork fauna and a Clarkforkian mammal age.

Plesiadapis cookei and the Clarkforkian have long been considered to be Late Paleocene in age. Two facts argue against that age assessment: a) the earliest Perissodactyla (Hyracotherium) and Rodentia, forms marking the beginning of the Eocene in Europe, are present in the Ples. cookei zone; b) Plesiadapis cookei itself resembles closely a new species of Plesiadapis from the earliest Sparnacian fauna of Meudon in the Paris Basin (whereas the North American Ples. simonsi closely resembles species from the European Cernay fauna). This suggests that the North American Clarkforkian should properly be considered Early Eocene in age (with the base of the Eocene defined as the base of the Paris Basin Sparnacian; see Gingerich, 1975, for discussion and references). Much of the confusion regarding both the Clark Fork fauna and the Sand Coulee fauna may be due to their synonymy -- both are now known to contain Plesiadapis cookei. The upper beds of the Ples. cookei zone yield Pelycodus ralstoni, a primate species characteristic of the Sand Coulee fauna, whereas a new larger species intermediate morphologically between P. ralstoni and P. trigonodus is found in the lower Gray Bull beds (Gingerich and Simons, in prep.).

NORTH AMERICAN PLESIADAPID ZONE

ADDITIONAL SPECIES

MAJOR LOCALITIES

CLARKFORKIAN	Plesiadapis cookei	Plesiadapis dubius Chiromyoides major ² Chiromyoides potior	² Bear Creek, Chappo-I2, ² Little Sand Coulee, [†] Paint Creek, Togwotee lower variegated seq., [†] Upper Sand Draw.	
TIFFANIAN	Plesiadapis simonsi	Plesiadapis fodinatus Nannodectes aff. gidleyi Chiromyoides potior	Bayfield, Chappo-I, 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, Mason Pocket, Malcolm's Loc.	
	Plesiadapis rex	Nannodectes simpsoni Chiromyoides minor	Battle Mountain, Cedar Point Q., Chappo-17, Ledge Loc., Love Q., Melville-13, Saddle Anne Twin Creek, West End Loc., Erickson's Landing.	
	Plesiadapis anceps	Nannodectes gazini	Highway Blowout, Saddle Loc., Scarritt Q.	
	Plesiadapis praecursor	Nannodectes intermedius	Douglass Q., Keefer Hill.	
TORFEJCHÄN	Pronothodectes jepi		Rock Bench Q.	
	Pronothodectes matthewi		Gidley Q.	

Upper part of zone only.

TEXT-FIG. 2—Sequence of plesiadapid zones and a correlation of the major plesiadapid-bearing deposits in North America. The *Plesiadapis cookei* zone appears to be divisible, with *Chiromyoides potior* occurring in the lower part, *C. major* in the upper.

²Lower part of zone only.

Lists of the major plesiadapid-bearing localities in North America are presented in text-fig. 2, with correlative localities listed alphabetically within each division. The relative stratigraphic position of each locality was determined by identifying the species of Plesiadapidae from that locality, and then referring the locality to the proper plesiadapid zone.

Finally, it should be noted that while the zonation illustrated in text-fig. 2 was derived from a study of Plesiadapidae, the stratigraphic position of the localities listed will be the same for any other taxonomic group of vertebrates, and this sytem of zones thus provides a stratigraphic framework for studying the evolution of other groups as well. As additional evolutionary lineages of Paleocene mammals are studied in detail, it should be possible to increase further the resolution of the zonation through the precise definition of concurrent range zones.

LITERATURE CITED

- BERGGREN, W. A., 1972, A Cenozoic time-scale some implications for regional geology and paleobiology: Lethaia, v. 5, p. 195-215.
- CRACRAFT, J., 1974, Phylogenetic models and classification: Syst. Zool., v. 23, p. 71-90.
- GAZIN, C. L., 1956, Paleocene mammalian faunas of the Bison Basin in south-central Wyoming: Smithson. Misc. Coll., v. 131, no. 6, p. 1-57.
- ——, 1969, A new occurrence of Paleocene mammals in the Evanston Formation, southwestern Wyoming: Smithson. Contrib. Paleobiology, v. 2, p. 1-17.
- ——, 1971, Paleocene primates from the Shotgun member of the Fort Union Formation in the Wind River Basin, Wyoming: Proc. Biol. Soc. Washington, v. 84, p. 13-38.
- GERVAIS, P., 1877, Enumération de quelques ossements d'animaux vertébrés recueillis aux environs de Reims par M. Lemoine: Jour. Zool. (Paris), v. 6, p. 74-79.
- GIDLEY, J. W., 1923, Paleocene primates of the Fort Union, with discussion of relationships of Eocene primates: Proc. U.S. Nat. Mus., v. 63, p. 1-38.
- GINGERICH, P. D., 1973, First record of the Paleocene primate *Chiromyoides* from North America: Nature, v. 244, p. 517-518.
- ——, 1974a, Cranial anatomy and evolution of Early Tertiary Plesiadapidae (Mammalia, Primates): Ph.D. Dissertation, Yale University, p. 1-370. Abstract in: Dissert. Abstr. Internat., v. 35, p. 2340-2341.
- , 1974b, Platychoeropidae Lydekker, 1887 (Mammalia): proposed suppression of family name under the plenary powers; together with validation of *Platychoerops* Charlesworth, 1855 (Mammalia) not Klunzinger, 1879 (Pisces): Bull. Zool. Nomencl., v. 30, p. 207-209.
- ----, 1974c, Size variability of the teeth in living mammals and the diagnosis of closely related sympatric fossil species: Jour. Paleontology, v. 48, p. 895-903.
- _____, 1975, Discussion what is type Paleocene? Amer. Jour. Sci., v. 275, in press.
- HOFFSTETTER, R., 1974, Apidium et l'origine des Simiiformes (=Anthropoidea): C. R. Acad. Sci. Paris, v. 278, p. 1715-1717.
- LEMOINE, V., 1887, Sur le genre *Plesiadapis*, mammifère fossile de l'éocène infèrieur des environs de Reims: C. R. Acad. Sci. for 1887, p. 190-193.
- MATTHEW, W. D., 1915, A revision of the lower Eocene Wasatch and Wind River faunas. Part IV Entelonychia, Primates, Insectivora (part): Bull. Amer. Mus. Nat. History, v. 34, p. 429-483.
- PITON, L.-E., 1940, Paléontologie du gisement éocène de Menat (Puy-de-Dome): Clermont-Ferrand, Vallier, 303 p.
- RUSSELL, D. E., 1964, Les mammifères paléocènes d'Europe: Mém. Mus. Nat. d'Histoire Natur., ser. C, v. 13, p. 1-324.
- SCHAEFFER, B., HECHT, M. K., and ELDREDGE, N., 1972, Phylogeny and paleontology: Evol. Biology, v. 6, p. 31-46.
- SIMONS, E. L., 1972, Primate evolution: Macmillan, New York, 322 p.

- SIMPSON, G. G., 1937, The Fort Union of the Crazy Mountain Field, Montana and its mammalian faunas: Bull. U.S. Nat. Mus., v. 169, p. 1-287.
- STEHLIN, H. G., 1916, Die Säugetiere des schweizerischen Eocaens. *Caenopithecus*, etc.: Abh. Schweiz. Paläont. Gesell., v. 41, p. 1299-1552.
- SZALAY, F. S., 1973, New Paleocene primates and a diagnosis of the new suborder Paromomyiformes: Folia Primat., v. 19, p. 73-87.
- VAN VALEN, L., and SLOAN, R. E., 1966, The extinction of the multituberculates: Syst. Zool., v. 15, p. 261-278.
- WOOD, H. E., et al., 1941, Nomenclature and correlation of the North American continental Tertiary: Bull. Geol. Soc. Amer., v. 52, p. 1-48.
- WOOD, R. C., 1967, A review of the Clark Fork vertebrate fauna: Breviora, no. 257, p. 1-30.