

CONTRIBUTIONS FROM THE MUSEUM OF PALEONTOLOGY

THE UNIVERSITY OF MICHIGAN

VOL. 26, No. 8, p. 141-155

December 31, 1983

---

***BARYLAMBDA CHURCHILLI*, A NEW SPECIES OF  
PANTOLAMBIDAE (MAMMALIA, PANTODONTA) FROM THE  
LATE PALEOCENE OF WESTERN NORTH AMERICA**

BY

PHILIP D. GINGERICH AND CONDUFF G. CHILDRESS, JR.



MUSEUM OF PALEONTOLOGY  
THE UNIVERSITY OF MICHIGAN  
ANN ARBOR

## CONTRIBUTIONS FROM THE MUSEUM OF PALEONTOLOGY

Philip D. Gingerich, Director

Gerald R. Smith, Editor

This series of contributions from the Museum of Paleontology is a medium for the publication of papers based chiefly upon the collection in the Museum. When the number of pages issued is sufficient to make a volume, a title page and a table of contents will be sent to libraries on the mailing list, and to individuals upon request. A list of the separate papers may also be obtained. Correspondence should be directed to the Museum of Paleontology, The University of Michigan, Ann Arbor, Michigan, 48109.

VOLS. II-XXVI. Parts of volumes may be obtained if available. Price lists available upon inquiry.

**BARYLAMBDA CHURCHILLI, A NEW SPECIES OF PANTOLAMBDIDAE  
(MAMMALIA, PANTODONTA) FROM THE LATE PALEOCENE OF WESTERN  
NORTH AMERICA**

By

Philip D. Gingerich and Conduff G. Childress, Jr.

*Abstract.*—Morphological variation in late Paleocene and early Eocene pantolambdid pantodonts, studied in geographic and stratigraphic context, indicates that *Leptolambda schmidti* is a junior synonym of *Barylamba faberi*. *B. faberi* is known from faunas of Clarkforkian age in Colorado and southern Wyoming. Late Tiffanian specimens from northern Wyoming previously referred to *L. schmidti* are here placed in a new species *Barylamba churchilli*. The genera *Barylamba*, *Haplolambda*, and *Titanoides* represent distinct lineages of North American Tiffanian and Clarkforkian Pantolambdidae. *Caenolambda*, if sufficiently distinct to warrant separate generic status, may be a common ancestor of *Barylamba* and *Haplolambda*. All of these genera can plausibly be regarded as descendants of middle Paleocene *Pantolambda*. During the Clarkforkian, *Barylamba* and other large pantolambdids appear to have been replaced in a north to south progression by the more advanced immigrant *Coryphodon*.

INTRODUCTION

Pantodonta played an important role as large-bodied herbivores in middle Paleocene through early Eocene mammalian faunas of North America. The most recent revision of North American pantodonts is by Simons (1960), who recognized four families and eight genera: Pantolambdidae, including *Pantolambda* and *Caenolambda*; Barylambdidae, including *Barylamba*, *Haplolambda*, *Leptolambda*, and *Ignatiolambda*; Titanoideidae, including *Titanoides*; and Coryphodontidae, including *Coryphodon*. One additional family, Cyriacotheriidae, has been erected subsequent to Simons' review for the highly specialized genus *Cyriacotherium* (Rose and Krause, 1982).

*Coryphodon* and *Cyriacotherium* are very distinct from each other and from remaining North American pantodonts, but the genera placed in Pantolambdidae, Titanoideidae, and Barylambdidae are much more similar. Comparative study suggests that only four or five of the seven genera allocated to Pantolambdidae, Titanoideidae, and Barylambdidae by Simons (1960) are sufficiently distinct to warrant continued recognition. These are *Pantolambda*, *Titanoides*, *Barylamba*, *Haplolambda*, and possibly *Caenolambda*. We group all of these in a single family, for which the name Pantolambdidae has priority. *Titanoides* could be placed in a separate subfamily Titanoideinae, and *Barylamba*, *Haplolambda*, and *Caenolambda* could be placed in a subfamily Barylambdinae to show relationships within Pantolambdidae. Further study may show that additional taxa are represented, but we do not feel that present evidence of

morphological diversity justifies recognition of seven genera (most of which are monotypic) and three families (two of which would contain a single genus) in a balanced classification.

A thorough study of the morphological variability, sexual dimorphism, geographic distribution, and stratigraphic range of each of the species of North American pantolambdid pantodonts, with a modern systematic treatment of the group as a whole, is badly needed. Such a full review is, however, beyond the scope of this study. We concentrate instead on a narrower systematic problem concerning *Barylambda*. Among pantodonts, *Barylambda* is one of the few genera containing species known from large enough samples to permit characterization of dental variation and sexual dimorphism.

As presently conceived, *Pantolambda* includes middle Paleocene species of pantolambdid pantodonts of moderate body size that retain simple conical canines and generalized pantodont cheek teeth. *Titanoides* includes late Paleocene and earliest Eocene species of moderate to large body size that have specialized canines, exaggerated crest-like parastyles and metastyles on triangular upper molars, and relatively long, narrow, low-crowned lower molars. *Caenolambda* (if valid), *Haplolambda*, and *Barylambda* include late Paleocene and early Eocene species of moderate to large body size that have specialized canines, moderate parastylar and metastylar crests on rectangular upper molars, and relatively short, broad, high-crowned lower molars. *Ignatiolambda* is very similar to *Caenolambda*, *Haplolambda*, and *Barylambda*, and it is probably a synonym of *Haplolambda*. As we shall show, *Leptolambda* is clearly a junior synonym of *Barylambda*.

The following museum acronyms are used in the text and figures: AMNH, American Museum of Natural History (New York); CMNH, Carnegie Museum of Natural History (Pittsburgh); FMNH [CNHM of some authors], Field Museum of Natural History (Chicago); PU, Princeton University Museum of Natural History (Princeton); and UM, University of Michigan Museum of Paleontology (Ann Arbor). The stratigraphic and chronological sequence of localities yielding Tiffanian and Clarkforkian pantodonts is much better known today than it was when Simons' (1960) study was published. The biostratigraphy of Paleocene and early Eocene faunas is reviewed in Gingerich (1976), Gingerich, Rose, and Krause (1980), Rose (1981), and Gingerich (1983).

## SYSTEMATIC PALEONTOLOGY

The genus *Barylambda* was proposed by Patterson (1937) to receive a large pantodont from western Colorado that he originally described as *Titanoides faberi* (Patterson, 1933). The type specimen of *Barylambda faberi* was found in the lower valley of Plateau Creek, in "Plateau Valley" beds, which are generally regarded as latest Tiffanian and Clarkforkian in age (transitional Paleocene-Eocene; Rose, 1981, p. 132). A smaller pantodont, *Haplolambda quinni*, was described from these beds by Patterson (1939). Patterson recognized that *Haplolambda* was closely related to *Barylambda*, and grouped the two genera in a new family Barylambdidae. Nineteen years later, Patterson and Simons (1958) described a third barylambdid genus and species, *Leptolambda schmidti*, from Plateau Valley beds, with referred specimens from the Bighorn Basin and Clark's Fork Basin of northern Wyoming. The specimen designated as the holotype of *L. schmidti*, FMNH P-26075, has cheek teeth the same size as those of *Barylambda faberi*, while many other specimens referred to this species, including all figured dentitions, are smaller and come from an older faunal zone in northern Wyoming. We here synonymize *Leptolambda schmidti* from Plateau Valley with *Barylambda faberi*, and propose a new species

to include the smaller specimens of "*Leptolambda*" from Wyoming. These differ significantly from specimens of *Barylambda faberi*, but the difference is not sufficient to warrant placement in a distinct genus.

Order PANTODONTA Cope, 1873  
Family PANTOLAMBIDIDAE Cope, 1883  
Genus *Barylambda* Patterson, 1937

*Titanoides* (in part), Patterson, 1933, p. 415; 1934, p. 72; 1935, p. 144.  
*Barylambda* Patterson, 1937, p. 229; 1939, p. 361. Simons, 1960, p. 27.  
*Leptolambda* Patterson and Simons, 1958, p. 2. Simons, 1960, p. 28.

*Type species.*—*Barylambda faberi* (Patterson, 1933).

*Included species.*—Type species and *B. churchilli*, new species.

*Age and distribution.*—Late Paleocene and early Eocene (late Tiffanian and Clarkforkian Land-Mammal Ages) in western North America.

*Diagnosis.*—Species of *Barylambda* differ from those of *Haplolambda* and other pantolambdid genera principally in being larger and in having relatively broader and higher-crowned lower cheek teeth. *Barylambda* also differs from *Haplolambda* in having all upper molars more nearly equal in size. *Barylambda* differs from *Titanoides* in having high-crowned lower molars, and in having more rectangular upper molars with less well developed parastyles and metastyles.

*Barylambda faberi* (Patterson, 1933)

*Titanoides faberi* Patterson, 1933, p. 417, figs. 1-4; 1934, p. 73, Pl. 1-2, figs. 1-12; 1935, p. 144, figs. 1-6.  
*Barylambda faberi*, Patterson, 1937, p. 229; 1939, p. 365, figs. 104-105. Patterson and Simons, 1958, p. 4, figs. 2a, 3a, c. Simons, 1960, p. 27, figs. 1b, 4e, f, 5d, 11a.  
*Leptolambda schmidtii* (in part) Patterson and Simons, 1958, p. 3, figs. 3b, d. Simons, 1960, p. 29.  
Cf. *Titanoides primaevus*(?), Dorr and Gingerich, 1980, p. 109.

*Holotype.*—FMNH P-14637, skull and mandibular rami of a young individual with partial dentition.

*Type locality.*—Lower part of Plateau Creek Valley, NW 1/4, Section 15, T 10 S, R 96 W, Mesa County, Colorado. The holotype was found in the Atwell Gulch Member of the Wasatch Formation, 10-15 meters above the contact with the underlying Cretaceous Hunter Canyon Formation of the Cretaceous Mesa Verde Group (Patterson, 1933; Rose, 1981; A. Kihm, in litt. 1983).

*Type of synonym.*—Holotype of *Leptolambda schmidtii*, here synonymized with *B. faberi*, is FMNH P-26075, an incomplete skull with mandibles and a fragmentary postcranial skeleton. The type of *L. schmidtii* was found in the Atwell Gulch Member of the Wasatch Formation four miles south-southeast of DeBeque in the NW 1/4 of Section 11 or SW 1/4 of Section 2, T 10 S, R 97 W, Mesa County, Colorado. This locality is approximately 30 m higher stratigraphically than the type locality of *Barylambda faberi* (Patterson and Simons, 1958; Rose, 1981; A. Kihm, in litt. 1983).

*Age and distribution.*—*Barylambda faberi* is known only from localities of Clarkforkian age (transitional latest Paleocene - early Eocene) in western Colorado and southwestern Wyoming.

*Typodigm.*—The holotype is the only specimen known with certainty to have come from the type locality. Other Plateau Valley specimens come from a stratigraphic interval approximately 50 meters thick. These include AMNH 32511, CMNH 11353, FMNH P-14898, 14902, 14904, 14908, 14944, 14945, 14946, 15558, 25617, 26075, 26076, and 26077. FMNH P-15571 may belong to *B. faberi*, but it may also be a large specimen of *Haplolambda quinni*. The one specimen known from Buckman Hollow in southwestern Wyoming is UM 71339.

*Discussion.*—The age of the Plateau Valley beds yielding *Barylambda faberi* is variously given as late Tiffanian or Clarkforkian (Patterson, 1935; Gingerich, 1976; Rose, 1981). A composite faunal list for Plateau Valley localities compiled by Kihm (in Rose, 1981) includes 21 species, of which only four are diagnostic of age, given our present state of knowledge. The diagnostic taxa are *Plesiadapis dubius*, cf. *Haplomylus* sp., *Esthonyx* sp., and *Coryphodon* sp. All four indicate a Clarkforkian rather than Tiffanian age for the Plateau Valley fauna. Recent work by Kihm (pers. comm., 1983) indicates that *Plesiadapis dubius* and *Haplomylus* sp. are present in the same stratigraphic interval as *Barylambda faberi* (including "*Leptolambda schmidtii*"). *Esthonyx* sp. and *Coryphodon* sp. occur above the stratigraphic interval yielding *Barylambda*. A Clarkforkian age assignment for the Plateau Valley fauna is further corroborated by discovery of a large high-crowned lower molar of *Barylambda faberi* at Buckman Hollow, in southwestern Wyoming, in a fauna of undoubted Clarkforkian age (this tooth was incorrectly compared to *Titanoides* when first published by Dorr and Gingerich, 1980, but its large size and great crown height are diagnostic of *B. faberi*).



FIG. 1— Eastern part of locality SC-228 on the south side of Polecat Bench. View is to the east. The type specimen of *Barylambda churchilli* was found by W. Churchill in 1941 weathering out of a dark grey bed on a small hill in the foreground. A marsh pick rests at the exact location (see arrow).

It is worth noting that *Barylambda faberi* is not known from Clarkforkian faunas in northwestern Wyoming, an area where *Barylambda* was abundant during the late Tiffanian. This suggests that *Barylambda* became restricted to faunas in the southern part of North America before it became extinct (see discussion of phylogeny and biogeography below).

***Barylambda churchilli*, new species**

Figs. 2B, 3B, 4

*Leptolambda schmidti* (in part), Patterson and Simons, 1958, p. 3, fig. 1. Simons, 1960, p. 29, figs. 6b, d, g, 11b, 13a.

*Holotype*.—PU 14681, nearly complete dentary with moderately worn lower dentition.

*Type locality*.—Airport Locality [SC-228] on south side of Polecat Bench, center of NE 1/4, Section 9, T 56 N, R 99 W, Park County, Wyoming (see Figure 1). This locality is at the 550 m level in the Fort Union ("Polecat Bench") Formation, 150 m below the level of Princeton Quarry and 400 m below the Tiffanian-Clarkforkian boundary. It is stratigraphically just above a normal polarity interval interpreted as magnetozone 26N (Butler et al., 1981).

*Age and distribution*.—Late Paleocene (late Tiffanian Land-Mammal Age; *Plesiadapis churchilli* and *Ples. simonsi* biochrons of Gingerich, 1976). *Barylambda churchilli* is known from several localities in the northern Bighorn Basin and adjacent Clark's Fork Basin of northwestern Wyoming.

*Diagnosis*.—*Barylambda churchilli* differs from middle Tiffanian "*Caenolambda*" *jepseni* and its probable synonym *Barylambda jackwilsoni* in being 17-18% larger in linear dimensions of most cheek teeth (Table 1). *B. churchilli* differs from Clarkforkian *B. faberi* in being 10-13% smaller in linear dimensions of most cheek teeth (Table 1, see also Fig. 7).

*Typodigm*.—Two specimens of *Barylambda churchilli* are known from the type locality: PU 14680 and 14681 (holotype). Other specimens from late Tiffanian localities in the Fort Union Formation of the northern Bighorn Basin, Wyoming, include PU 14879, 14990, 14992, 14996, 16485, and UM 69248, 73710, and 77155.

*Etymology*.—Named for Mr. Winston Churchill of Powell, Wyoming, who found the holotype in 1941 while helping his father, Frederick Churchill, excavate a less well preserved specimen (PU 14680) nearby.

*Description*.—The holotype of *Barylambda churchilli*, PU 14681, is a nearly complete dentary missing only the crowns of left and right  $P_1$ . The lower incisors have simple pointed crowns bordered by medial and lateral crests flaring near the base of the crown. These crests are worn from occlusion with opposing upper incisors. Crown size increases from  $I_1$  to  $I_3$ . The lower canine in the holotype (a putative male) is considerably larger than  $I_3$ . It has a simple, high, pointed crown with a flaring medial crest like that on  $I_3$ , but no lateral crest. The lateral surface is worn from occlusion with the upper canine.

Judging from its alveolus,  $P_1$  had a single thick root. The crown of  $P_1$  is not preserved in the holotype. The remaining lower premolars are double-rooted and similar to each other in form. All have distinct protoconids, paraconids, and metaconids defining a distinct trigonid, followed by a short, narrow, basined talonid. The size of the lower premolar crowns increases from  $P_2$  to  $P_4$ , and the width of both trigonids and talonids increases markedly in this progression.

The lower molars are moderately worn in the holotype. Each has an anteroposteriorly short, broad trigonid, with the protoconid, paraconid, and metaconid distinct. The trigonid is followed by a moderately developed talonid. Talonids on  $M_1$  and  $M_2$  are slightly basined and similar in

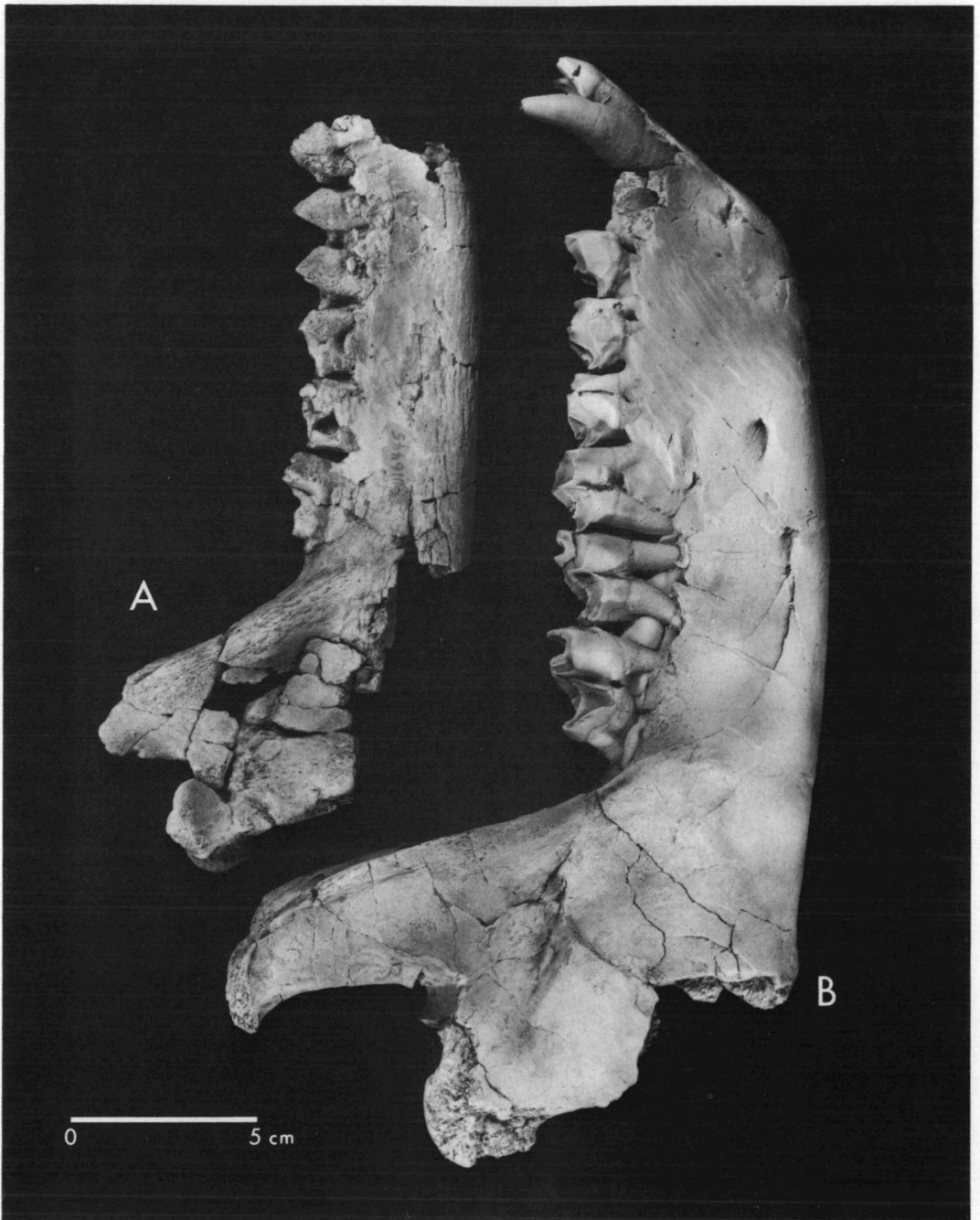


FIG. 2— Comparison of dentaries of *Haplolambda quinni* (A, PU 16445) and *Barylamba churchilli* (B, holotype PU 14681) from the late Tiffanian of the Bighorn Basin, Wyoming. Both photographed in right lateral view at the same scale (approximately 0.5 x natural size).



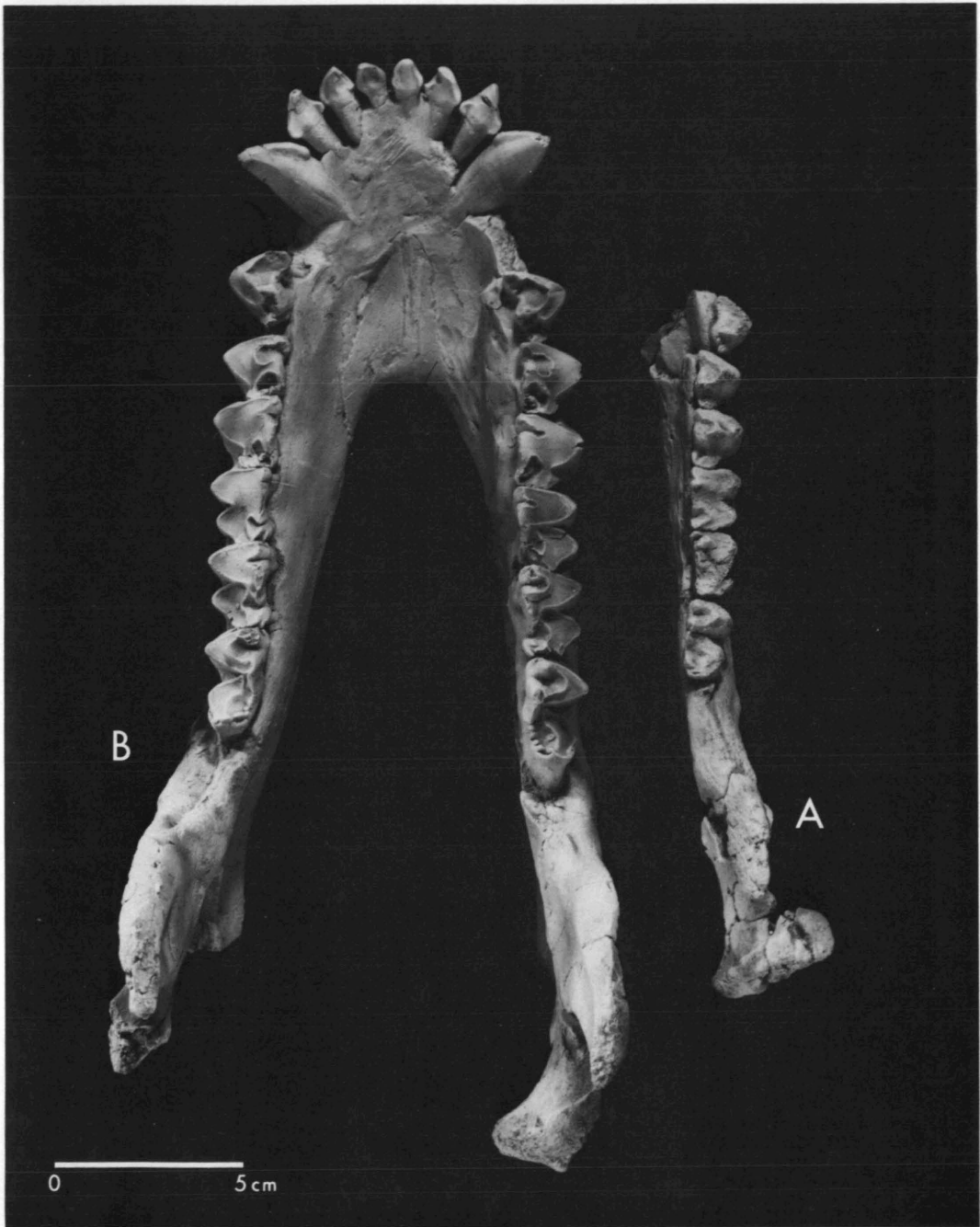


FIG. 3.— Comparison of dentaries of *Haplolambda quinni* (A, PU 16445) and *Barylamba churchilli* (B, holotype PU 14681) from the late Tiffanian of the Bighorn Basin, Wyoming. Both photographed in occlusal view at the same scale (approximately 0.5 x natural size).

width to the trigonids. There is a prominent crest running posteriorly from the metaconid, but there is no distinct metastylid (a small cuspule formerly present here may have been removed by wear). The talonid on  $M_3$  is narrower than the trigonid, and it is bordered medially by a series of beaded cuspules continuous with the metastylid crest. All three molars are relatively high-crowned. The mandibular ramus is moderately deep beneath all of the cheek teeth, and left and right rami are solidly fused at the symphysis. The mandibular condyles have two distinct but confluent articular surfaces, one covering the entire dorsal surface of each condyle and the other limited to the posterior surface of the medial half of each condyle. The holotype, PU 14681, is illustrated and compared to a dentary of contemporary *Haplolambda quinni* in Figures 2 and 3.

A second specimen from the type locality, PU 14680, resembles the holotype very closely, differing only in having a much smaller, almost incisiform, lower canine. The crown of  $P_1$  is also preserved in this specimen, and it is incisiform like the lower canine. These differences are plausibly attributed to sexual dimorphism, the holotype representing a male individual and PU 14680 representing a female. Another probable female specimen, PU 14990, conforms very closely to PU 14680 in the relative size and form of  $I_3$ ,  $C_1$ , and  $P_1$ . PU 14680 is compared to the holotype dentary in Figure 4, where the magnitude of presumed sexual differences in the anterior dentition of *Barylambda churchilli* is illustrated.

A partial upper dentition of *Barylambda churchilli* is preserved in PU 14680. The crowns of the upper incisors in this specimen resemble crowns of the lower incisors very closely, but the axes of the crowns of upper incisors are oriented at a greater angle to the long axis of the roots. The upper canine in PU 14680, a female, is a relatively small tooth with a simple pointed crown (the form of the upper canine in males is unknown).  $P^3$  and  $P^4$  have pronounced protocone and paracone cusps at the apices of sweeping curved crests. The external margins of the crowns  $P^3$  and  $P^4$  are deeply but not acutely invaginated. Crowns of  $M^1$  and  $M^2$  are similar in size, being relatively symmetrical with broadly based protocones and smaller paracones and metacones that are equal in size. There is a distinct paraconule but no metaconule on  $M^1$  and  $M^2$ . Distinct anterior and posterior cingula border the protocone, and there is a distinct external cingulum as well. The crown of  $M^3$  is similar in width to that of  $M^1$  and  $M^2$ , but the metacone is reduced and the crown is shorter anteroposteriorly. A partial upper dentition of "*Caenolambda*" *jepseni* (or possibly *Barylambda churchilli*) is illustrated in Figure 5. It shows the general form of upper cheek teeth of *Barylambda*.

Measurements of the dentition of individual specimens of *Barylambda churchilli*, including the holotype, were published by Simons (1960). These are summarized in Table 1 for comparison with other species most similar to *B. churchilli*.

#### PHYLOGENY AND BIOGEOGRAPHY OF LATE PALEOCENE PANTOLAMBIDAE

There are at least three lineages of pantolambdid pantodonts represented in North American Tiffanian faunas. The most distinct of these is included in *Titanoides*. Species of *Titanoides* have long, narrow, low-crowned lower molars with open trigonids, and triangular upper molars lacking paraconules but having exaggerated parastylar and metastylar crests (Figure 6). The only Torrejonian record of *Titanoides* is the type specimen of *T. simpsoni*, a partial maxilla described by Simons (1960, p. 38). It is from Gidley Quarry, the type locality of *Pantolambda intermedium* Simpson (1935). The type maxilla of *T. simpsoni* is the right size to occlude with the type dentary of *P. intermedium* and, considering that the two were found at the same locality, *T. simpsoni* is

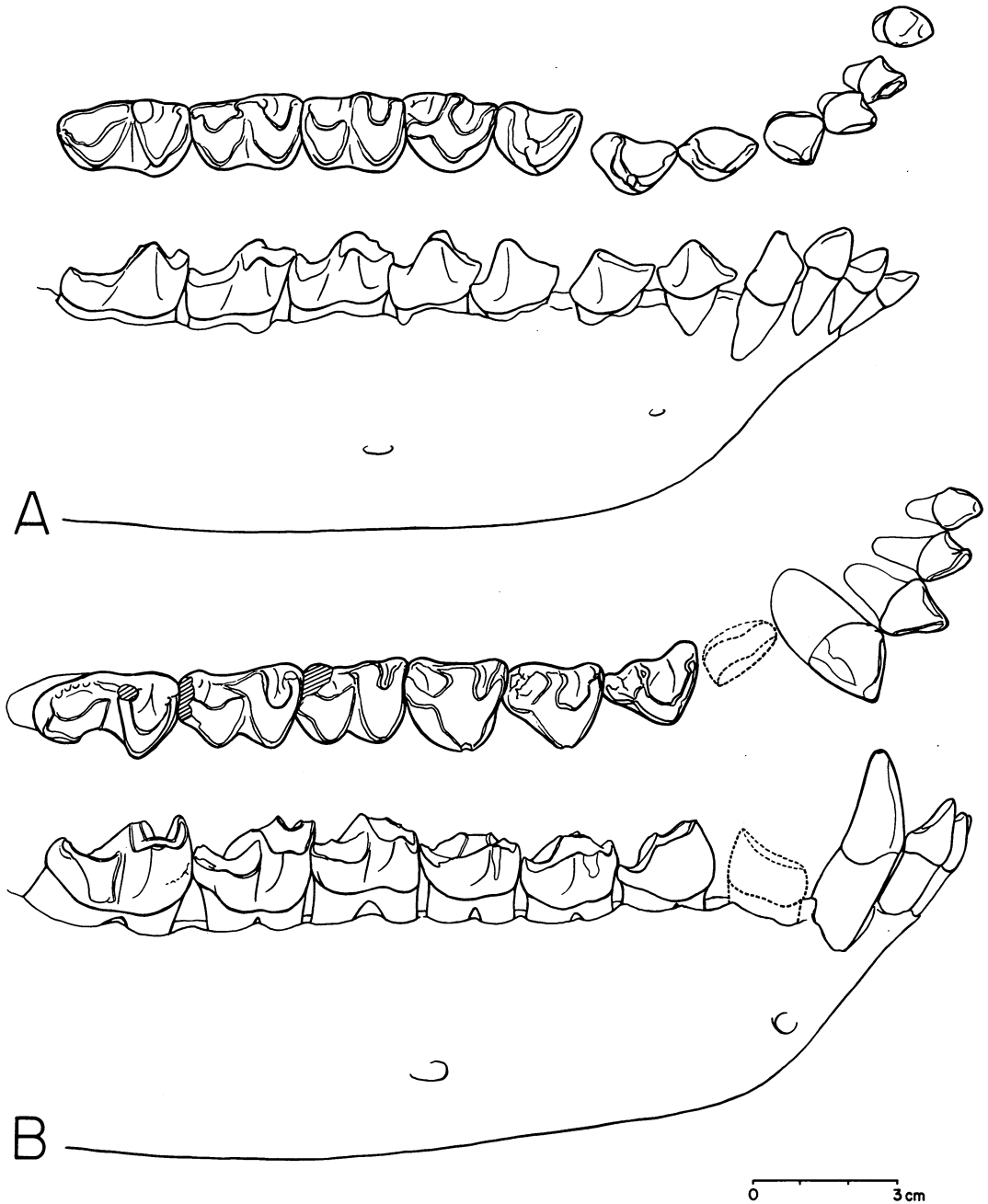


FIG. 4— Comparison of right lower dentition of female (A, PU 14990) and male (B, holotype PU 14681) *Barylambda churchilli* from the late Tiffanian of the Bighorn Basin, Wyoming. Each specimen is shown in occlusal and lateral view. Sexual dimorphism is expressed principally in the size and form of the upper and lower canines and honing P<sub>1</sub>. The crown of P<sub>1</sub> in PU 14681 is reconstructed after that in PU 14863, holotype of “*Caenolambda*” *jepseni*, which is also a male. Both drawn at the same scale (0.67 x natural size).

TABLE 1.—Comparative measurements of the upper and lower dentitions of species referred to *Barylambda*. All measurements are from Simons (1960), except those of *B. "jackwilsoni,"* which are from Schiebout (1974). *L* and *W* are maximum crown length and width, respectively. Italicized numbers in parentheses following means are sample size and standard deviation. Note that molars of *B. churchilli* are significantly larger than those of "*Caenolambda jepseni*" and *B. "jackwilsoni,"* and significantly smaller than those of *B. faberi* in most dimensions.

Tooth position	M. Tiffanian <i>Barylambda</i> " <i>jackwilsoni</i> " Type TMM 40537-83 (female)		M. Tiffanian " <i>Caenolambda</i> " <i>jepseni</i> Type PU 14863 (male)		L. Tiffanian <i>Barylambda</i> <i>churchilli</i> Bighorn Basin	Clarkforkian <i>Barylambda</i> <i>faberi</i> Plateau Valley
	UPPER DENTITION					
I <sup>1</sup>	L	-	6.0(?)	-	-	6.25 (2, ----)
	W	-	5.1(?)	-	-	5.10 (2, ----)
I <sup>2</sup>	L	-	-	7.7	-	8.55 (2, ----)
	W	-	-	6.3	-	8.05 (2, ----)
I <sup>3</sup>	L	-	-	9.1	-	10.60 (4, 1.39)
	W	-	-	6.8	-	11.20 (4, 1.63)
C <sup>1</sup>	L	-	28.5	10.9	-	17.14 (5, 3.14)
	W	-	15.4	8.8	-	16.80 (5, 2.61)
P <sup>1</sup>	L	-	14.7	14.70 (3, 0.95)	-	16.70 (4, 1.54)
	W	-	7.3	8.53 (3, 0.61)	-	12.80 (4, 1.51)
P <sup>2</sup>	L	-	14.4	18.2	-	18.43 (7, 1.77)
	W	-	21.0	25.5	-	27.83 (7, 3.14)
P <sup>3</sup>	L	-	15.0	17.40 (2, ----)	-	19.37 (7, 1.71)
	W	-	24.1	26.00 (2, ----)	-	30.44 (7, 2.00)
P <sup>4</sup>	L	-	15.0	-	-	20.14 (7, 2.19)
	W	-	24.4	-	-	34.11 (7, 2.78)
M <sup>1</sup>	L	-	18.7	23.00 (3, 1.50)	-	27.42 (6, 2.17)
	W	-	26.2	32.10 (3, 0.95)	-	35.49 (7, 2.18)
M <sup>2</sup>	L	-	-	24.00 (4, 1.09)	-	27.71 (8, 1.42)
	W	-	-	34.23 (4, 1.26)	-	39.15 (8, 3.25)
M <sup>3</sup>	L	-	-	18.43 (3, 1.23)	-	21.99 (8, 1.53)
	W	-	-	31.53 (3, 1.72)	-	35.39 (8, 4.98)

almost certainly the upper dentition of *P. intermedium*. We regard *Titanoides simpsoni* as a junior synonym of *Pantolambda intermedium*.

Four other species of *Titanoides* described in the literature may represent one or two evolutionary lineages. These include *T. zeuxis* Simpson (1937) from the early(?) and middle Tiffanian, and *T. gidleyi* Jepsen (1930) from the middle and late(?) Tiffanian. Larger *T. primaevus* Gidley (1917) [= *Sparactolambda looki* Patterson, 1939] is from the late Tiffanian(?) and Clarkforkian. The systematic position of large *Titanoides major* Simons (1960) is problematical because the type and only specimen (PU 16447) is fragmentary. The type locality, near Sage Point on Polecat Bench [UM locality SC-264 in the SE 1/4, NE 1/4, Section 2, T 56 N, R 99 W], is clearly early Tiffanian in age. PU 16446, a partial maxilla referred to *T. primaevus* by Simons (1960, P. 34-35) is also from this area [UM locality SC-263 in the center of Section 2, T 56 N, R 99 W], and it is almost certainly the upper dentition of *T. major*.

*Caenolambda*, *Haplolambda*, and *Barylambda* represent a more complex radiation including a minimum of two evolutionary lineages (Figure 7). All species in this complex have relatively short, broad, high-crowned lower molars, and rectangular upper molars with moderate

TABLE 1, cont.

Tooth position		M. Tiffanian <i>Barylambda</i> "jackwilsoni" Type TMM 40537-83 (female)	M. Tiffanian "Caenolambda" <i>jepseni</i> Type PU 14863 (male)	L. Tiffanian <i>Barylambda</i> <i>churchilli</i> Bighorn Basin	Clarkforkian <i>Barylambda</i> <i>faberi</i> Plateau Valley
LOWER DENTITION					
I <sub>1</sub>	L	-	6.4	8.27 (3, 0.46)	6.80 (3, 0.89)
	W	-	6.0	6.13 (3, 0.12)	6.97 (3, 0.91)
I <sub>2</sub>	L	-	7.4	10.50 (3, 0.50)	9.55 (2, ----)
	W	-	7.0	6.67 (3, 0.42)	8.20 (2, ----)
I <sub>3</sub>	L	-	9.0	11.57 (3, 1.10)	11.25 (2, ----)
	W	-	7.3	7.23 (3, 0.40)	9.65 (2, ----)
C <sub>1</sub>	L	-	16.0	13.60 (3, 1.84)	17.67 (3, 3.79)
	W	-	15.0	9.13 (3, 2.12)	14.40 (4, 3.09)
P <sub>1</sub>	L	-	20.6	14.75 (2, ----)	18.05 (4, 0.99)
	W	-	8.0	8.60 (2, ----)	10.57 (3, 0.75)
P <sub>2</sub>	L	-	13.8	20.33 (3, 1.26)	19.97 (3, 2.28)
	W	-	12.5	13.53 (3, 1.88)	15.13 (3, 0.64)
P <sub>3</sub>	L	16.4	15.6	20.00 (3, 0.87)	20.93 (4, 1.41)
	W	14.2	14.0	16.43 (3, 1.69)	17.40 (4, 0.95)
P <sub>4</sub>	L	17.3	16.0	20.20 (4, 1.57)	20.48 (5, 1.56)
	W	17.0	14.4	17.88 (4, 1.18)	18.30 (5, 1.76)
M <sub>1</sub>	L	17.1	16.6	22.13 (4, 0.94)	25.06 (5, 1.10)
	W	14.4	14.2	17.70 (4, 0.83)	19.46 (5, 1.53)
M <sub>2</sub>	L	19.8	20.0	23.43 (4, 0.81)	27.04 (5, 1.78)
	W	17.3	15.8	17.38 (4, 0.62)	20.70 (5, 1.82)
M <sub>3</sub>	L	25.5	25.1	27.88 (4, 2.18)	33.62 (5, 2.44)
	W	16.1	13.9	17.25 (4, 0.80)	19.54 (5, 1.82)

parastyles and metastyles and distinct paraconules. *Caenolambda*, if sufficiently different from *Haplolambda* and *Barylambda* to warrant separate generic status, includes one or two valid species. The type species of *Caenolambda*, *C. pattersoni* Gazin (1956), is known from the early Tiffanian. "*C.*" *jepseni* Simons (1960) [probably = *Barylambda jackwilsoni* Schiebout, 1974] comes from the middle Tiffanian. "*C.*" *jepseni* may well prove to represent an early species of *Barylambda* when better specimens are known. *Caenolambda*, if valid, appears to be old enough and sufficiently generalized morphologically to be a common ancestor of both *Haplolambda* and *Barylambda*.

*Ignatiolambda barnesi* Simons (1960) is not clearly separable from *Haplolambda quinni* Patterson (1939), and together these constitute a lineage of medium-sized late Tiffanian and Clarkforkian pantodonts. *Barylambda churchilli*, described here, and *Barylambda faberi* (Patterson, 1933) constitute a lineage of larger pantodonts in late Tiffanian and Clarkforkian faunas, respectively.

*Barylambda* and other large pantolambdids appear never to occur in the same local fauna with the large coryphodontid pantodont *Coryphodon*, although pantolambdids and *Coryphodon* are both known from the Clarkforkian Land-Mammal Age. In northern Wyoming, the beginning of the Clarkforkian is marked by the first appearance of *Coryphodon* (and several other immigrant genera; Rose, 1981), while *Barylambda*, abundant during the late Tiffanian, disappears. *Barylambda* is present in Clarkforkian faunas in southern Wyoming (Buckman Hollow) and

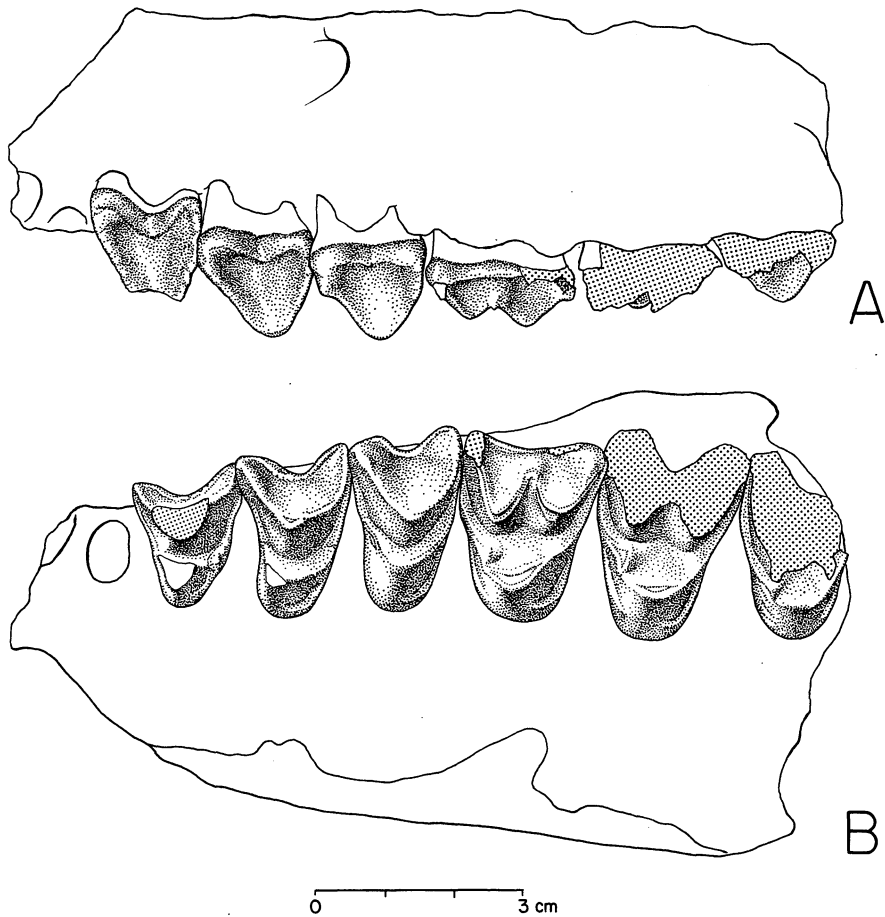


FIG. 5— Left maxillary dentition of large “*Caenolambda*” *jepseni* or small *Barylambda churchilli*, PU 16662, from the middle-to-late Tiffanian Seaboard Well locality. *A*, lateral, and *B*, occlusal view. Note the more shallowly invaginated external margins and sweeping protocristae on upper premolars, together with moderate development of styler crests, distinct paraconules, and quadrate occlusal outlines of upper molars distinguishing the upper cheek tooth dentition of barylambdines “*Caenolambda*,” *Barylambda*, and *Haplolambda* from that of the titanoideine *Titanoides* (Figure 6).

western Colorado (Plateau Valley) before *Coryphodon* appears, but here again they do not overlap in time. Coexistence of *Barylambda* with the Wasatchian immigrant perissodactyl *Hyracotherium* in southern Texas (Schiebout, 1974) and Baja California (Morris, 1966; Ferrusquia, 1978) suggests that *Barylambda* persisted into the Wasatchian Land-Mammal Age in southern faunas, again apparently in the absence of *Coryphodon*. As a result, we can envision a slow replacement of *Barylambda* and other pantolambdids by *Coryphodon*, this replacement progressing from northern to southern North America during the course of the Clarkforkian. *Barylambda churchilli* was replaced by *Coryphodon* in northern Wyoming at the beginning of the Clarkforkian. The more advanced species *B. faberi* was replaced by *Coryphodon* in southern Wyoming and Colorado in the middle to late Clarkforkian. Finally, unnamed forms of *Barylambda* were replaced by *Coryphodon* in Texas (Wilson, 1967), and

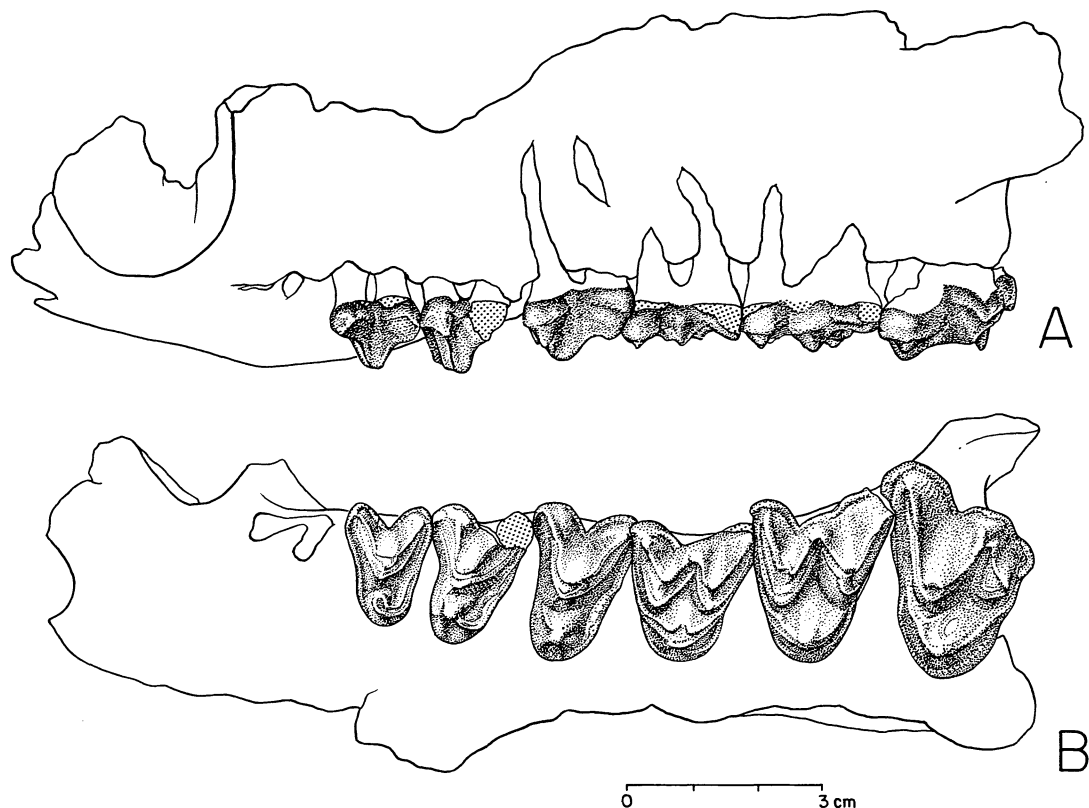


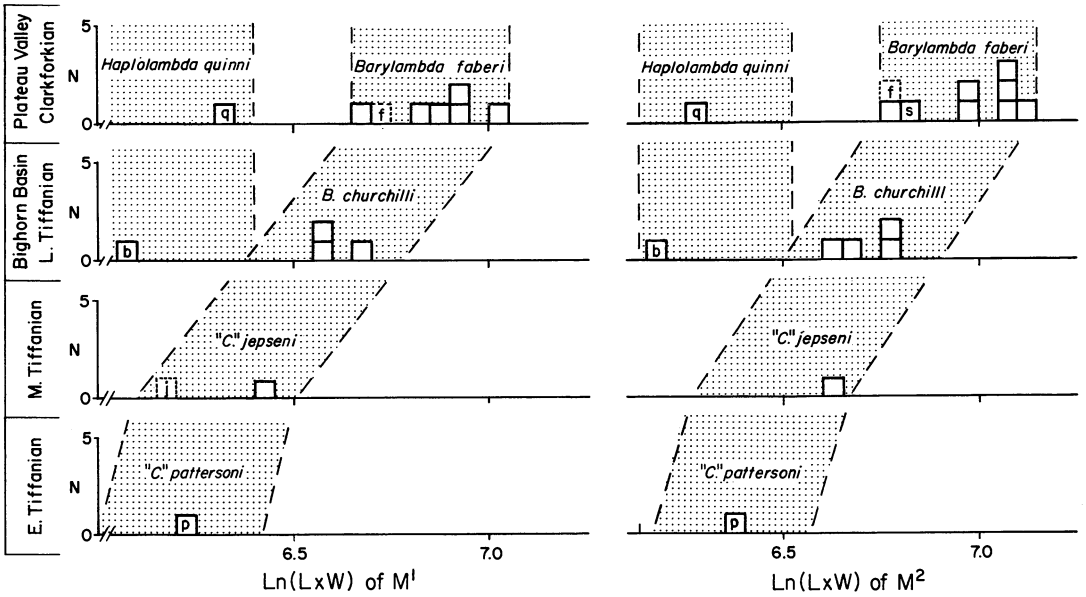
FIG. 6.— Left maxillary dentition of *Titanoides zeuxis* or *T. gidleyi*, PU 14974, from late Tiffanian Witter Quarry (Crocodile Tooth Quarry of Simons, 1960, and “Croc Tooth” Quarry of authors). *A*, lateral, and *B*, occlusal view. Note the deeply invaginated external margins and simple cusps on upper molars, together with the exaggerated development of styler crests, absence of distinct paraconules, and triangular occlusal outlines on upper molars distinguishing the upper cheek tooth dentition of titanoideine *Titanoides* from that of barylambdines “*Caenolambda*,” *Barylamba*, and *Haplolambda* (Figure 5).

possibly Baja California, in the early Wasatchian. Whether this progressive replacement of *Barylamba* by *Coryphodon* was a consequence of direct competition or an indirect result of changing environmental conditions cannot be determined at present.

#### ACKNOWLEDGMENTS

We thank Drs. Donald Baird, Princeton University; Malcolm C. McKenna, American Museum of Natural History; and William Turnbull, Field Museum of Natural History, for access to specimens and casts analyzed here. Dr. Kenneth D. Rose, Johns Hopkins University; Dr. Judith A. Schiebout, Louisiana State University; and Mr. Allen J. Kihm, University of Colorado, reviewed the manuscript. Mr. Kihm generously provided information on the type localities of *Barylamba faberi* and *Leptolambda schmidtii*, and a current assessment of the stratigraphic ranges of Plateau Valley mammals. We are particularly indebted to Winston

UPPER DENTITION



LOWER DENTITION

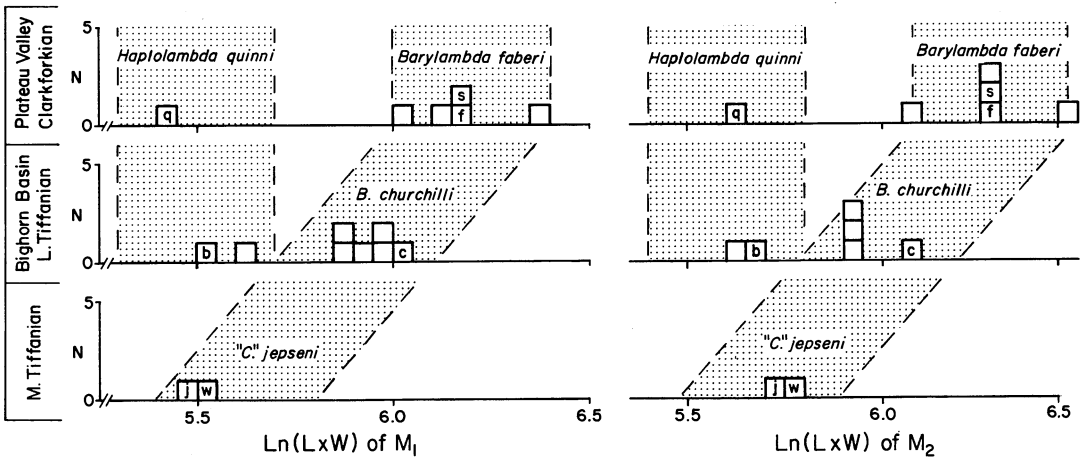


FIG. 7— Distribution of variation in the size of upper and lower molars in “*Caenolambda*,” *Haplolambda*, and *Barylambda* from western North America. Tooth size is plotted for successive subdivisions of the Tiffanian and Clarkforkian land-mammal ages, showing in outline the possible phylogenetic relationships of “*Caenolambda*” *pattersoni* (p), “*Caenolambda*” *jepseni* (j), *Haplolambda quinni* (q), *Barylambda churchilli* (c), and *Barylambda faberi* (f). Each square represents an individual specimen. Letters within squares identify type specimens of the five valid species listed above. In addition, types of probable synonyms are plotted and identified as follows: *Barylambda jackwilsoni* (w), *Ignatiolambda barnesi* (b), and *Leptolambda schmidtii* (s). Note that *Barylambda churchilli* is intermediate stratigraphically and intermediate in form between “*C.*” *jepseni* and *Barylambda faberi*. *Haplolambda quinni* may represent a late Tiffanian immigrant into the Bighorn Basin. Original measurements taken from Simons (1960) and Schiebout (1974).



Churchill of Powell, Wyoming, for showing us exactly where he found the type specimen of *Barylambda churchilli*. Photography in Figures 1-3 is by George Junne. Figures 4-7 were drawn by Karen Klitz. This research was supported by a grant from the National Science Foundation (DEB 82-06242).

## LITERATURE CITED

- BUTLER, R. F., P. D. GINGERICH, and E. H. LINDSAY. 1981. Magnetic polarity stratigraphy and biostratigraphy of Paleocene and lower Eocene continental deposits, Clark's Fork Basin, Wyoming. *Journal of Geology*, 89:299-316.
- DORR, J. A. and P. D. GINGERICH. 1980. Early Cenozoic mammalian paleontology, geologic structure, and tectonic history in the overthrust belt near LaBarge, Wyoming. *University of Wyoming Contributions to Geology*, 18:101-115.
- FERRUSQUÍA-VILAFRANCA, I. 1978. Distribution of Cenozoic vertebrate faunas in middle America and problems of migration between North and South America. *In*, I. Ferrusquía-Villafranca (ed.), *Conexiones Terrestres entre Norte y Sudamérica*. Universidad Nacional Autónoma de México, Boletín Instituto de Geología, 101:193-321.
- GAZIN, C. L. 1956. Paleocene mammalian faunas of the Bison Basin in south-central Wyoming. *Smithsonian Miscellaneous Collections*, 131(6):1-57.
- GIDLEY, J. M. 1917. Notice of a new Paleocene mammal, a possible relative of the titanotheres. *Proceedings of the United States National Museum*, 52:431-435.
- GINGERICH, P. D. 1976. Cranial anatomy and evolution of early Tertiary Plesiadapidae (Mammalia, Primates). *University of Michigan Papers on Paleontology*, 15:1-140.
- \_\_\_\_\_. 1983. Paleocene-Eocene faunal zones and a preliminary analysis of Laramide structural deformation in the Clark's Fork Basin, Wyoming. *Wyoming Geological Association Guidebook*, in press.
- \_\_\_\_\_, K. D. ROSE, and D. W. KRAUSE. 1980. Early Cenozoic mammalian faunas of the Clark's Fork Basin - Polecat Bench area, northwestern Wyoming, p. 51-68. *In*, P. D. Gingerich (ed.), *Early Cenozoic Paleontology and Stratigraphy of the Bighorn Basin, Wyoming*. University of Michigan Papers on Paleontology, No. 24.
- JEPSEN, G. L. 1930. Stratigraphy and paleontology of the Paleocene of northeastern Park County, Wyoming. *Proceedings of the American Philosophical Society*, 69:463-528.
- MORRIS, W. J. 1966. Fossil mammals from Baja California: new evidence on early Tertiary migrations. *Science*, 153:1376-1378.
- PATTERSON, B. 1933. A new species of the amblypod *Titanoides* from western Colorado. *American Journal of Science*, 25:415-425.
- \_\_\_\_\_. 1934. A contribution to the osteology of *Titanoides* and the relationships of the Amblypoda. *Proceedings of the American Philosophical Society*, 73:71-101.
- \_\_\_\_\_. 1935. Second contribution to the osteology and affinities of the Paleocene amblypod *Titanoides*. *Proceedings of the American Philosophical Society*, 75:143-162.
- \_\_\_\_\_. 1937. A new genus, *Barylambda*, for *Titanoides faberi*, Paleocene amblypod. *Geological Series, Field Museum of Natural History*, 6:229-231.
- \_\_\_\_\_. 1939. New Pantodonta and Dinocerata from the upper Paleocene of western Colorado. *Geological Series, Field Museum of Natural History*, 6:351-384.
- \_\_\_\_\_ and E. L. SIMONS. 1958. A new barylambdid pantodont from the late Paleocene. *Breviora, Museum of Comparative Zoology*, 93:1-8.
- ROSE, K. D. 1981. The Clarkforkian Land-Mammal Age and mammalian faunal composition across the Paleocene-Eocene boundary. *University of Michigan Papers on Paleontology*, 26:1-196.
- \_\_\_\_\_ and D. W. KRAUSE. 1982. Cyriacotheriidae, a new family of early Tertiary pantodonts from western North America. *Proceedings of the American Philosophical Society*, 126:26-50.
- SCHIEBOUT, J. A. 1974. Vertebrate paleontology and paleoecology of Paleocene Black Peaks Formation, Big Bend National Park, Texas. *Bulletin of the Texas Memorial Museum*, 24:1-88.
- SIMONS, E. L. 1960. The Paleocene Pantodonta. *Transactions of the American Philosophical Society*, 50(6):1-98.
- SIMPSON, G. G. 1935. New Paleocene mammals from the Fort Union of Montana. *Proceedings of the United States National Museum*, 83:221-244.
- \_\_\_\_\_. 1937. Additions to the upper Paleocene fauna of the Crazy Mountain field. *American Museum Novitates*, 940:1-15.

