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Additional Middle Eocene (Bridgerian) Mammals from Tabernacle Butte, Sublette County, Wyoming

BY ROBERT M. WEST¹ AND EDWARD G. ATKINS²

INTRODUCTION

Fossil vertebrates from the upper part of the Bridger Formation (Middle Eocene) at Tabernacle Butte in the northeastern part of the Green River Basin have been collected and studied primarily by personnel of the University of Wyoming and of the American Museum of Natural History. P. O. McGrew and others (1959) described the stratigraphy and the fauna known at that time. Supplementary reports have since been published by Simpson (1959a, 1959b), M. C. McKenna and Simpson (1959), and McKenna, P. Robinson, and D. W. Taylor (1962). The present paper adds data on mammalian material collected by the American Museum of Natural History parties in 1959 and 1967.

During the senior author's study of the phenacodont condylarths in the American Museum of Natural History collection, McKenna pointed out a specimen recovered from the "*Hyopsodus* Hill" locality (Locality 5 of McGrew and others) in 1967. Examination of this specimen confirmed its tentative identification as *Phenacodus*, a genus not previously known to have survived later than the time of the Lost Cabin fauna (early

¹ Department of Geological and Geophysical Sciences, Princeton University, New Jersey; present address: Department of Biology, Adelphi University, Garden City, New York.

² Department of Biological Sciences, Columbia University, New York.

Eocene) in North America. A specimen in the collection of the Carnegie Museum, discussed below, may also come from strata younger than the Lost Cabin fauna, although the physical stratigraphy as well as the biostratigraphy of the area in which it was found are not yet clear (Black and Dawson, 1966). Further investigation of the undescribed material in the Tabernacle Butte collection in the American Museum of Natural History produced additional new records for the area: *Apatemys* sp., *Microslops* sp. [cf. *M. annectens* (Marsh, 1872)], and a new dichobunid artiodactyl, *Neodiadocodexis emryi*. This latter specimen extends the range of the Diadocodinae, a Wasatchian subfamily, well into the Bridgerian.

The artiodactyl maxilla is described by Atkins, and the remainder of the paper is by West.

ACKNOWLEDGMENTS

We are grateful to Dr. Malcolm C. McKenna, Frick Curator of Fossil Mammals at the American Museum of Natural History, for calling this material to our attention and allowing us to study it. McKenna also critically read the manuscript and offered many helpful suggestions. Drs. Craig C. Black and Mary R. Dawson, Division of Vertebrate Fossils, Carnegie Museum, Pittsburgh, permitted the discussion of the Wind River Basin *Phenacodus*, although the opinions expressed here do not necessarily reflect their ideas. Dr. Elwyn L. Simons of the Peabody Museum of Natural History, Yale University, allowed the discussion of the Yale *Apatemys* specimens, located in the Yale collection several years ago by Dr. Peter Robinson of the University of Colorado Natural History Museum.

ABBREVIATIONS

A.M.N.H., the American Museum of Natural History
C.M., Carnegie Museum
F.M., Field Museum of Natural History
P.U., Princeton University
U.S.N.M., U.S. National Museum of the Smithsonian Institution
Y.P.M., Peabody Museum of Natural History

SYSTEMATICS

CLASS MAMMALIA

ORDER CONDYLARTHRA

FAMILY PHENACODONTIDAE

PHENACODUS COPE, 1873

Phenacodus primaevus Cope, 1873

Figures 1–5

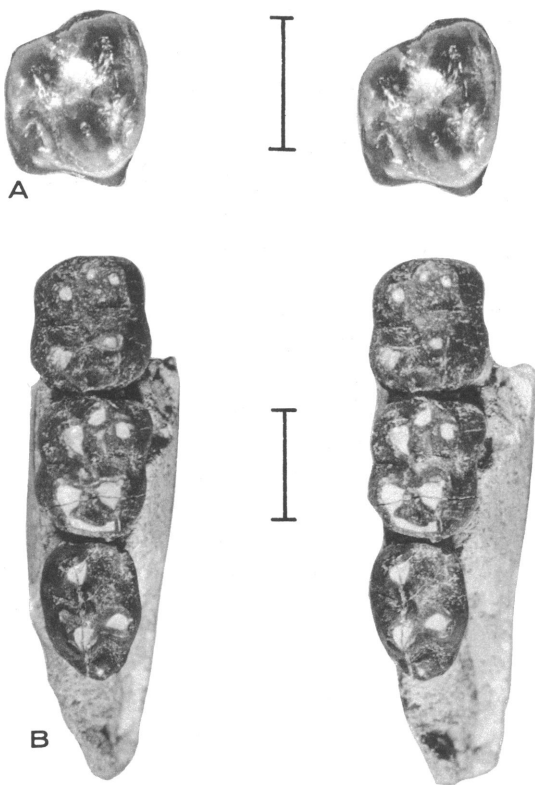


FIG. 1. A. Stereophotographs of A.M.N.H. No. 56053, *Phenacodus primaevus* M² from Tabernacle Butte. B. Stereophotographs of C.M. No. 12476, *Phenacodus primaevus* dentary from beds presumably younger than the Lost Cabin in the northern Wind River Basin.

The lines indicate lengths of 10 mm. for both specimens.

MATERIAL: A.M.N.H. No. 56053, isolated right upper molar, collected by M. C. McKenna, 1967.

HORIZON AND LOCALITY: Upper part of Bridger Formation, Middle Eocene, Tabernacle Butte. "Hyopsodus Hill" locality (Locality 5 of McGrew and others, 1959), NE. $\frac{1}{4}$, SE. $\frac{1}{4}$, SE. $\frac{1}{4}$, sect. 5, T. 28 N., R. 105 W., Sublette County, Wyoming.

DESCRIPTION: This single tooth (fig. 1A), a right upper molar, probably M², is thus far the sole representative of the Phenacodontidae in the upper Bridger Formation at Tabernacle Butte. It is preserved in a peculiar manner, as only the crown is present and it is encrusted with a

siliceous deposit which somewhat obscures the surface of the tooth and cannot be removed without harming the specimen. The tooth displays features characteristic of Wasatchian specimens of *Phenacodus primaevus*,¹ a large mesostyle and a rather small parastyle (compared with much earlier and smaller species of *Phenacodus*), which results in the rounded anterolabial margin; strong anterior, posterior and labial cingula; poor lingual cingulum; paraconule situated well in advance of a line from the protocone to the metacone; and metaconule situated posterior to a line from the hypocone to the metacone. The paraconule is considerably larger than the metaconule. This specimen differs from many specimens of M² of *P. primaevus* in that the hypocone is much smaller than the protocone, and is almost confluent with the rather lingually placed metaconule, although the metaconule is a variable cuspule in *P. primaevus*.

A.M.N.H. No. 56053 does not compare favorably with the bunodont artiodactyls, the group with the most similar dental anatomy during the middle Eocene. Several artiodactyls of the Bridgerian are as large as or larger than *Phenacodus primaevus*. Most of the phenacodontid characters of the Tabernacle Butte specimen, however, exclude it from the Artiodactyla. Only in the most general way does A.M.N.H. No. 56053 resemble artiodactyls such as *Helohyus* (present in the Tabernacle Butte assemblage), *Parahyus*, or *Lophiohyus*.

One more Bridgerian genus must be considered briefly in reference to A.M.N.H. No. 56053. *Ithygrammodon camelooides* (P.U. No. 10084), described by Osborn, Scott and Speir in 1878 on the basis of an edentulous premaxillary-maxillary fragment, was considered an artiodactyl by Sinclair (1914, p. 279). Because of the poor quality of the specimen, the affinities of this genus (and its probable synonymy) have never been precisely determined, and no published effort has been made since 1914. It is a large animal, considerably larger than any known phenacodont, and comparison with the corresponding area of P.U. No. 14854, a superbly preserved *P. primaevus* from the Graybull of the Bighorn Basin, establishes that *Ithygrammodon* is morphologically quite different from *Phenacodus*. This decreases the possibility of A.M.N.H. No. 56053 being a specimen of *Ithygrammodon*, although it does not help to determine the taxonomic position of *Ithygrammodon*.

¹ The species *P. primaevus* is used here in the sense of Simpson (1937), which includes within the species *P. primaevus* that material considered a separate species, *P. intermedius*, by Granger in 1915. No attempt is made to utilize the subspecific categories of either Granger, 1915, or Simpson, 1937. It is believed that work presently in progress by the senior author will clarify the taxonomy of the Phenacodontidae.

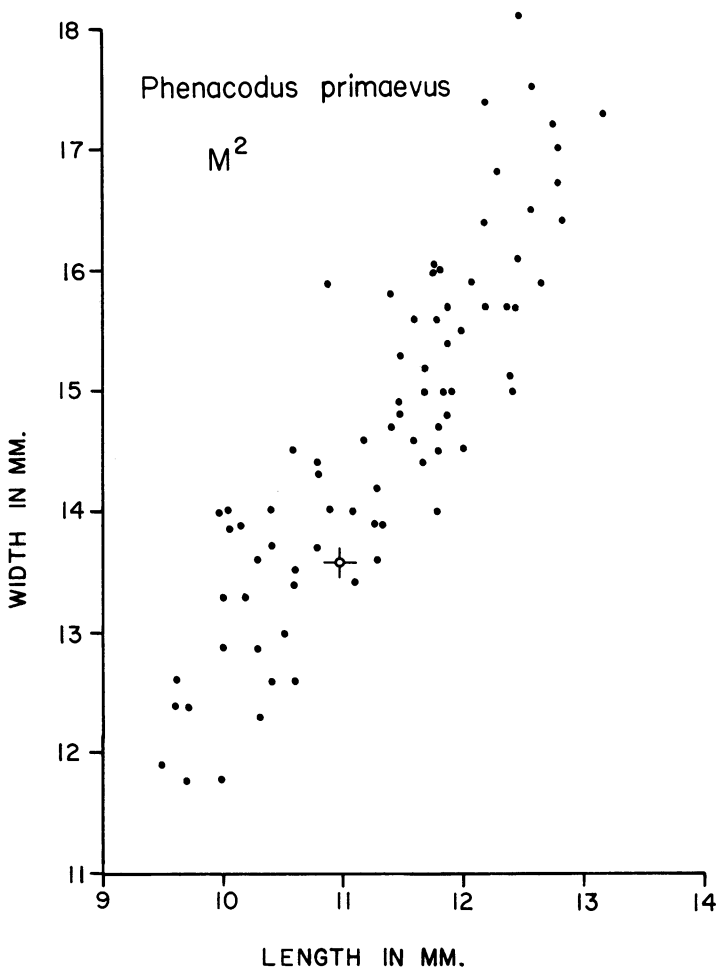


Fig. 2. Scatter diagram of second upper molars showing dimensional relationships between A.M.N.H. No. 56053, represented by the open, starred circle, and an assemblage of Wasatchian specimens of *Phenacodus primaevus* from the Graybull beds (early Wasatchian) in the Bighorn Basin, Wyoming.

Figure 2 shows that the Tabernacle Butte specimen fits well with *P. primaevus* in its external dimensions, despite the considerable temporal gap from early Wasatchian to late Bridgerian. Because of the great similarity to the earlier *P. primaevus*, and because A.M.N.H. No. 56053 is a single, isolated tooth, it is here referred to *P. primaevus*. Additional

collecting at “*Hyopsodus* Hill” and other localities of equivalent age may produce additional material which might necessitate the naming of a new species for the Bridgerian material, but this is not justified now.

A partial dentary of *Phenacodus primaevus* in the collection of the Carnegie Museum may also come from sediments younger than those that produce the Lost Cabin fauna, although the rock-stratigraphic placement of the locality where the specimen was found is much less certain than at Tabernacle Butte. C.M. No. 12476 (fig. 1B) was found by the Carnegie Museum party of 1963 in the NE. $\frac{1}{4}$, SE. $\frac{1}{4}$, sect. 5, T. 38 N., R. 88 W., Natrona County, Wyoming (Locality 17 of Black and Dawson, 1966), near the northern edge of the Wind River Basin. This area is one of considerable distortion along the post-Eocene Cedar Ridge Fault and its subsidiaries (Tourtelot, 1957, p. 7), and continuous strata are difficult to trace. Although Tourtelot (1957, fig. 2) mapped Carnegie Museum Locality 17, north of the Cedar Ridge Fault, as being in the late Eocene Tepee Trail Formation,¹ Black and Dawson (1966, pp. 302–303) regarded the sediment as older than ?middle to late Eocene, and believed that the presence of *Phenacodus* is adequate evidence for a late Wasatchian (Lost Cabin zone) age.

The beds at Carnegie Museum Locality 17 may be the uppermost part of the Lost Cabin Member of the Wind River Formation² physically separated from the main part of the unit by the movement of the Cedar Ridge Fault. They then would represent deposition later than the beds containing the Lost Cabin fauna a few miles away, if we distinguish between biostratigraphic and rock-stratigraphic units bearing the same name. The sediment in which C.M. No. 12476 was found is tuffaceous

¹ Tourtelot considered all the beds north of the Cedar Ridge Fault as belonging to the Tepee Trail Formation. This unit was divided into a lower “green and brown member” and an upper “Hendry Ranch Member” in the Badwater area. The green and brown member included “. . . bedded rocks rich in volcanic material . . .”

² Although the late Wasatchian fauna from the Lost Cabin area has been used as the basis for the correlation of this time period in North America since early this century (see Sinclair and Granger, 1911, p. 104, and Granger, 1914, p. 208), it was not until 1965 that a type section for the Lost Cabin Member of the Wind River Formation was defined. Keefer (1965, p. 48) designated a type section “. . . east of Lost Cabin along Alkali Creek and on the drainage between Alkali and Poison Creeks (northeastern part of T. 38 N., R. 89 W.).” The top of the Lost Cabin Member is missing as it has been removed by erosion there as well as at most places throughout its exposure area. The upper part of the member, as far as it is known, contains volcanic derivatives in varying quantities, especially toward the northwestern end of the Wind River Basin. The Lost Cabin fauna, the correlative basis for the late Wasatchian, comes mostly from a thin band of sediment near the bottom of the member; it does not necessarily serve to date the upper part of the Lost Cabin Member of the Wind River Formation.

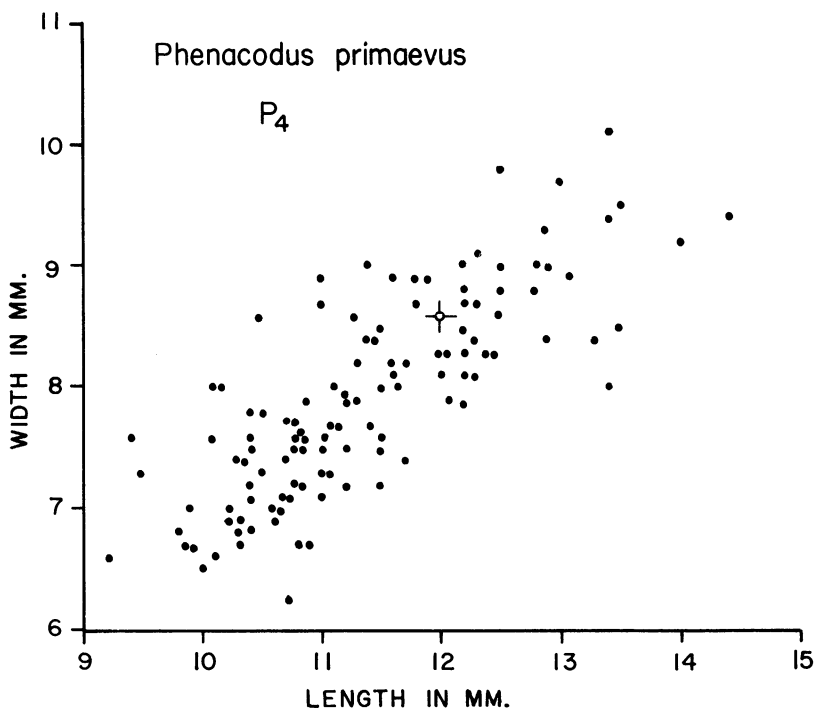


FIG. 3. Scatter diagram of fourth lower premolars showing dimensional relationships between C.M. No. 12476, represented by the open, starred circle, and an assemblage of Wasatchian specimens of *Phenacodus primaevus* from the Graybull beds (early Wasatchian) in the Bighorn Basin, Wyoming.

(being part of Tourtelot's green and brown member), a feature suggestive of other sediments producing faunas younger than the Lost Cabin fauna and possibly of temporal equivalence to the Cathedral Bluffs Tongue of the Wasatch Formation in the Green River Basin. There the fossil assemblage from the upper part of the Wasatch Formation is later than the Lost Cabin fauna (West [In press a]). The fauna accompanying C.M. No. 12476 is not yet sufficiently known to confirm that these tuffaceous beds were deposited after the time of deposition of the strata containing the Lost Cabin fauna. Consequently this conclusion rests on the stratigraphic information given above. In view of the possibility of the specimen being a second late occurrence of *Phenacodus*, it is illustrated and briefly described here in conjunction with the Tabernacle Butte *Phenacodus primaevus*.

C.M. No. 12476 consists of the right P₄-M₂ of a normal *Phenacodus*

primaevus. P_4 is the same length as M_1 , and displays a low, median conical paraconid, equal protoconid and metaconid, a relatively large metastylid, a low cristid obliqua, and a large hypoconid which is the only talonid cusp. M_1 and M_2 are similar to each other, differing in that M_1 has much better paraconid development and a relatively narrower

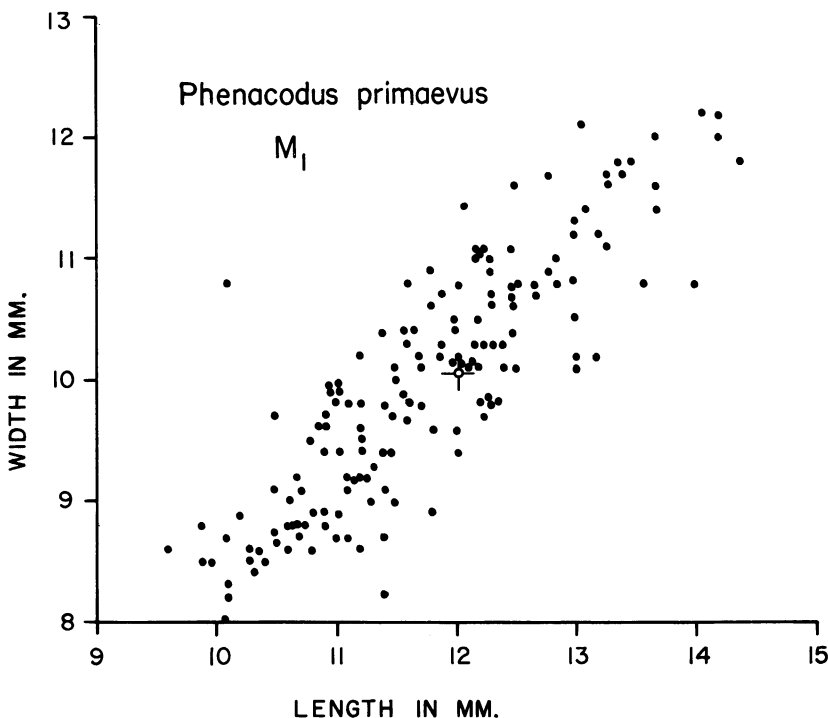


FIG. 4. Scatter diagram of first lower molars showing dimensional relationships between C.M. No. 12476, represented by the open, starred circle, and an assemblage of Wasatchian specimens of *Phenacodus primaevus* from the Graybull beds (early Wasatchian) in the Bighorn Basin, Wyoming.

trigonid. In both molars the hypoconid is the largest talonid cusp, and the entoconid and hypoconulid are approximately equal in size with the hypoconulid medial and slightly extended posteriorly. No features of this dentition are outside the range of variation of the well-known *P. primaevus*. As shown in figures 3, 4, and 5, its size is well within the range of Graybull *P. primaevus*. Table 1 gives the measurements for both C.M. No. 12476 and A.M.N.H. No. 56053.

ORDER INSECTIVORA

FAMILY APATEMYIDAE

APATEMYS MARSH, 1872*Apatemys* sp.

Figures 6, 7

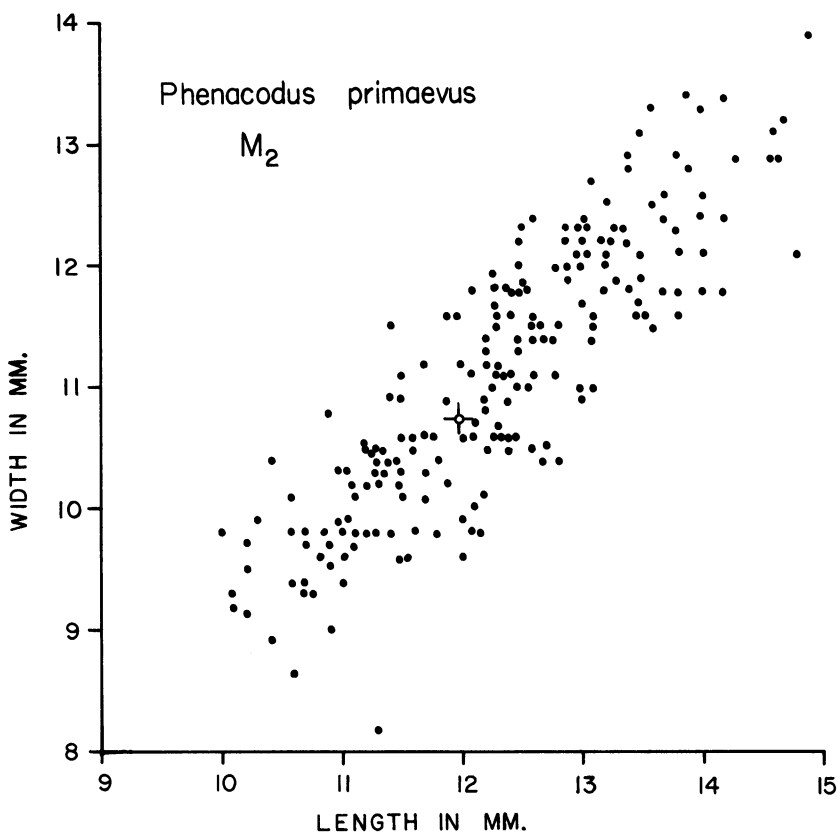
MATERIAL: A.M.N.H. No. 56046, fragment of right maxilla with M².HORIZON AND LOCALITY: Upper part of Bridger Formation, Middle Eocene, Tabernacle Butte. "*Hyopsodus* Hill" locality (Locality 5 of

FIG. 5. Scatter diagram of second lower molars showing dimensional relationships between C.M. No. 12476, represented by the open, starred circle, and an assemblage of Wasatchian specimens of *Phenacodus primaevus* from the Graybull beds (early Wasatchian) in the Bighorn Basin, Wyoming.

McGrew and others, 1959), NE. $\frac{1}{4}$, SE. $\frac{1}{4}$, SE. $\frac{1}{4}$, sect. 5, T. 28 N., R. 105 W., Sublette County, Wyoming, 1967.

DESCRIPTION: A maxillary fragment, A.M.N.H. No. 56046 (fig. 6) with the right M² in place, is assignable to *Apatemys*. Upper teeth of apatemyids are rare, therefore this is an interesting specimen; its interest is also enhanced by the presence of much of the maxillary bone.

TABLE 1
MEASUREMENTS (IN MILLIMETERS) OF *Phenacodus* SPECIMENS

	Tooth	Length	Anterior Width	Posterior Width
A.M.N.H. No. 56053	M ²	11.0	13.6	11.8
C.M. No. 12476	P ₄	12.0	8.6	8.6
	M ₁	12.0	9.8	10.1
	M ₂	12.0	10.7	10.0
	P ₄ -M ₂	37.0	—	—

No species assignment is attempted for A.M.N.H. No. 56046. All three presently valid species of middle Eocene *Apatemys*, *A. bellus* Marsh, *A. bellulus* Marsh, and *A. rodens* Troxell, are based on lower teeth. No upper teeth are yet definitely associated with any of these species. *Apatemys bellus* and *A. bellulus* are quite similar in size, differing by only about 10 to 15 per cent (based on the measurements given by Gazin, 1958, p. 89). They are also presumed to be separable on the basis of the number of roots and size of P₄, although this particular feature may well be merely intraspecific variation. It is probable that A.M.N.H. No. 56046 is referable to one of these two species (if both are valid), but without associated upper and lower teeth for comparison, it is at present impossible to tell which one. A review of the Eocene Apatemyidae planned by the senior author may help resolve this situation.

The dental morphology and size of A.M.N.H. No. 56046, shown in figure 6A, 6B, and 6C, compares favorably with that of U.S.N.M. No. 17765, a maxilla with M¹⁻³, illustrated in McKenna (1963, p. 34, fig. 5), which is referred only to *Apatemys* sp. The measurements of A.M.N.H. No. 56046, along with the Yale specimens to be discussed below, are given in table 2.

M² preserved in A.M.N.H. No. 56046 is characterized by the following features: large prominent parastyle and metastyle, separated by a

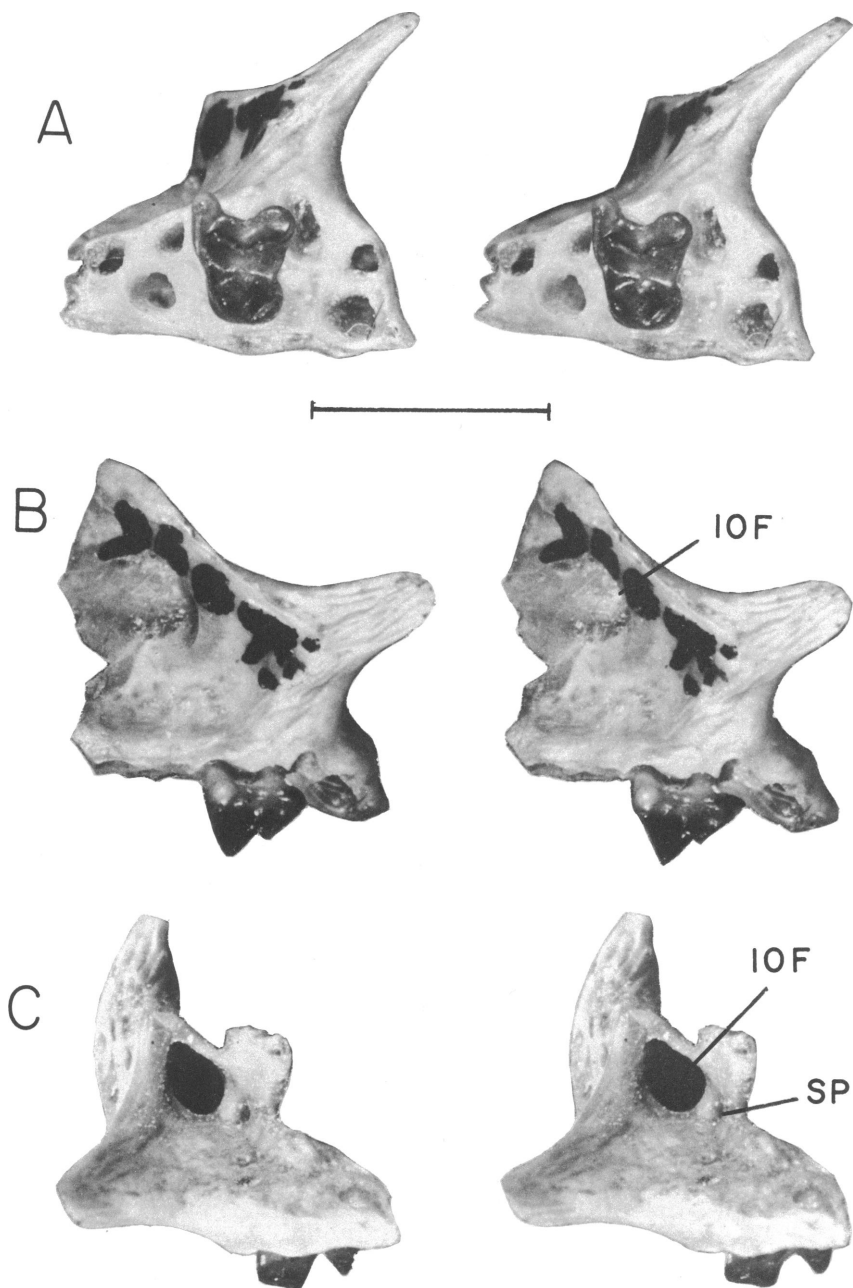


FIG. 6. A. A.M.N.H. No. 56046, *Apatemys* sp., occlusal view, showing M² in place. B. Labial side with anterior end to the left. The process directed to the upper right is the zygomatic process of the maxillary bone. IOF = infraorbital foramen. C. Lingual view, anterior end to the rear left. IOF = infraorbital foramen; SP = sphenopalatine duct. The line indicates a length of 5 mm.

wide ectoflexus; distinct paracrista and metacrista; paracone slightly higher than metacone; prominent protocone slightly posterior of the midline of the tooth; distinct posterointernal hypocone, smaller than any other cusp, forming a small bulge on the posterolingual flank of the protocone base; no intermediate conules; a slight posterolingual crest from the back of the protocone parallels the crest of the hypocone and has one very small cuspule, but not in the position of the metaconule;

TABLE 2
MEASUREMENTS (IN MILLIMETERS) OF UPPER TEETH OF MIDDLE EOCENE *Apatemys* SP.

	Tooth	Length	Width
A.M.N.H. No. 56046	M ²	2.2	2.6
Y.P.M. No. 16214	P ³	2.7	1.6
Y.P.M. No. 15284	M ²	2.5	2.9
	M ³	1.9	3.1
Y.P.M. No. 15267	P ³	2.5 ^a	1.4
	P ⁴	2.2	2.1 ^a
	M ¹	2.7 ^a	2.6 ^a

^a Estimated.

and a low crest on the anterior side of the central basin, extending from the protocone to the paracone-paracrista junction, elevates the anterior half of the central basin. The tooth is slightly skewed posteriorly, as the lingual alveolus, for the protocone root, is posterior to the midline of the tooth.

The fourth premolar and first and third molars of A.M.N.H. No. 56046 are represented only by empty alveoli; three are present for each molar, and the posterior two for the fourth premolar. On the basis of this evidence alone, M¹ was longer and narrower than M², and M³ was much more skewed with a reduced posterior part. The anterobuccal alveolus of M³ is transversely elongate, suggesting the presence of a root beneath at least part of the greatly enlarged parastyle. Such features of M¹ and M³ are shown in McKenna's illustration of U.S.N.M. No. 17765, as well as in the Yale *Apatemys* specimens shown in figure 7. The narrowing of the maxillary bone plus the small, closely appressed posterior alveoli for the roots of P⁴ suggests a P⁴ considerably smaller than M¹, and this is shown in the Yale material.

UPPER DENTITION OF BRIDGERIAN *Apatemys*

Three specimens from the collection of the Yale Peabody Museum permit illustration of all the recognized upper teeth of Bridgerian *Apatemys*, although they are certainly not from the same individual, and possibly not even the same species. This material adds the premolars to the molar row present in U.S.N.M. No. 17765 illustrated by McKenna. The three Yale specimens were collected by parties directed by O. C. Marsh in 1873 and 1874 in the upper Bridger Formation beds of the southern Green River Basin, in the Fort Bridger vicinity.

The third premolar, complete in Y.P.M. No. 16214 (fig. 7C) and badly spalled in Y.P.M. No. 15267 (fig. 7A) is a large, single-rooted tooth. It has a high, slightly posteriorly curved main cusp, flanked in front and behind by low cuspules. The entire tooth has a trenchant shape, with only a hint of a posterolingual expansion, which has no cuspule development. The over-all lateral appearance is leaflike. This tooth is very similar to the same tooth in late Eocene *Stehlinella* (A.M.N.H. No. 1903) and is much larger than the double-rooted P³ of early Oligocene *Sinclairiella* (P.U. No. 13585).

The fourth premolar is preserved in Y.P.M. No. 15267 (fig. 7A). It has a large buccal paracone and a well-developed parastyle. A posterior crest extends from the paracone to a weak metastyle, largely obscured by the parastyle of M¹. The lingual cusp of this tooth is broken on Y.P.M. No. 15267, but there appears to have been a moderately large protocone, similar to that seen in Wasatchian *Apatemys* material. The tooth has three roots, like the molars, with the anterolingual root rather small. It is much more molariform than P⁴ of *Stehlinella* or *Sinclairiella*, both of which have a smaller, trenchant, double-rooted P⁴. This feature is evidence for the validity of a generic separation between *Apatemys* and *Stehlinella*, a distinction which has been questioned (Gazin, 1962, p. 90).

The first upper molar is present in Y.P.M. No. 15267 (fig. 7A) as well as in U.S.N.M. No. 17765. It has a large parastyle in front of a slight ectoflexus, which is deeper than that in *Sinclairiella*. The metacone area is broken off, but judged from U.S.N.M. No. 17765, it was much like the corresponding area of M². The protocone is large and slightly lower than the buccal cusps. The hypocone is a low cusp, placed far posterolingual. Slight crests extend from the protocone to the paracone and metacone, creating a small, shallow internal basin. The tooth is three-rooted and much larger than P⁴.

The second molar is present in Y.P.M. No. 15284 (fig. 7B). It is adequately described above in the discussion of A.M.N.H. No. 56046; there are no significant differences between the two specimens.

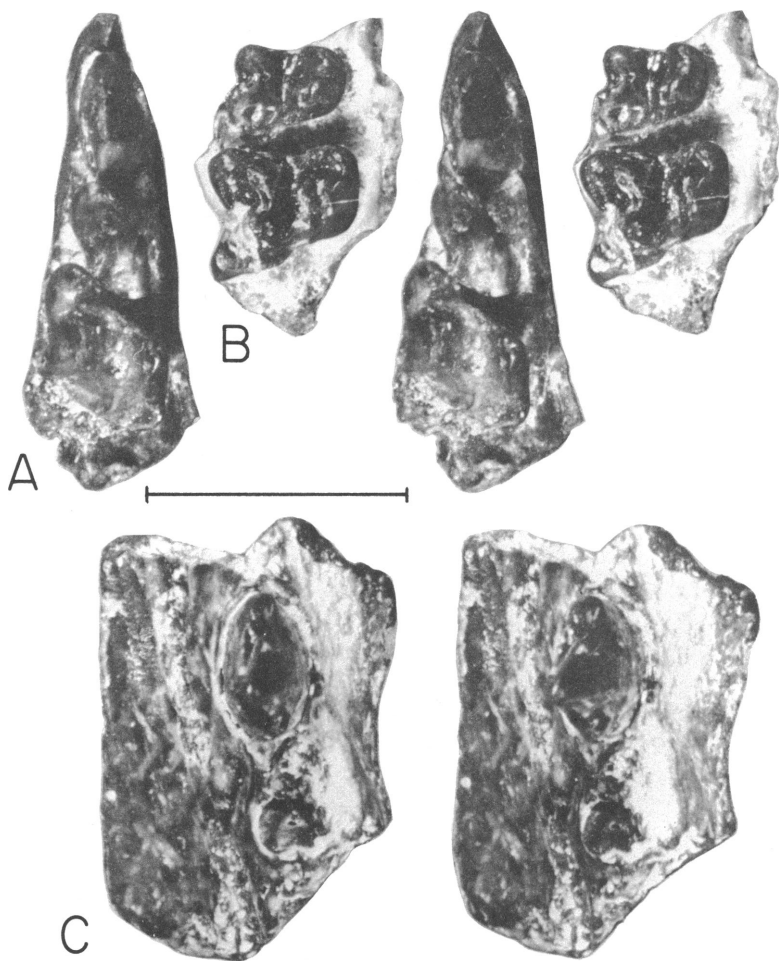


FIG. 7. Upper teeth and maxillae of *Apatemys* sp., Bridgerian of the Green River Basin, from the Yale Peabody Museum collection. A. Y.P.M. No. 15267, P³-M¹, anterior end upward. B. Y.P.M. No. 15284, M²-M³, anterior end downward. C. Y.P.M. No. 16214, P³, anterior end upward.

The line represents a length of 5 mm. for all three specimens.

The third upper molar, shown in Y.P.M. No. 15284 (fig. 7B), is smaller than M². The parastyle is partially missing in this specimen, but it was obviously large and extended far anterobuccally. The metacone and metastyle are reduced from their condition in the anterior molars. There is no true hypocone; it is suggested only by a small flat-

tened area behind the protocone. A weak crest extends along the anterior margin of the central basin, slightly raising the anterior part of the basin. This tooth also has three roots. It is quite similar to the third molar of *Sinclairiella*.

MAXILLARY BONE OF BRIDGERIAN *Apatemys*

Much of the posterior part of the maxillary bone is preserved in A.M.N.H. No. 56046, and a number of features of that bone are visible (fig. 6A, 6B, 6C). This specimen permits discussion of a small part of the Bridgerian apatemyid skull, despite the fact that no reasonably complete specimens are known from rocks of that age. Data on the skulls of Uintan *Stehlinella* (A.M.N.H. No. 1903) and Chadronian *Sinclairiella* (P.U. No. 13585) are available, but there are no published cranial data for North American apatemyids any older than Uintan. Teilhard (1921, pp. 90-93) described a skull of *Heterohyus quercyi* from the Quercy Phosphorites of France (late Eocene-early Oligocene), but the specimen has since been lost (M. C. McKenna, pers. comm.).

The infraorbital canal of A.M.N.H. No. 56046, present in its entirety, is short and wide. Its anterior end emerges above M^1 , in about the same position as in *Stehlinella* but posterior of the position in *Sinclairiella*. Just internal to the posterior opening of the infraorbital canal, within the orbit, the sphenopalatine duct exits forward from the orbit through the maxillary bone. It may be traced forward, as far as the bone is preserved, as a bony sheath.

The posterior zygomatic process of the maxillary bone is grooved, presumably for the reception of the jugal in the orbital border. Anteriorly the maxillary bone shows a pronounced narrowing into a reduced snout. A.M.N.H. No. 56046 is not adequate for estimates of the amount of maxillary-palatine, maxillary-frontal, maxillary-nasal, or maxillary-lacrimal contacts.

ORDER ?PRIMATES

FAMILY MICROSYOPIDAE

MICROSYOPS LEIDY, 1872

Microsyops sp. [cf. *annectens* (Marsh, 1872)]

Figure 8

MATERIAL: A.M.N.H. No. 56055, broken lower incisor.

HORIZON AND LOCALITY: Upper part of Bridger Formation, Middle Eocene, Tabernacle Butte. "*Hyopsodus* Hill" locality (Locality 5 of McGrew and others, 1959), NE. $\frac{1}{4}$, SE. $\frac{1}{4}$, SE. $\frac{1}{4}$, sect. 5, T. 28 N., R.

105 W., Sublette County, Wyoming, 1959.

DESCRIPTION: A broken left lower incisor found in the 1959 collection from "*Hyopsodus* Hill" now adds *Microsypops* to the Tabernacle Butte assemblage. The incisors of *Microsypops* are quite distinctive, as they have slightly serrated edges on a trowel-shaped, recumbent tooth. Figure 8 illustrates this as well as the concave upper surface of A.M.N.H. No. 56055.

A specimen such as this is virtually impossible to place in a particular species when two or more species are known to be present. However, Szalay (1969a, p. 246, table 7) recognized only *M. annectens* in the upper Bridger and illustrated a partial lower right incisor of this species on plate 54. Complete lower incisors of other species are illustrated elsewhere in his paper. As A.M.N.H. No. 56055 is the proper size for *M. annectens* and as there are no other species of *Microsypops* known from the late Bridgerian, the specimen from Tabernacle Butte is tentatively assigned to that species.

ORDER ARTIODACTYLA

FAMILY DICHOBUNIDAE

SUBFAMILY DIACODEXINAE GAZIN, 1955

NEODIACODEXIS ATKINS, NEW GENUS

TYPE: *Neodiacodexis emryi* Atkins, new species.

KNOWN DISTRIBUTION: Upper Bridger Formation, Middle Eocene, western Wyoming.

DIAGNOSIS: Medium-sized artiodactyl, probably closely related to *Diacodexis* and *Tapochoerus*. P⁴ with two large, sharp cusps, slightly flattened labiolingually. M¹ and M² tritubercular; metacone and paracone co-equal in size, conical, sharp and high; paraconule and metaconule well developed, and relatively independent of the major cones; metaconule not hypertrophied; mesostyle present; cingulum interrupted lingually by rugose enamel, and tends to develop small cuspules.

Neodiacodexis emryi Atkins, new species

Figure 9

TYPE: A.M.N.H. No. 56054, left maxilla with P⁴-M², collected by Robert Emry in 1967, hence the specific nomen.

HORIZON AND LOCALITY: Upper part of Bridger Formation, Middle Eocene, Tabernacle Butte. "*Hyopsodus* Hill" locality (Locality 5 of McGrew and others, 1959), NE. ¼, SE. ¼, SE. ¼, sect. 5, T. 28 N., R. 105 W., Sublette County, Wyoming.



FIG. 8. Stereophotographs of A.M.N.H. No. 56055, *Microsyops* sp. [cf. *M. annexans* (Marsh, 1872)] lower left incisor. A. Lower (buccal) surface. B. Upper (lingual) surface.
The line indicates a length of 5 mm.

DIAGNOSIS: Sole known species of the genus. Measurements are in table 3.

DESCRIPTION OF TYPE SPECIMEN: This maxilla (fig. 9) is excellently preserved and the teeth show little evidence of wear. The enamel is dark brown and the bone of the maxilla is off-white, with a remarkably fresh appearance. The specimen was not found in association with other material, such as tarsal elements, so the placement in the order Artiodactyla is based only on dental morphology.

The fourth upper premolar has a large conical protocone with a well-developed crista on its anterior border. A small tubercle is situated in the

TABLE 3
MEASUREMENTS (IN MILLIMETERS) OF *Neodiadocodexis emryi*

	Tooth	Length	Width
A.M.N.H. No. 56054	P ⁴	5.1	5.9
	M ¹	5.9	6.9
	M ²	6.0	7.5
	P ⁴ -M ²	21.7	—

middle of the postcingulum. Both cusps of P^4 are high and sharp, and appear slightly flattened labiolingually.

The first and second upper molars have a tritubercular pattern. The paracone and metacone are about equal in size, rather high and pointed, with a paracrista, centrocrista, and metacrista present on the sides of the otherwise conical cusps. A deep trigon basin is formed by the high metacone, paracone, and protocone. A small mesostyle is present. The conules are well developed and about equal in size. The paraconule is situated anterior to a line from the paracone to the protocone, and the

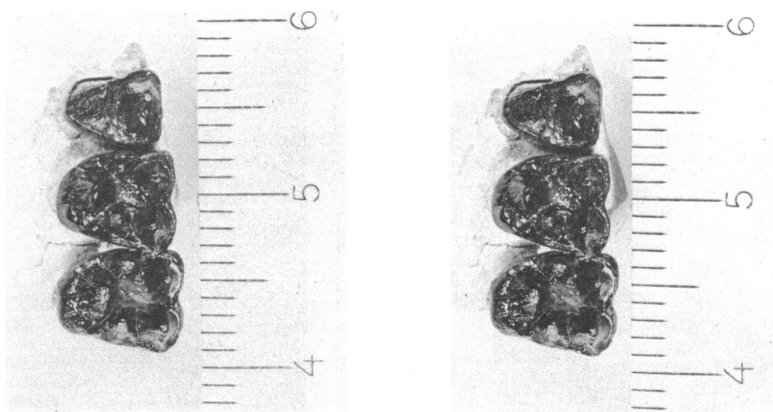


FIG. 9. Stereophotographs of occlusal view of A.M.N.H. No. 56054, *Neodiacodexis emryi*, maxilla with P^4 - M^2 . The rule is marked in millimeters.

metaconule is situated slightly posterior to a line from the metacone to the protocone.

The cingulum is continuous, except for a slight lingual interruption by enamel rugosity. A number of small tubercles rise from the cingulum. One (the pericone) is situated on the precingulum between the protocone and paraconule, a second on the postcingulum between the protocone and metaconule, and a third tubercle is on the postcingulum just internal to the second. This third tubercle is in the position of a hypocone, but since it is no larger than the other tubercles and because the crown retains a triangular shape, the teeth are regarded as tritubercular. The protocone is lower but more massive than the paracone and metacone and rather rugose on its internal surface. The enamel of all the teeth is finely crenulated.

AFFINITIES: The upper molars of other Bridger artiodactyls are quadri-

tubercular, either through the development of a cingular hypocone, as in *Homacodon*, *Microsus*, and *Antiacodon*, or by hypertrophy and relocation of the metacone, as in *Helohyus* (Gazin, 1955, p. 20). The M^2 described above has the same dimensions as that of *Diacodexis robustus*, A.M.N.H. No. 15510, described by Sinclair (1914, p. 294). *Neodiacodexis* molars closely resemble those of *Diacodexis* in their tritubercular form: high, sharp cusps; development of paraconule and metaconule; and general appearance. The reference of A.M.N.H. No. 56054 to a new genus is based on the presence of a mesostyle in M^1 and M^2 (a feature not present in *Diacodexis*), larger conules than those of *Diacodexis*, the crenulated enamel and rugose internal surface of the protocone, the tendency for development of cuspules on the cingula, and a difference in the basic outline of the upper molars. *Diacodexis* upper molars have a characteristic lopsided outline, giving the impression that the more lingual part of the tooth is pushed posteriorly whereas the labial part remains in line. *Neodiacodexis* lacks this lopsided outline.

The *Neodiacodexis* maxilla and dentition were also compared with the upper dentition of *Hexacodus*, a genus thought to be in the lineage of *Homacodon*, a genus with well-developed molar hypocones. The teeth of *Hexacodus* are considerably more rectangular than those of *Neodiacodexis*. There is no apparent close relationship between *Hexacodus* and *Neodiacodexis*, and they are here placed in different subfamilies.

Neodiacodexis does compare favorably with *Tapochoerus* (McKenna, 1959), a Uintan dichobunid artiodactyl. Although the molars of *Tapochoerus* lack mesostyles, this genus appears to be derived from the same lineage as *Neodiacodexis*. *Diacodexis* of the Wasatchian, *Neodiacodexis* of the Bridgerian, and *Tapochoerus* of the Uintan form a fairly coherent temporal and morphologic series that could provide an ancestry for the early Oligocene Leptochoeridae. This may not be a direct linear relationship, but the morphologic similarities strongly suggest that these genera belong to the same subfamily.

The subfamily Diacodexinae is now extended to include the later genera *Neodiacodexis* and *Tapochoerus*. Previously the Diacodexinae were limited to the Wasatchian and included only *Wasatchia*, *Bunophorus*, and *Diacodexis*, with the last occurrence in the Lost Cabin fauna.

Tapochoerus, with its affinity to *Neodiacodexis* and thus the earlier diacodexines, is moved to the Diacodexinae from the Homacodontinae. At the time *Tapochoerus* was assigned to the Homacodontinae (McKenna, 1959), *Neodiacodexis* was not yet known, nor were the upper molars of *Hexacodus*, the presumed predecessor of *Tapochoerus*. *Hexacodus* is now known to be too far advanced dentally to be closely related to *Tapochoerus*.

DISCUSSION

The sediments at Tabernacle Butte belong to the upper Bridger Formation, on the basis of both lithostratigraphic and biostratigraphic evidence. The fossiliferous levels, in a tuffaceous sandy mudstone similar to upper Bridger Formation rocks in the central and southern parts of the Green River Basin, are in a graben downdropped between limbs of the Continental Fault system. The magnitude of this faulting cannot be determined precisely, but is on the order of 250–300 feet at this, the western end of the system (McGrew and others, 1959). Northwest of Tabernacle Butte, within the graben block and several hundred feet lower than the Tabernacle Butte localities, West has made large collections of early Bridgerian (Bridger B) mammals from Bridger Formation strata considerably less tuffaceous than those at Tabernacle Butte (West, [In press b]). On the upthrust side of the fault the early Bridgerian Laney Shale Member of the Green River Formation is in faulted contact with the lower Bridger Formation, and 20 miles to the northwest and considerably below the Laney Shale Member, Lost Cabin (late Wasatchian) mammals have been found in the arkosic facies of the New Fork Tongue of the Wasatch Formation (West [In press a]).

The fauna collected at the various upper Bridger Formation Tabernacle Butte localities (enumerated in McGrew and others, 1959, pp. 124–125, fig. 1), is late Bridgerian in age. McGrew and others, (1959, pp. 125–126) noted the geochronologic significance of each species in the original list, and the subsequent papers, cited earlier, have added to and modified that list. Following is a revised list for the mammalian assemblage, combining all the published information on the fauna and recent taxonomic revisions which affect the classification.

CLASS MAMMALIA

Infraclass Marsupialia

Order Marsupicarnivora

Family Didelphidae

Peratherium sp. (cf. *P. innominatum* Simpson, 1928)

Peratherium knighti McGrew, 1959

Peratherium sp.

Infraclass Eutheria

Order Insectivora

Family Palaeoryctidae

Didelphodus altidens (Marsh, 1872)

undescribed apternodontine (includes indeterminate soricid discussed by Simpson in McGrew and others, 1959)

Family Leptictidae

Palaeictops bridgeri (Simpson, 1959)

- Family Erinaceidae
 - Centetodon pulcher* Marsh, 1872
 - Centetodon bacchanalis* (McGrew, 1959) (generic assignment questionable)
 - Geolabis*, sp. [cf. *G. marginalis* (Cope, 1873)]
 - Scenopagus edenensis* (McGrew, 1959)
- Family Nyctitheriidae
 - Nyctitherium velox* Marsh, 1872
- Family Adapisoricidae
 - Talpavus* sp. (cf. *T. nitidus* Marsh, 1872)
- Family Apatemyidae
 - Apatemys* sp.
- Order Chiroptera
 - undetermined family, genus, and species
- Order Primates
 - Family Omomyidae
 - Washakius insignis* Leidy, 1873
 - Family Microsypidae (family uncertainly assigned to the Primates)
 - Microsyps* sp. [cf. *M. annectens* (Marsh, 1872)]
 - Uintasorex parvulus* Matthew, 1909
- Order Edentata
 - Family Epoicotheriidae
 - Tetrapassalus mckennai* Simpson, 1959
- Order Rodentia
 - Family Ischyromyidae
 - Paramys delicatior* Leidy, 1873
 - Paramys* sp. (cf. *P. excavatus* Loomis, 1907)
 - Paramys wyomingensis* (Wood, 1959)
 - Leptotomus* sp.
 - Reithroparamys delicatissimus* (Leidy, 1873)
 - Family Sciuravidae
 - Sciuravus nitidus* Marsh, 1871
 - Taxymys lucaris* Marsh, 1872
 - Tillomys senex* Marsh, 1872
- Order Condylarthra
 - Family Hyopsodontidae
 - Hyopsodus lepidus* Matthew, 1909
 - Family Phenacodontidae
 - Phenacodus primaevus* Cope, 1873
- Order Dinocerata
 - Family Uintatheriidae
 - Uintatherium* sp.
- Order Perissodactyla
 - Family Equidae
 - Orohippus* sp. (large form)
 - Orohippus* sp. (small form)
 - Family Brontotheriidae
 - Telmatherium cultridens* (Osborn, Scott and Speir, 1878)
 - Manteoceras manteoceras* (Osborn, 1899)

Family Helaeletidae

Hyrachyus sp. (cf. *H. eximius* Leidy, 1871)

Order Artiodactyla

Family Dichobunidae

Helohyus validus Marsh, 1872*Neodiacodexis emryi* Atkins (the present paper)

The presence of *Phenacodus* among all the Bridgerian mammals listed above is unexpected. All prior work has indicated that the Phenacodontidae did not survive into the Bridgerian in North America, although *Phenacodus* is present in the Lutetian (approximately early Bridgerian) of western Europe (Russell, 1968). No phenacodonts have been reported from the poorly known early Tertiary faunas of eastern Asia.

The phenacodonts *Ectocion* and *Phenacodus* were common and significant members of virtually all known early Eocene faunas of North America, although their importance diminished considerably toward the end of Wasatchian time. Wasatchian collections, which have shown the nature of the later phenacodont record in North America, include extensive assemblages from the Bighorn and Wind River basins and smaller collections from elsewhere in Wyoming, as well as in Colorado and New Mexico.

Strata of Bridgerian age are known from a more restricted area than are the Wasatchian beds, and are centered in southwestern Wyoming and adjacent areas. The Green River and Washakie basins have been intensively prospected since the 1870's, whereas less work has been done in other areas. No specimens of *Phenacodus* have been reported previously from Bridgerian strata in any of these areas.

Neodiacodexis is the first occurrence of an artiodactyl with tritubercular molars in the middle Eocene Bridgerian fauna, but with *Tapochoerus* known from the Uintan and *Diacodexis* from the Wasatchian, its presence is not unexpected.

The unexpected discovery of *Phenacodus* at Tabernacle Butte may be explained in several ways. First, it is possible that the tooth was accidentally introduced. Although human error is always possible, and the chance for admixture of materials from various localities and levels does exist, this probably did not happen. Because of the geographic location of the Tabernacle Butte collecting area, collecting parties do not work it and a Wasatchian locality on the same day. As it is common practice to sort and label in the evening the production of each day to prevent any confusion, Wasatchian specimens would be most unlikely to find their way into the Tabernacle Butte locality or collection. A.M.N.H. No. 56053 does not have the general appearance of a Wasatchian specimen; aside from the above-mentioned surface encrustation it is similar

to all other specimens from "*Hyopsodus* Hill" in color and preservation.

Second, the tooth might have been introduced in material reworked from older beds and redeposited at Tabernacle Butte late in the Bridgerian. The nature of the Tabernacle Butte sediment, generally fine, volcanic-rich sandstone with the only large clasts being volcanic-rich clay fragments derived from the slumping of contemporaneous stream banks, indicates this possibility to be remote. During the Bridgerian in the northern Green River Basin, sediments of Wasatchian age were being buried beneath Bridger Formation sediments, not being exhumed. Erosion, which has exposed both the Wasatch Formation and the Bridger Formation in the area, took place much later, during the past few million years.

If the specimen had been brought in as reworked material from beds of Wasatchian age, it is probable that some of the more common late Wasatchian mammals, such as *Lambdaotherium*, *Hyracotherium*, *Meniscotherium*, and *Hyopsodus miticulus* would also be present. No Tertiary beds earlier than Lost Cabin age are known to occur within 20 miles of Tabernacle Butte, and those are not in a place from which sediment, even if it were being eroded during the Bridgerian, would have been carried to Tabernacle Butte.

Third, and the conclusion favored here, is that A.M.N.H. No. 56053 does indeed represent a late Bridgerian *Phenacodus*. The lack of previous reports¹ of such a late occurrence of this genus probably reflects the facts that the genus was rare at this time, as well as that its occurrence might be governed by any number of undecipherable paleoecologic variations. The possibility that C.M. No. 12476 represents another post-Lost Cabin *Phenacodus* lends some support to the suggestion of the persistence of the genus into the middle Eocene in North America.

The recognition of late occurrences of *Phenacodus* and the presence of a new diacodexine at Tabernacle Butte is indication of the continual improvement of the fossil record. As samples become larger and more environments and localities are sampled, the temporal and geographic ranges of many animals are being enlarged.

A number of such extensions of early Tertiary mammalian ranges have recently been discussed. Morris (1965; 1968) described a new species of *Hyracotherium* from the late Paleocene Punta Prieta beds of Baja California. Prior to this announcement, the presence of *Hyraco-*

¹One tooth in West's Bridger B collection mentioned earlier, P.M. No. 15847, may prove to be an aberrant lower third or fourth premolar of *Phenacodus*; this identification is uncertain, and does not suffice to establish positively the presence of *Phenacodus* in the lower Bridger strata of the northern Green River Basin.

therium was considered a positive indicator of Wasatchian time. Morris' discovery and interpretation was strengthened by Jepsen and Woodburne (1969) who likewise reported a Paleocene horse, but from the late Paleocene of the Bighorn Basin of Wyoming. At the other end of the spectrum, Robinson, Black and Dawson (1964) reported a late Eocene multituberculate, *Ectypodus* sp., from the Wind River Basin; the multituberculates were previously assumed to have become extinct early in the Wasatchian. Additional evidence for this extension into the late Eocene was found by Black (1967) who recovered multituberculates from the late Eocene Climbing Arrow Formation of southwestern Montana.

Phenacodus and the Diacodexinae are now added to the list of early Tertiary taxa for which the temporal range is greatly extended by recent discoveries. The continued collecting effort at Tabernacle Butte is proving most fruitful, as numerous new discoveries have been made since the first compilation of paleontologic work in the area (McGrew and others, 1959). Further collection and interpretation of situations such as this should lead to an improved reconstruction of the environments and faunas of the early Tertiary.

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