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Paleontology and Geology of the Bridger Formation, Southern Green River Basin, Southwestern Wyoming. Part 7. Survey of Bridgerian Artiodactyla, including description of a skull and partial skeleton of *Antiacodon pygmaeus*.

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Paleontology and Geology of the Bridger Formation, Southern Green River Basin, Southwestern Wyoming. Part 7. Survey of Bridgerian Artiodactyla, including description of a skull and partial skeleton of *Antiacodon pygmaeus*.

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ABBREVIATIONS

Collections are indicated by the following abbreviations:
AMNH—American Museum of Natural History, New York, NY;
ANSP—Academy of Natural Sciences, Philadelphia, PA;
CM—Carnegie Museum of Natural History, Pittsburgh, PA;
MPM—Milwaukee Public Museum, Milwaukee, WI;
PU—Princeton University, Princeton, NJ;
TMM—Texas Memorial Museum, University of Texas, Austin, TX;
USNM—U.S. National Museum of Natural History, Washington, D.C.;
YPM—Peabody Museum, Yale University, New Haven, CT.

ABSTRACT

Five genera and nine species of dichobunid artiodactyls have been recovered from the Bridger Formation. Recent collecting has produced new materials of all species but *Neodiacodexis emryi*. Of particular importance is a skull and partial skeleton of the the uncommon homacodontine *Antiacodon pygmaeus*. This new material is described and illustrated and numerical data for all Bridgerian artiodactyls is made available. Middle Eocene artiodactyls represent the termination of the initial bunodont episode of artiodactyl evolution and suggest the initiation of the selenodont radiation which was dominant in the late Eocene.

INTRODUCTION

Artiodactyls are uncommon elements in the fauna of the Bridger Formation. Gazin (1976) reported only 53 artiodactyls among 3151 identified specimens or 1.6% of the U.S. National Museum Bridger Formation collection. Two more were found by K.D. Rose (pers. comm., 1983). The present collection, with its emphasis on collection of small vertebrates via screen-washing, contains a far lower percentage; to date 39 artiodactyl specimens have been recognized in a collection of approximately 15,000 specimens. In addition there are 41 specimens in the American Museum collection and 51 in the Yale collection. The vast majority of these 186 specimens are isolated teeth, jaw fragments or readily recognizable pedal elements (astragli). There are few associations of dentitions and postcranial elements and only five skulls are known, two of *Homacodon,* one of *Helohyus* and two of *Antiacodon* (one of the latter reported and described below).

Sinclair (1914) wrote the seminal paper on Bridger Formation artiodactyls. In it he consolidated the inadequate and often conflicting reports of Cope and Marsh and added substantial materials collected by the American Museum of Natural History at the turn of the century. He did not, however, provide clear diagnoses of the various artiodactyl taxa. Gazin (1955) constructed a key to the Eocene Artiodactyla which is an important aid in identification. The diagnoses given below are derived and modified from that key with additional data from recently collected specimens. Subsequent work has dealt with Bridgerian artiodactyls either as preliminaries to the late Eocene radiation (Gazin, 1955; Golz, 1976; Black, 1978), as small parts of large faunas (Robinson, 1966; McGrew *et al.,* 1958; West, 1973, 1982; West and Atkins, 1970) or as the subjects of basicranial anatomy studies (Coombs and Coombs, 1982).

All five genera and nine species of Bridger Formation artiodactyls fit comfortably in the primitive family Dichobunidae, characterized by bunodont dentitions, some with upper molar hypocones and some without, generally small size and four or five toes. The Dichobunidae are commonly broken into at least three (Gazin, 1955) and up to five (Van Valen, 1971) subfamilies. Species thus far known from the Bridger Formation are placed in the subfamilies Diacodexinae, Homacodontinae, and Helohyinae.

The paucity and low diversity of Bridger Formation artiodactyls stands in marked contrast with their abundance and rapidly increasing diversity in later Eocene rocks (Gazin, 1955; Golz, 1976; Black, 1978). The Dichobunidae continue on into the Uintan, apparently simultaneously giving rise to several groups of more advanced selenodont artiodactyls. The development of selenodonty now may be traced back into the late Bridgerian Homacodontinae.

This paper surveys the major collections of artiodactyls from the Bridger Formation, illustrates most of all the species, and gives simplified dental morphometric data. The combined collections are neither large enough nor possess consistent enough stratigraphic data for any detailed stratigraphic analysis. Further, as is clear from the tables of dental measurements, individual sample sizes are small. In the absence of adequate data on distribution and variation, a full systematic revision is not attempted.

Bridger Formation Artiodactyls

Family Dichobunidae
- Subfamily Homacodontinae
  - *Microsus cuspidatus*
  - *Antiacodon pygmaeus*
  - *Antiacodon venustus*
  - *Homacodon vagans*
- Subfamily Helohyinae
  - *Helohyus plicodon*
  - *Helohyus milleri*
  - *Helohyus lentus*
- Subfamily Diacodexinae
  - *Neodiacodexis emryi*
  - *Neodiacodexis* sp.

REPOSITORIES AND LOCALITIES

All the newly collected specimens reported here were recovered by field parties under my direction between 1970 and 1981. Those found between 1970 and 1972 are the property of the American Museum of Natural History; those collected subsequent to 1972 are in the collection of the Milwaukee Public Museum. All localities for these specimens are designated in the Appendix by MPM numbers; detailed locality data is available in MPM files. Older specimens (those collected prior to my study) are also listed in the appendix; locality data is abbreviated from the various museum catalogues and is frequently incomplete and/or cryptic. The general geology and distribution of localities and collecting areas within the Bridger Formation may be found in West (1976) and references therein.

Systematic Review
Order Artiodactyla
Family Dichobunidae Gill 1872
Subfamily Homacodontinae Peterson 1919

Diagnosis: Small bunodont artiodactyls with conical molar protocones, well-developed hypocones, and the hypoconulid of M_1 and M_2 developed from the cingulum posterior to the saddle between the hypoconid and entoconid.

Microsus Leidy 1870

Diagnosis: Upper molars lack mesostyle, possess distinct conules, and M^1 and M^2 have prominent hypocones. P_4 has a metaconid. The paraconid on M_1 is closely appressed to the metaconid and is vestigial or absent on the posterior lower molars. The hypoconulid on M_1 and M_2 is located on the posterior cingulum. The cusps are high and crescentic. M_1 length 4.2-4.6mm.

Microsus cuspidatus Leidy 1870
Fig. 1 & 2, Table 1

Holotype: ANS 10260, lower molars, Bridger B (Specimen missing [Gillette and Colbert 1976]).

Diagnosis: As for the genus.

Microsus cuspidatus, which ranges through the entire thickness of the Bridger Formation, is the smallest Bridgerian artiodactyl. *Microsus* is a typical homacodontine in the absence of a paraconid on M_3 coupled with a large conical M_3 heel and a well-developed upper molar hypocone. It is readily differentiated from *Antiacodon* by the virtual absence of a paraconid on M_2 and M_3 and the absence of upper molar mesostyles. The astragalus (Fig. 2a) shows no appreciable angulation, and the deeply grooved calcaneum has a tuber that is more than one-half the total length of the bone. Although the proximal tibia fragment of MPM 6709 is distorted, there is no indication of the presence of a proximal fibula.

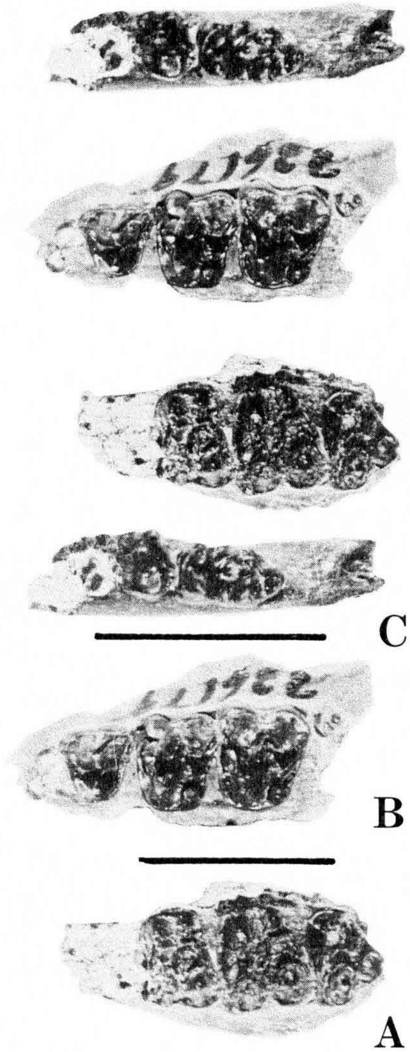


Fig. 1. Microsus cuspidatus. *Stereoscopic pairs.*
A. and B. Maxillae, right M^1-M^3, left P^4-M^2, USNM 336179. c. Mandible, right partial M_2 and M_3, MPM 6709. Scales represent a length of 10 mm.

Antiacodon Marsh 1872

Diagnosis: Upper molars with well-developed hypocone on M^1 and M^2 which may be double, a small cusp anterior to the protocone, and a small but distinct mesostyle. Conules are prominent. P_4 has a metaconid. Lower molars with metaconid reduced and paraconid and metaconid closely appressed but nonetheless distinct.

Antiacodon pygmaeus (Cope 1872)

Figs. 2-14, Tables 2 and 3

Holotype: AMNH 5006, dentary with P_4-M_1, Bridger B

Diagnosis: Small species of *Antiacodon,* M_1 length 4.3-4.4mm.

Antiacodon pygmaeus is the stratigraphically lower of the two species here regarded as valid, and is the more abundant.

Until recovery of MPM 5896 and 6721 and Rose's recognition in 1983 that USNM 336202 belongs here, *Antiacodon pygmaeus* had been known only from isolated jaw fragments and teeth. There had been no positive associations of upper and lower dentitions, and no cranial or postcranial remains could be referred to the genus with any certainty.

The three specimens mentioned above now allow positive dental associations and the description of cranial and some postcranial anatomy. Recent studies by Franzen (1981), Rose (1982 and pers. comm.) and Coombs and Coombs (1982) have greatly improved our knowledge of the biology of dichobunid artiodactyls and provide comparison for the *Antiacodon pygmaeus* materials described here. The following discussion concentrates on MPM 5896 and 6721; elements of USNM 336202 are being studied by K.D. Rose (pers. comm., March 1983).

Table 1

Measurements, in millimeters, of teeth of *Microsus cuspidatus*

	N	L	$\bar{X}$	N	W_a	$\bar{X}$	N	W_p	$\bar{X}$
P_4	2	4.0-4.3	4.15	2	2.2-2.5	2.35	4	2.5-2.9	2.78
M_1	4	4.1-4.4	4.28	4	2.3-2.7	2.5	4	2.5-2.9	2.78
M_2	5	4.0-4.6	4.3	5	2.4-3.2	2.9	6	2.8-3.4	3.2
M_3	4	4.7-5.4	5.05	4	2.8-3.2	3.03	4	2.7-3.2	2.95
P^4	1	4.1		1	4.0				
M^1	1	4.3					1	5.3	
M^2	1	4.8		1	5.8		1	5.4	
M^3	1	4.2		1	5.2				

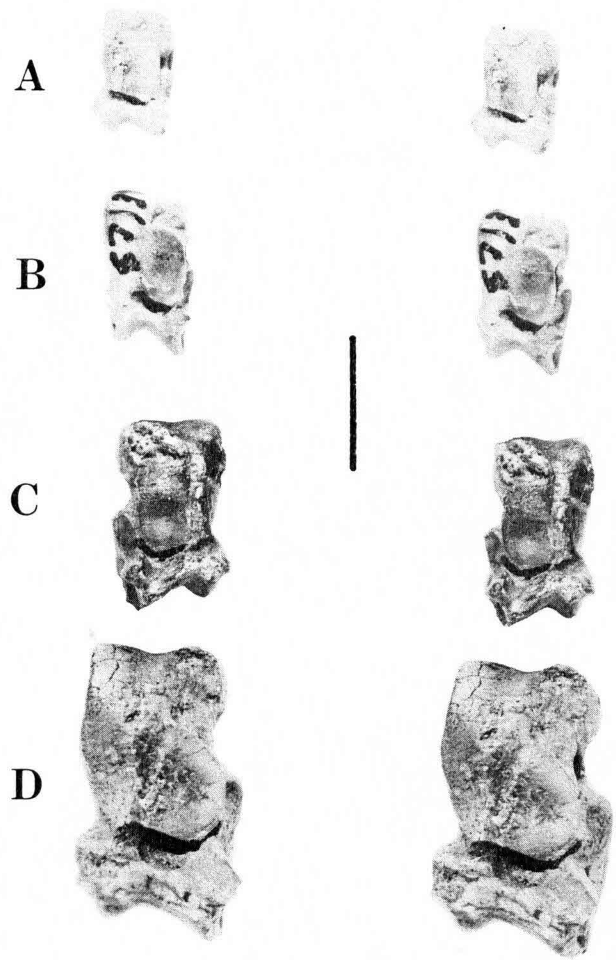


Fig. 2. *Bridgerian artiodactyl astragali. Stereoscopic pairs.*
A. Microsus cuspidatus, *USNM 108128.*
B. Antiacodon pygmaeus, *MPM 6713.*
C. Homacodon vagans, *MPM 6716.*
D. Helohyus lentus, *MPM 6701.*
Scale represents a length of 10 mm.

SKULL
Figs. 3-5

MPM 5896 is dorsoventrally crushed to an estimated 50% of its natural depth; this estimate is confirmed by the uncrushed skull of USNM 336202. While this has resulted in the artificial opening of some cranial sutures, most of the bones are readily recognizable and their position and relationships comprehensible. The snout has been subjected to some lateral distortion.

The skull of *Antiacodon* is relatively delicate. It is snub-nosed with an arcuate cheek tooth row. The snout is not drawn out or narrowed, as it is in *Homacodon* (AMNH 12695), but is proportionately more like that of early Eocene *Diacodexis* (AMNH 16141). The dorsal surface of the skull is relatively planar, without a noticeable interruption of the dorsal plane in the vicinity of the orbits.

Although the crushing of the snout of MPM 5896 makes interpretation of this area difficult, the nasal bones are narrow, terminating anteriorly above an apparently shallow nasal incision. Posteriorly, the frontals broaden between and behind the orbits. Medial to the anterior end of the orbits are the origins of the prominent supraorbital sulci. They are directed antero-posteriorly and flatten and open out at the frontal-nasal suture. Each has a single opening. In contrast, the supraorbital sulci of *Diacodexis* have paired openings, are shorter, and considerably less obvious. The posterolateral part of the frontal produces a shelf that overlaps the dorsal border of the orbit.

The lacrimal bone is equally divided between its external preorbital exposure and its internal exposure on the anterior wall of the orbit. The single nasolacrimal canal opens internally in the orbit.

The premaxillary and anterior end of the maxillary are missing. Posteriorly, the maxillary contains, immediately dorsal to the anterior root of P^3, a small, round infraorbital foramen. It is somewhat smaller than the equivalent structure in *Diacodexis;* the infraorbital canal is not preserved in either skull of *Homacodon*.

The zygomatic arch is wide and delicate, with approximately equal contributions from the jugal and squamosal. There is no postorbital bar; rather there is a weak dorsal projection from the posterior end of the jugal widely separated from an equally weak ventrolateral process from the posterolateral corner of the frontal bone. The other early and middle Eocene artiodactyl skulls are inadequately preserved to allow interpretation of zygomatic morphology.

The cranium is bulbous (Fig. 4) with a modest sagittal crest only along the posterior area of the parietal suture; it merges into a prominent but narrow supraoccipital crest. This supraoccipital crest-

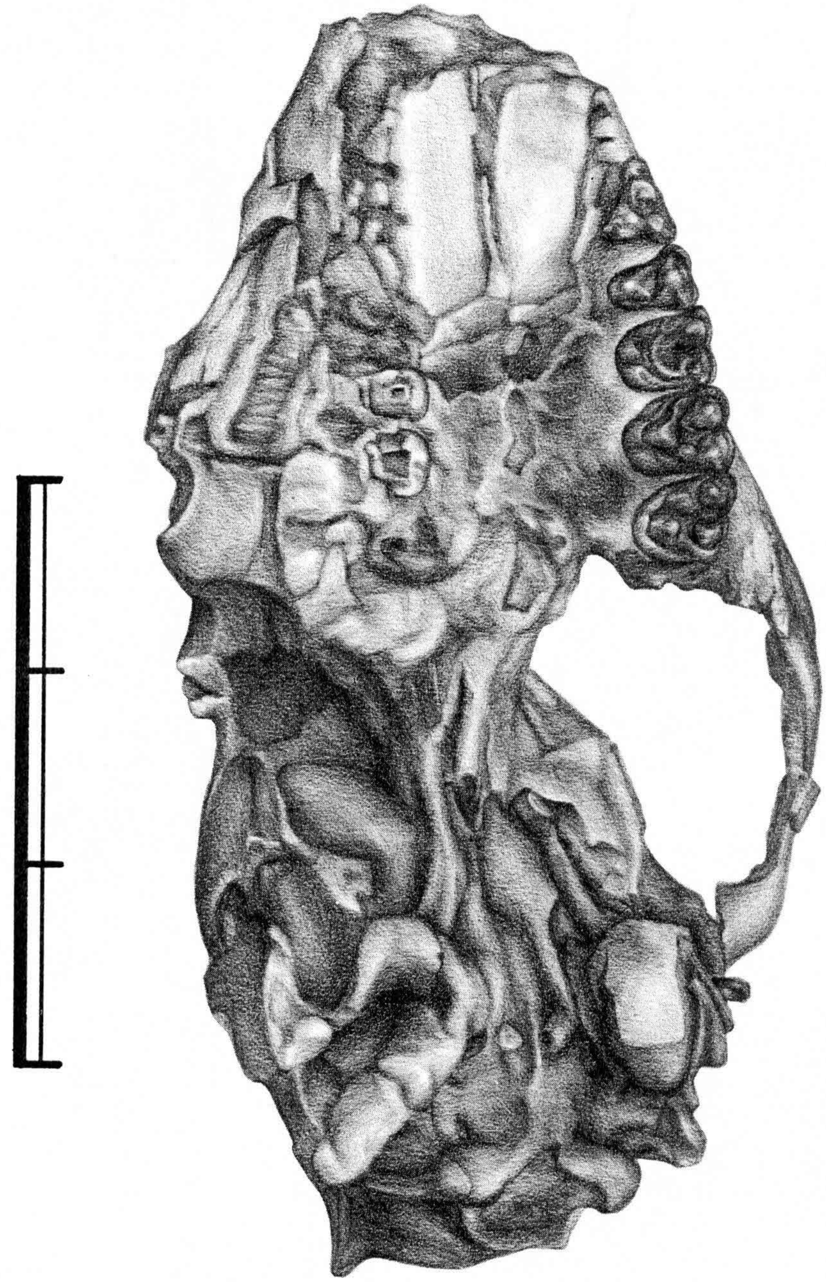


Fig. 3. Antiacodon pygmaeus *skull, palatal view, MPM 5896. Scale units represent a length of 10 mm.*

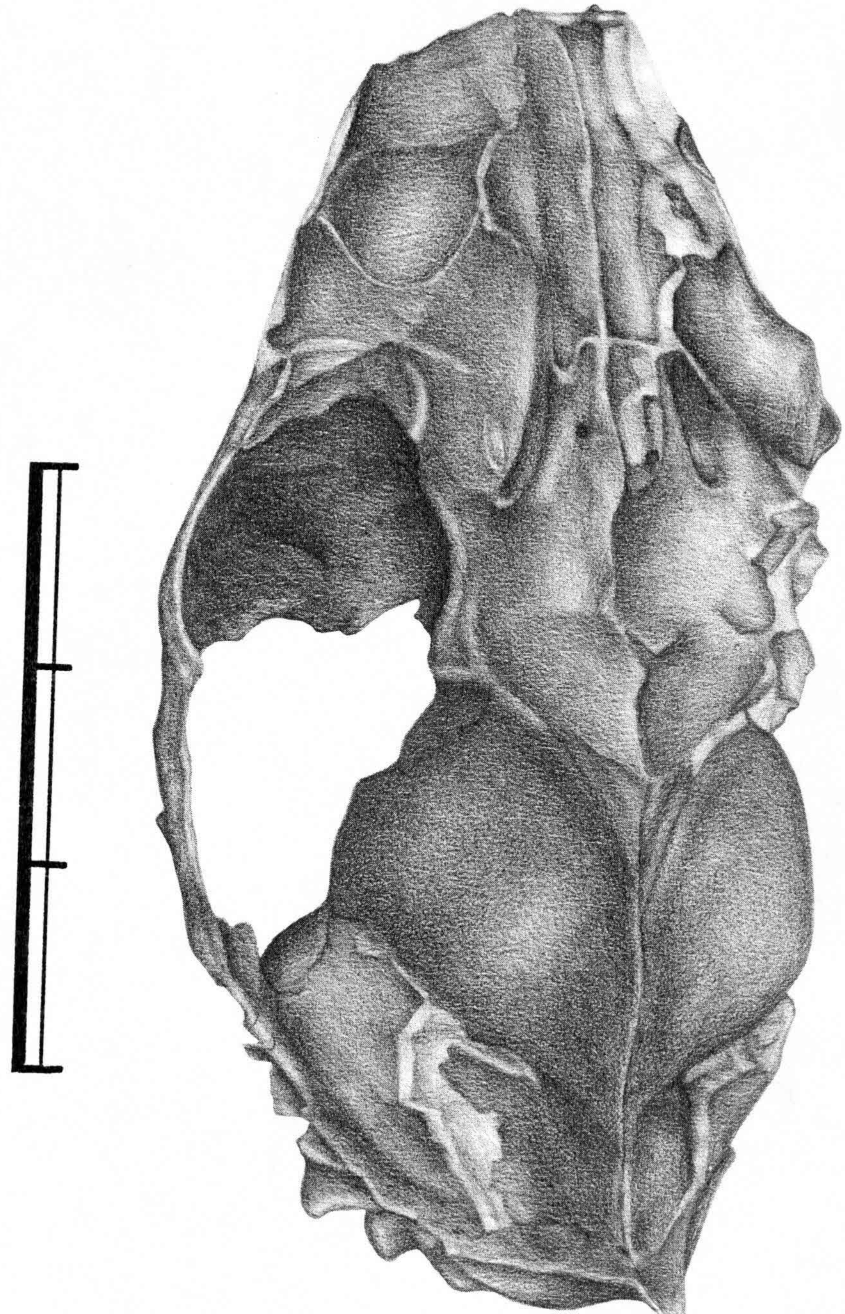


Fig. 4. Antiacodon pygmaeus *skull, dorsal view, MPM 5896. Scale units represent a length of 10 mm.*

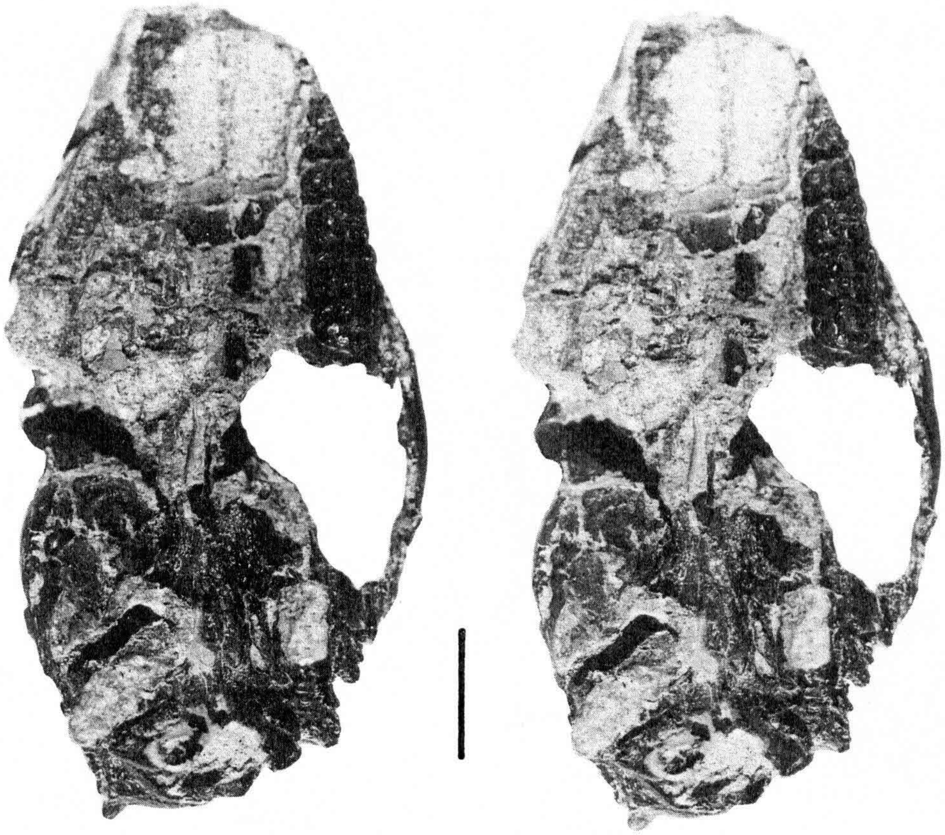


Fig. 5. Antiacodon pygmaeus *skull, stereoscopic views of palate and basicranium, MPM 5896. Scale represents a length of 10 mm.*

ing in *Antiacodon* is considerably more prominent than it is in *Diacodexis* and the posterior part of the *Antiacodon* braincase shows more constriction.

The glenoid fossa is flat and broad, buttressed posteriorly by a thin extended postglenoid process and medially by the posterior end of the pterygoid process. Its surface is slightly above the occlusal plane of the upper dentition, as in the other Eocene dichobunids.

Details of the *Antiacodon* palate are not available because of distortion and poor preservation in MPM 5896 (Figs. 3 and 5).

The study of Eocene bunodont artiodactyl basicrania by Coombs and Coombs (1982) pointed out their general similarity. *Antiacodon* is a typical bunodont, although it clearly has ossified bullae. Bullae were not preserved on any of the skulls studied by Coombs and Coombs, although ridges and rugosities on the promontoria suggested their presence. The retention of a complete bulla on the left side of MPM 5896 and parts of the bulla on the right side preclude complete comparison with the basicranium of *Diacodexis*.

The *Antiacodon* basisphenoid is wide medially, and narrows both posteriorly (where it is pinched between flanges from the basioccipital), and anteriorly, where it forms the border of the median lacerate foramen, as in *Diacodexis* and *Homacodon*. The contact between the lateral edge of the basisphenoid and the medial border of the alisphenoid is marked by the pterygoid process of the alisphenoid. This process is directed antero-medially from the medial edge of the glenoid fossa and posteriorly from the internal border of the glenoid fossa. It becomes more prominent anteriorly.

The foramen ovale, doubled in *Antiacodon,* is located in the lateral wall of the pterygoid process antero-medial to the anterior border of the glenoid fossa. This opening is single and located slightly more posteriorly in *Diacodexis*.

A prominent, though delicate, postglenoid process buttresses the rear of the flattened glenoid fossa. Posteriorly it is penetrated by a small vertically-directed postglenoid foramen. The opening of the postglenoid foramen is obscured by the antero-external part of the tympanic tube, a feature not noted on other Eocene bunodont artiodactyls (Coombs and Coombs, 1982).

The external auditory meatus is roofed by the squamosal and anteriorly, ventrally, and posteriorly enclosed in a cylindrical tube, preserved on the right side only, which extends onto the lateral surface of the bulla. This tube flares moderately laterally, and is quite unlike structures recorded in the external auditory meatus of other Eocene artiodactyls. Where the tube is missing on the left side, a minor depression between the external auditory meatus and the middle ear cavity may be regarded as a semilunar depression. Posterior to the external auditory meatus, a prominent ventrally-directed process is formed of the mastoid process of the petrosal fused with the lateral part of the exoccipital. The process is composed primarily of the mastoid, which is roughly triangular in shape and has a substantial external ventral exposure. The mastoid is grooved on its external surface, but no such pattern can be seen on the ventromedial side as in *Diacodexis*. No mastoid foramen is evident and a stylomastoid foramen was not found in MPM 5896.

The promontorium, globular and bulbous, unlike that of either *Diacodexis* or *Homacodon*, is exposed on both sides. On the left, the medial part of the promontorium is visible medial to the bulla. The posterior lacerate foramen lies posterior to the promontorium and is connected with the median lacerate foramen by a groove along the medial edge of the promontorium, as in *Diacodexis*, although, because of the shape of the promontorium in *Antiacodon*, the groove is much more restricted. Posterior to the posterior lacerate foramen are paired condylar foramina, and an opening possibly referable to the hypoglossal foramen is near the internal base of the paraoccipital process.

The bulla, well preserved on the left side, is bulbous and extended laterally by the prominent tympanic tube. It covers the medial part of the promontorium, though there is no prominent ridge or rugose area on the promontorium marking the contact area as is presumed in *Diacodexis* (Coombs and Coombs, 1982). The presence of the bulla on the left side, and bone destruction in the middle ear on the right, preclude detailed study of the middle ear anatomy of *Antiacodon*.

In summary, the organization of the basicranium of *Antiacodon* is generally similar to that of other Eocene bunodont artiodactyls studied by Coombs and Coombs (1982). They present extensive comparisons of *Diacodexis, Gobiohyus, ?Helohyus,* and *Homacodon* with a great variety of North American, European, and Asian taxa and concluded that all four are at essentially the same stage of organization. All have external mastoid exposure, a conservative primitive character lost in most advanced artiodactyls. None of the specimens examined by Coombs and Coombs retain a bulla but MPM 5896 suggests it was present and is merely a postmortem loss in each.

There are minor differences among the taxa, but most appear to have neither functional or phylogenetic significance. Coombs and Coombs (1982) were able, however, to suggest that *Diacodexis* and *Homacodon* are part of a group separate from *Gobiohyus* and *?Helohyus* (the Helohyidae of their usage, Helohyinae of this paper). *Antiacodon* has more in common with the *Diacodexis-Homacodon* group, confirming the unity of the Homacodontinae and suggesting a close affinity with the Diacodexinae.

MANDIBLE

MPM 6721 preserves both mandibles (Figs. 6 & 7). The left one, more complete, retains P_3-M_3 and a pair of alveoli for P_2. This specimen is compatible with the features described by Burke (1968) from a Powder Wash locality specimen (CM 10930). In particular it shows double-rooted P_2 and P_3 and mental foramina beneath both P_2 and P_3. MPM 6721 is preserved somewhat farther posteriorly than CM 10930 and confirms the presence of a well excavated masseteric fossa, and a gently rising ascending ramus. It also suggests a very long, straight angular process. The coronoid height and position of the condyle cannot be determined from this specimen.

DENTITION

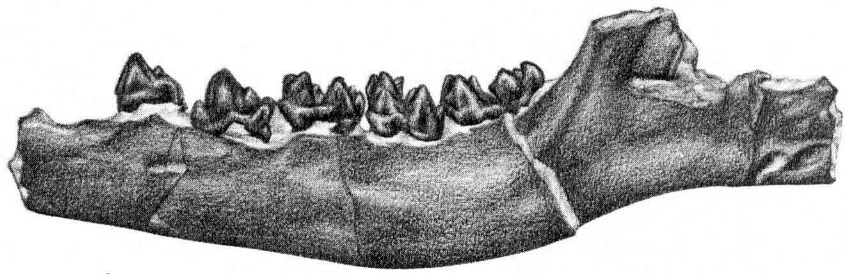
Figs. 3, 5-7

P^3-M^3 are present in both MPM 5281 and MPM 6721 (Fig. 6a). P^3 (Figs. 3 and 5) is prominently triangular and three-rooted, with anterior, posterior and internal cingula. The paracone is high, almost connate with the lower, elongate metacone. A low prominent parastyle rises from the anterior cingulum; the posterior cingulum is equally prominent but is not developed into a cusp. The protocone is lower than the other two primary cusps and is quite separate from them.

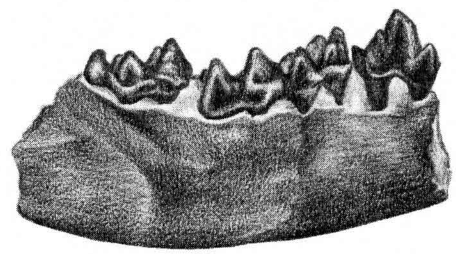
P^4 is three-rooted, but shorter anteroposteriorly and broader labiolingually than P^3. The cingulum is weak externally, and modest on the other sides. The high triangular protocone is flanked anteriorly by a low parastyle. There is neither a metacone nor a posterior style. The protocone is low with a low crest going antero-externally to the parastyle, and a low median crest extends through the central basin to the internal base of the paracone.

M^1 and M^2 are very similar. Each has a strong anterior cingulum, with a prominent parastyle and minor mesostyle, slightly better developed on M^2. The paracone and metacone are subequal, aligned, with anterior and posterior crests to the anterior and posterior styles. The protocone, with an anterior cingulum on its internal side, is lower than the metacone. A well-developed posterior cingulum has a paired hypocone as an outgrowth on its posterior end. The conules are strong. The paraconule is anterior of the paracone-protocone line, with an anterior-external crest extending to just inside the parastyle and a low crest to the center of the protocone. The metaconule is just posterior to the metacone-protocone line, with a

Fig. 6. Antiacodon pygmaeus, *stereoscopic views of dentition, MPM 6721.*
A. Left maxilla, P^4-M^3.
B. Left mandible, P_3-M_3.
Scale represents a length of 10 mm.



A



B

Fig. 7. Antiacodon pygmaeus, *lateral views of dentaries of MPM 6721.*
A. Left.
B. Right.
Scale units represent a length of 10 mm.

Table 2
Measurements, in millimeters, of teeth of *Antiacodon pygmaeus*

	N	L	$\bar{X}$	N	W_a	$\bar{X}$	N	W_p	$\bar{X}$
P_4	2	4.8-5.0	4.9	2	2.6-3.1	2.85			
M_1	8	4.3-4.5	4.4	8	2.6-2.9	2.8	8	2.9-3.3	3.11
M_2	6	4.1-4.8	4.38	6	3.1-3.4	3.22	6	3.3-3.7	3.48
M_3	3	5.2-5.7	5.47	3	3.3-3.4	3.33	3	3.1-3.2	3.13
P^4	2	3.7-3.8	3.75	2	4.5	4.5			
M^1	2	4.1-4.6	4.35	2	4.8-4.9	4.85	2	4.6-4.7	4.65
M^2	2	4.4-4.8	4.6	2	5.5-5.7	5.6	2	5.1-5.2	5.15
M^3	2	4.2-4.5	4.35	2	4.8-5.0	4.9			

similar crest to the posterior cingulum, but there is no connection with the protocone.

The subtriangular M^3 lacks a hypocone and the paracone is much larger than the metacone. The parastyle and mesostyle are better developed than in M^1-M^2. The protocone is approximately equal to the metacone, and the cingulum does not carry around the internal face of the tooth.

P_2 (not illustrated) is a narrow triangle with a high central cusp and a low posterior one. There is a posterior stylid and no cingulum.

P_3 (Fig. 6b and 7a) is similar to P_2, but shows an incipient talonid. There is a modest metaconid on the posterior flank of the high protoconid. The anterior and posterior margins are broken.

The P_4 of MPM 6721 is just erupting (Fig. 6b and 7a). The square trigonid has a high triangular protoconid which sends a sharp crest anterior to the paraconid. There then is an extra anterior cusp on the antero-internal corner of the tooth. A postero-internal crest extends from the protoconid to the low metaconid, and a postero-external crest extends from the protoconid to the talonid cusp. A ridge at the posterior edge of the tooth makes up the posterior talonid.

M_1 and M_2 are virtually identical (Figs. 6b and 7). The high trigonid, paraconid and protoconid are approximately equal, and the metaconid is smaller. The metaconid and paraconid have crests to the protoconid, closing the basin. There is a strong anterior cingulum. The hypoconid is large with a cristid obliqua to the posterior-internal corner of the metaconid. The entoconid is isolated on the postero-lingual corner of the tooth. The median hypoconulid is separate from the posterior cingulum with a lingually-directed ramp and a low crest to the hypoconid.

The trigonid of M_3 (Fig. 6b) is similar to that of M_1 and M_2, though the basin is not quite so thoroughly closed. The cristid obliqua extends to the midpoint between the metaconid and the protoconid. The large heel (hypoconulid) has a low irregular crest to the hypoconid and a large rounded posterior cusp.

Postcranial elements

MPM 6721 includes significant parts of the hind limb skeleton of an immature *Antiacodon*. Elements preserved include both femora (neither complete), both tibiae (left complete), both calcanei, left astragalus, two terminal phalanges, three metatarsals III or IV (one missing the epiphysis), five phalanges (two complete), one metatarsal II or V (incomplete proximally), two fragmentary innominates, one patella, six caudal vertebrae, one lumbar vertebra and nine thoracic vertebrae. Epiphyses on many of these bones are not fused because of the animal's age, as noted above by the early eruptive condition of P_4. Many of these elements are duplicated by USNM 336202.

These skeletal remains of *Antiacodon* have been compared with the Eocene bunodont artiodactyls *Diacodexis* (Rose, 1982 and pers. comm.) and *Messelobunodon* (Franzen, 1981), the Oligocene hypertragulid *Leptomeryx* (FMNH UC390), and modern *Tragulus* (MPM Mammalogy 543). Where comparable elements are available, *Antiacodon* shows a high degree of similarity with *Diacodexis,* less with *Messelobunodon,* and still less with *Leptomeryx* and *Tragulus*. All, however, are the same basic type of small, long-legged artiodactyl.

Most of the available vertebrae are isolated, although one group of three thoracics remains in contact in the matrix. Thus it is not possible to determine the total number, but it is likely that *Antiacodon* had 18 to 20 trunk vertebrae as in living artiodactyls. *Messelobunodon* (Franzen 1981) has 19. The tail length is assumed to be similar to that of *Diacodexis* and *Messelobunodon,* although only six caudals are present.

Fragments of both innominate bones have been preserved, although all that is available on each side is the acetabulum and nearby parts of the ilium. The ilium shows indications of dorsal flaring as in *Diacodexis* and some tragulids, but is not preserved as far dorsally as the sacral articulation. The ilium has a broad dorsolaterally facing gluteal surface and a much narrower ventrally-facing iliac surface. There is a well-developed tuberosity on the acetabular border of the ilium, as in *Diacodexis,* but *Antiacodon* also has a deep pit between the anterior border of the acetabulum and that tuberosity. This pit contrasts with the smoother surface of *Diacodexis*. Both taxa have a deep, circular acetabulum.

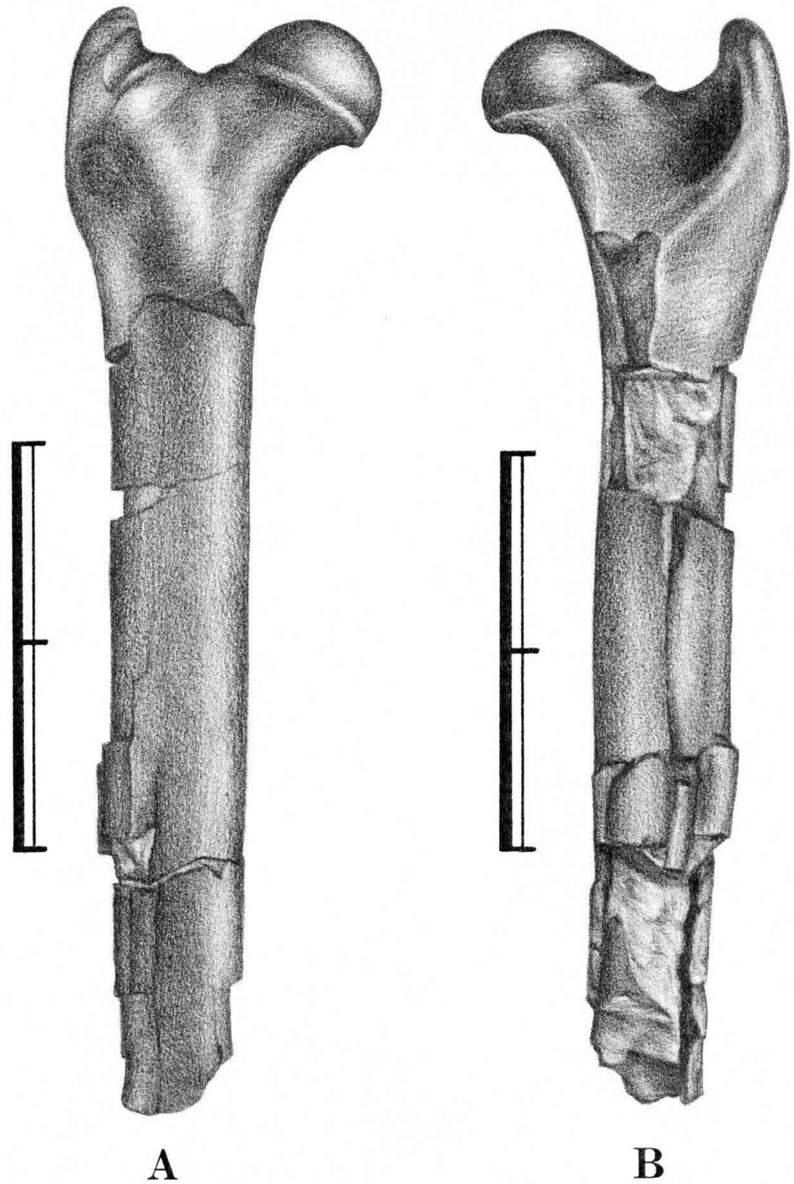
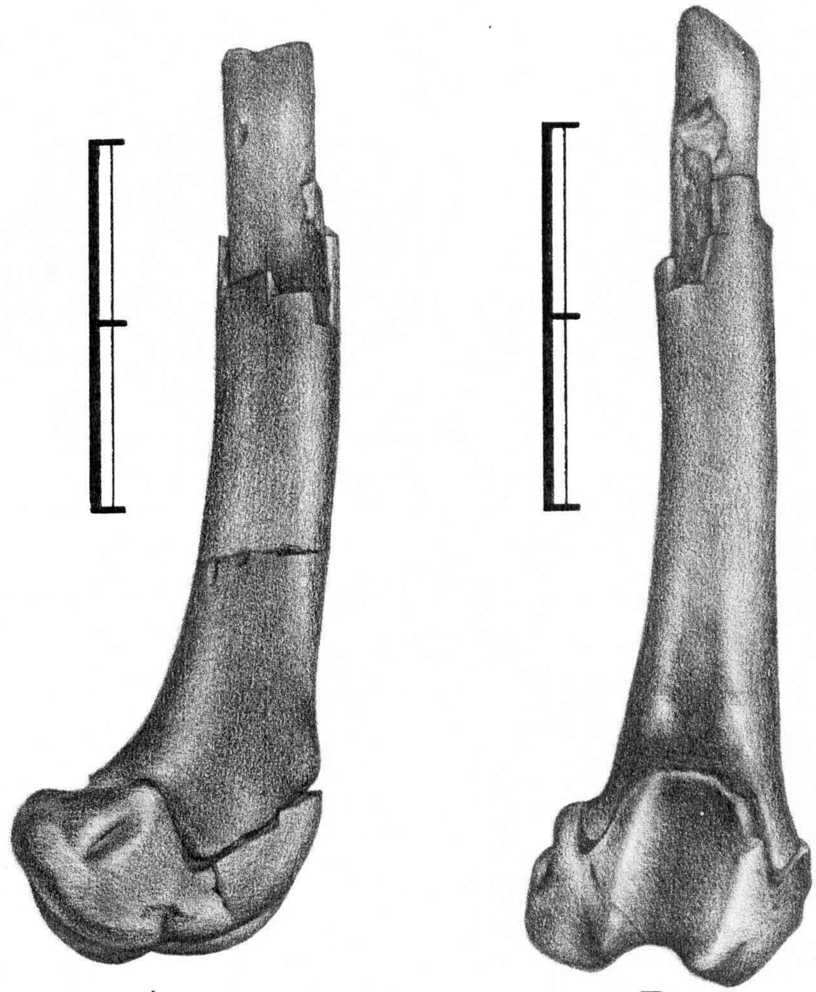


Fig. 8. Antiacodon pygmaeus, *proximal end of right femur, MPM 6721.*
A. Anterior view.
B. Posterior view.
Scale units represent a length of 10 mm.



A

B

Fig. 9. Antiacodon pygmaeus, *distal end of left femur, MPM 6721.*
A. Lateral view.
B. Anterior view.
Scale units represent a length of 10 mm.

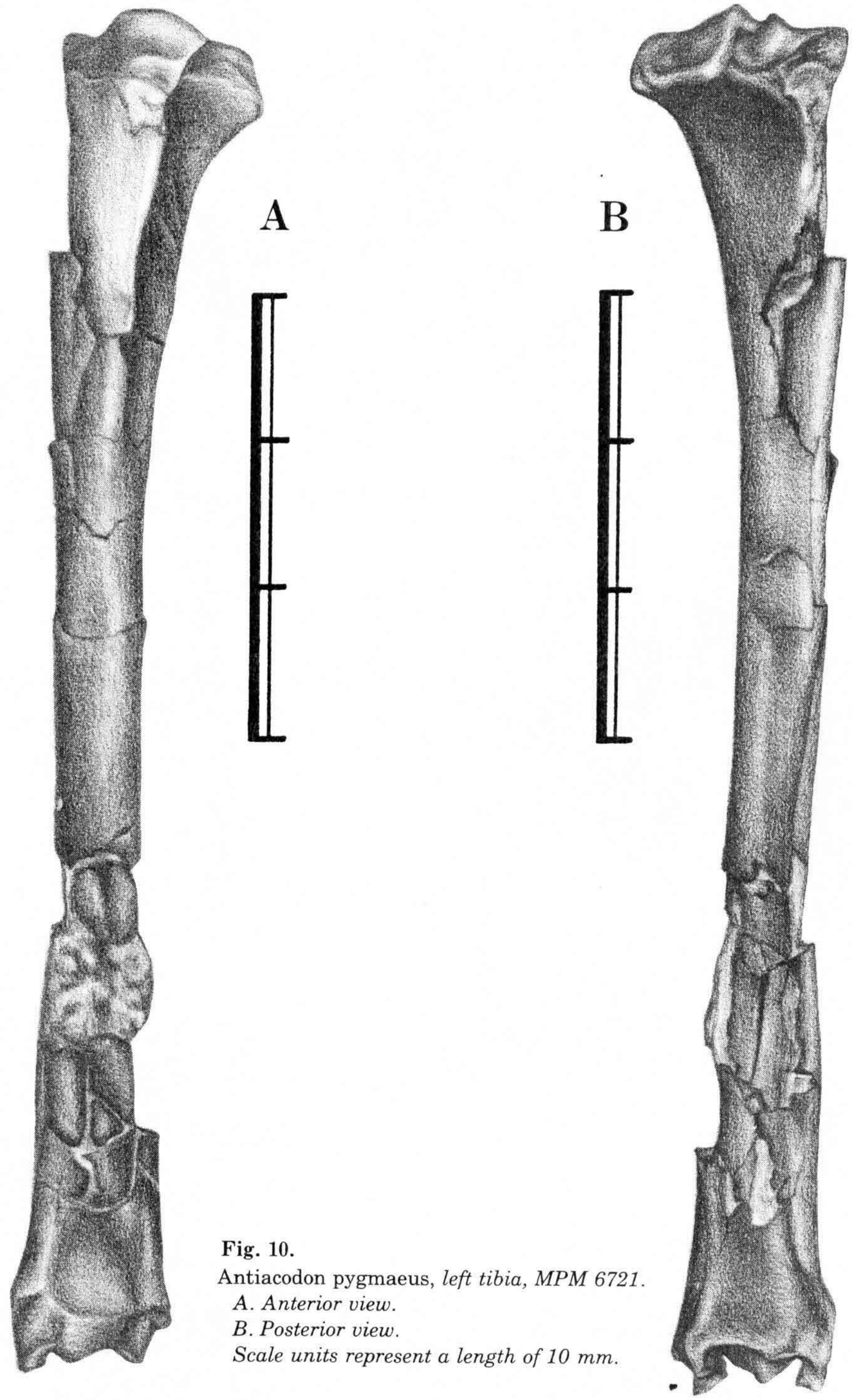


Fig. 10.
Antiacodon pygmaeus, *left tibia, MPM 6721.*
A. Anterior view.
B. Posterior view.
Scale units represent a length of 10 mm.

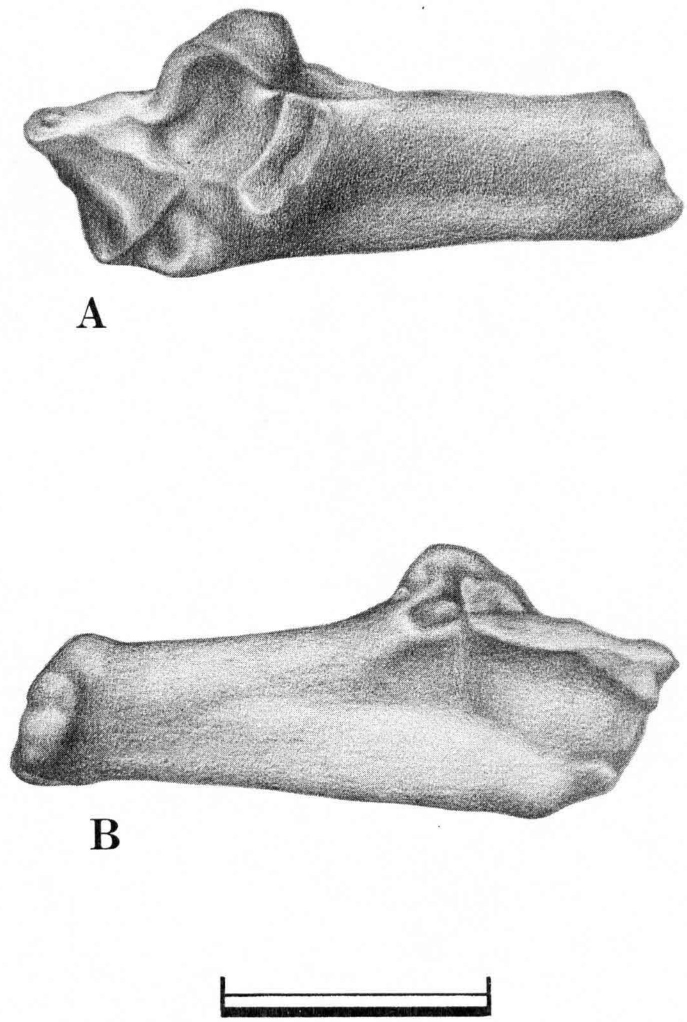


Fig. 11. Antiacodon pygmaeus, *right calcaneum, MPM 6721.*
A. Lateral view.
B. Interior view.
Scale represents a length of 10 mm.

Fig. 12. Antiacodon pygmaeus, *left astragalus, MPM 6721.*
A. Anterior view.
B. Posterior view.
Scale units represent a length of 10 mm.

Neither femur (Figs. 8 and 9) is complete, so length measurements (Table 3) are estimates. The slightly oval head has a robust neck and is broader than the femoral head in *Diacodexis*. The greater trochanter is prominent but does not project proximally past the

Table 3

Measurements (in mm) of *Antiacodon pygmaeus* (MPM 6721) with comparisons with *Diacodexis* (from Rose 1982)

Measurement	***Antiacodon*** **L**	**R**	***Diacodexis*** **(Rose 1982)**	***Antiacodon*** **as % of *Diacodexis***
Femur—length	80.0 Est	85.0 Est	70.8	113
breadth	14.2	—	11.8	120
depth distal	16.0	—	15.4	104
Patella—length	10.0		10.9	92
breadth	6.1		5.3	115
Tibia—length	89.7	—	82.6	109
breadth, prox.	15.5 Est		12.1	128
breadth, distal (incl. fibula)	10.2	10.5	—	
Max. Diameter, midshaft	5.5	5.5	5.2	106
Calcaneum—length	24.0		20.4	117
Astragalus—length	11.5		10.2	113
Metatarsal III, IV— prox. breadth	5.3	5.3		
Metatarsal II, V— prox. breadth	4.1			
Crural Index $\frac{\text{(Tibia lgth)}}{\text{(Femur lgth)}} \times 100$	112-120		117	100
Phalanges (position and number unknown)				
1. length	16.4			
prox. breadth	5.1			
distal breadth	—			
2. length	11.8			
prox. breadth	3.5			
distal breadth	2.3			
3. distal breadth	3.4			
4. proximal breadth	3.8			
5. proximal breadth	3.1			

head of the femur. There is a deeply excavated trochanteric fossa which extends farther distally than in *Diacodexis*. The lesser trochanter is broken on both specimens, but apparently had a triangular base and was of substantial size. A third trochanter is not present; a small one occurs on *Diacodexis*. The shaft is slightly curved posteriorly. The distal end of the femur is relatively broad and massive. A well-developed extensor fossa is located at the lower end of the lateral margin of the patellar groove. Several of the proportional distinctions from *Diacodexis* are likely to be ontogenetic, as MPM 6721 is a young animal with incompletely formed bones. The patellar groove is slightly shallower and broader than in *Diacodexis* and has a primary distal exposure; the patella is robust. The tibia (Fig. 10) is elongate and slender, longer than the femur giving a crural index of 112 to 120 (Table 3). It is virtually identical to that of *Diacodexis*. The fibula is synostosed distally. Although the bone is broken immediately proximal to the area of fusion, its impression can be traced about 60% of the length of the tibia. There is no indication of the presence of the proximal end of the fibula, unlike the situation in *Diacodexis*. The fibula of *Antiacodon* is a proximally incomplete splint, and thus is advanced over the condition shown by *Diacodexis*.

The calcaneum (Fig. 11) of *Antiacodon* is virtually identical to that of *Bunophorus* illustrated by Guthrie (1968). The tuber is half the length of the entire bone, and it has a deeply grooved lateral side. The calcaneum of *Diacodexis* has a deeper plantar groove.

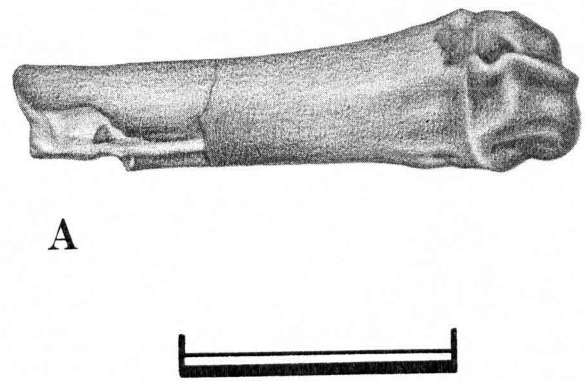
The astragalus (Figs. 2 and 12) is straighter than that of *Diacodexis*, and has a sharper tibial trochlea. The sustentacular facet is somewhat larger than in *Diacodexis*, as is the distal astragalar facet (Schaeffer 1947).

In the tarsal area, the cuboid is not fused with the navicular, a rather primitive artiodactyl condition similar to that described by Guthrie (1968) for *Bunophorus*.

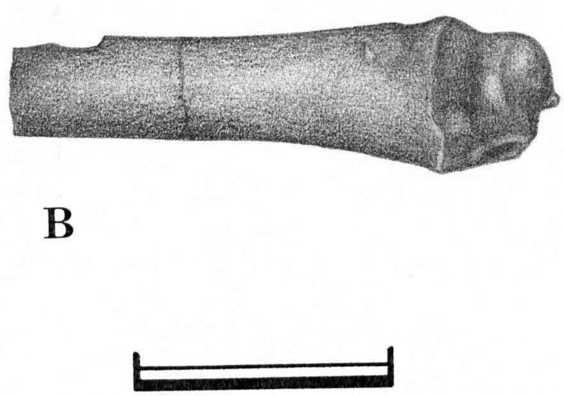
Metatarsals III and IV (Fig. 13) are the same size, although the total length cannot be measured. II and V are much smaller and presumably also much shorter. *Diacodexis* retains I; there is no evidence of its presence or absence in *Antiacodon*. The metatarsals of *Antiocodon* are substantially more robust than those of *Diacodexis*.

The phalanges are elongate, longer than in *Tragulus* and shorter than in *Messelobunodon*. The distal articular surfaces are rounded, extending well onto the dorsal surface as in all the comparison taxa. This strongly suggests unguiligrade posture for *Antiacodon*.

The terminal phalanges are somewhat flattened ventrally, but are dorsal-ventrally high and narrow. They are not flattened into hooves as in *Tragulus*, and are not as curved as in *Messelobunodon*.



A



B

Fig. 13. Antiacodon pygmaeus, *distal end of left metatarsal IV, MPM 6721.*
A. Ventral view.
B. Dorsal view.
Scale units represent a length of 10 mm.

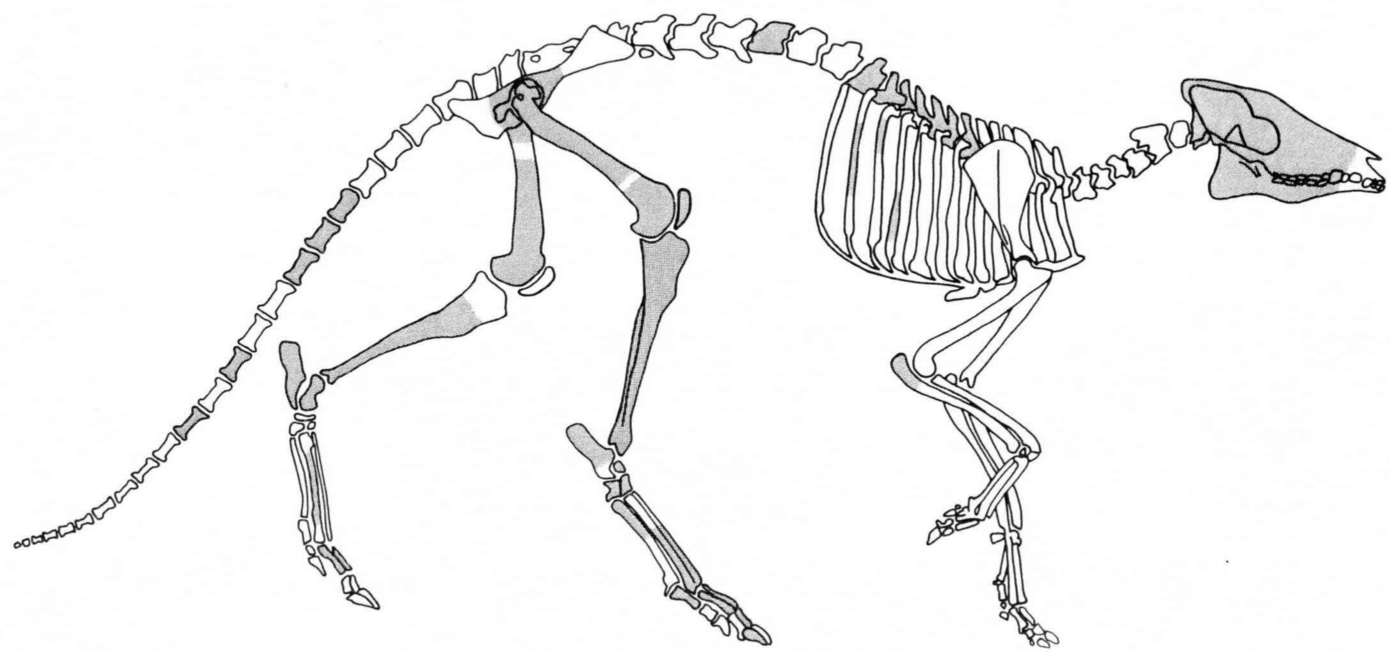


Fig. 14. *Reconstruction of the skeleton of* Antiacodon pygmaeus. *The stippled areas are represented by MPM 6721 and 5896; the remainder of the skeleton is based on* Messelobunodon *(Franzen 1981) and* Diacodexis *(Rose 1982).*

Both specimens show minor lateral grooving.

Apart from the massiveness of the patella, the incomplete fibula, and more robust metatarsals, the skeletal parts of *Antiacodon* that can be compared directly with *Diacodexis* (Rose, 1982) indicate a high degree of similarity (Table 3). Therefore in Fig. 14 *Antiacodon* is restored as a lithe, long-legged creature with highly developed cursorial locomotion. In fact, it possibly was more advanced in this respect than *Diacodexis,* based on the relatively smaller lateral toes and reduction of the fibula.

Antiacodon venustus **Marsh 1872**

Table 4

Holotype: YPM 11765, M_3, Henry's Fork (Bridger D)

Diagnosis: Large species of *Antiacodon,* M_1 length 5.0-5.1 mm.

A. venustus comprises only about one quarter of all *Antiacodon* specimens known and is differentiated from *A. pygmaeus* only by its larger size. To date it is known primarily from the upper part of the Bridger Formation.

Table 4

Measurements, in millimeters, of teeth of *Antiacodon venustus*

	N	L	$\bar{X}$	N	W_a	$\bar{X}$	N	W_p	$\bar{X}$
P_4	2	5.2-5.8	5.5	2	3.4-3.5	3.45			
M_1	3	5.0-5.1	5.03	3	3.4-3.8	3.53	3	3.6-4.3	4.0
M_2	3	5.2-5.3	5.23	3	3.2-3.9	3.57	3	3.5-4.6	4.17
M_3	4	6.1-7.0	6.33	3	3.5-3.9	3.7	3	3.5-3.6	3.53
P^4									
M^1	1	5.0		1	5.8		1	5.7	
M^2	2	5.1-5.3	5.2	2	6.7	6.7	2	6.0-6.3	6.15
M^3	1	4.0		1	6.1				

Homacodon **Marsh 1872**

Diagnosis: Upper molars with well-developed hypocone, parastyle, and conules, but lacking mesostyle. P_4 has no metaconid. Lower molars lack a paraconid (except occasionally on M_3). M_1 length 5.0-5.5 mm.

Homacodon vagans Marsh 1872
Figs. 2, 15 & 16; Table 5

Holotype: YPM 13129, skull and jaws, Henry's Fork (Bridger D)
Diagnosis: As for the genus.

Except for two suites of foot bones unassociated with teeth, specimens of *Homacodon vagans* are presently restricted to the Twin Buttes Member of the Bridger Formation (Bridger C and D) as previously noted by Gazin (1976) for the USNM collection and implied by Matthew (1909) for the older AMNH collection.

The dentition and skull of this species are rather well known from well-preserved and complete material in the American Museum collection (skull-AMNH 12695; dentary-AMNH 12138 and 12139) described by Sinclair (1914) and by the holotype skull in the Yale collection (YPM 13129). In addition, AMNH 12375 and YPM 10012 and 13129 have associated partial feet with articulated distal tibia and fibula, astragalus and calcaneum.

Both the preexisting and the recently-recovered material show *Homacodon* astragali (Fig. 2) with greater angulation than in either other Bridger homacodontine. However, similar to *Antiacodon*, the distal tibia and fibula are fused and the fibula thins rapidly proximally. Not enough tibia shaft is preserved to be able to compare apparent fibula length with that of *Antiacodon*. The tuber of the calcaneum is approximately half the length of the bone.

As the best known late Bridgerian homacodontine, *Homacodon* has been regarded as at or near the source of the sub-selenodont Uintan homacodontines (Gazin, 1955; Golz, 1976). However, typical *Homacodon* is markedly distinctive from its presumed Uintan derivatives.

Table 5

Measurements, in millimeters, of teeth of *Homacodon vagans*

	N	L	$\bar{X}$	N	W_a	$\bar{X}$	N	W_p	$\bar{X}$
P_4	3	5.1-5.4	5.23	3	2.7-2.9	2.77			
M_1	4	4.9-5.6	5.25	4	3.1-3.8	3.48	4	3.5-4.4	3.88
M_2	3	5.2-5.6	5.40	3	3.6-4.6	4.0	3	4.0-4.8	4.27
M_3	3	6.7-6.8	6.77	3	3.8-4.4	4.0	3	3.5-3.9	3.7
P^4	1	4.0		1	4.9				
M^1	2	5.0-5.2	5.3	2	5.4	5.4	2	5.4-5.5	5.45
M^2	2	5.2-5.4	5.3	2	5.8-6.4	6.1	2	5.6-6.1	5.85
M^3	2	5.0-5.4	5.2	2	6.4-6.5	6.45	2	4.9-5.0	4.95

MPM 6697 (Fig. 16) appears to partially bridge the morphologic gap between typical *Homacodon vagans* and Uintan homacodontines. It was found in 1977 at MPM locality 2188, in the upper part of the Bridger Formation 24 meters (75 feet) above the prominent Lone Tree White Layer marker bed which separates Bridger C from Bridger D (Matthew 1909). As far as can be determined from locality data at the American Museum of Natural History and the National Museum of Natural History, this specimen is probably the stratigraphically highest specimen of *Homacodon* yet collected in the Bridger Formation.

MPM 6697 is most of a left mandible, retaining P_2 and P_4-M_3 with the roots of P_1 and P_3. It thus is an adequate specimen for direct comparison with mandibles of the early Uintan homacodontines *Bunomeryx, Hylomeryx* and *Mesomeryx,* as well as with typical *Homacodon vagans* from elsewhere in the Bridger Formation.

Typical Bridger Formation *Homacodon vagans* (including AMNH 12139 from Matthew's Bridger D_2, (above the Lone Tree White Layer) has a more rounded anterior face to the trigonid, more rounded external faces to the hypoconids (producing subcrescentic cusps), and less pronounced M_3 heel than does MPM 6697. In addition, MPM 6697 has a higher degree of obliquity of the orientation of the cheek teeth relative to the line of the dentary bone. In all of these attributes, MPM 6697 is more similar to Uintan homacodontines which are distinctly "pre-selenodont" in their dental organization.

The mandible of 6697 is not advanced in morphology, as it is shallow for its entire length, shows a pronounced dorsal constriction at the base of the coronoid and, although the posterior part of the ramus is broken, the angle is probably modestly downturned. In contrast, Uintan homacodontine dentaries are distinctly deeper at their posterior ends, not constricted, and show no indication of a downturned angle.

The upper dentition of *Homacodon vagans* is best known from AMNH 12695, a skull collected in 1905 by Walter Granger "on Henry's Fork, opposite the mouth of Burnt Folk." The outcrop and vegetation pattern in that area on the south side of Cedar Mountain strongly suggest that this specimen was collected high in the Bridger C and thus from a level well below that which yielded MPM 6977. The specimen was briefly described by Sinclair in 1914, and its basicranium was exhaustively analysed by Coombs and Coombs (1982).

Dentally it does not appear to be as advanced as 6977, as the upper molars do not show prominent stylar development and retain strong hypocones. The subcrescentic internal molar cusps that are obvious in *Bunomeryx, Mesomeryx* and *Hylomeryx* are not developed in AMNH 12695.

Homacodon vagans, thus, shows several dental attributes which are predictive of the preselenodont condition of a number of genera of Uintan homacondontines, while retaining a dentary bone structure typical of middle Eocene artiodactyls. This suite of attributes corroborates previous interpretations of close relationship of Bridgerian and Uintan homacondontines and suggests that artiodactyl selenodonty in North America began developing as early as late Bridgerian time.

Subfamily Helohyinae Marsh 1877

Diagnosis: Modest-sized bunodont artiodactyls. Upper molars with hypocone small or absent and with a conical molar protocone. Mesostyle absent. P_4 lacks a metaconid; M_1 and M_2 have a weak, sometimes doubled hypoconulid in the early stages.

Helohyus Marsh 1872

Diagnosis: Upper molars with small, often indistinct cingular hypocone and a pronounced protoconule. The P_4 lacks a metaconid. The paraconid of the lower molars is distinct but located very close to the metaconid. The hypoconulid on M_1 and M_2 is weak and may be developed from the cingulum posterior to and in the saddle between the hypoconid and entoconid. Includes *Lophiohyus* of Sinclair.

This genus includes the largest of the Bridger Formation artiodactyls, and is the only one which has sympatric species. The distinction between these species is primarily size. I concur with Coombs and Coombs (1977) that *Lophiohyus alticeps* (the holotype and only speci-

Table 6

Measurements, in millimeters, of teeth of *Helohyus plicodon*

	N	L	$\bar{X}$	N	W_a	$\bar{X}$	N	W_p	$\bar{X}$
P_4	8	7.4-9.2	8.23	8	3.8-4.9	4.3			
M_1	15	7.4-9.2	8.29	15	4.8-5.6	5.26	15	5.5-6.0	5.79
M_2	16	7.7-10.0	8.94	14	5.5-7.2	6.46	15	5.6-7.3	6.68
M_3	14	9.3-13.4	11.46	13	6.1-7.4	6.88	14	5.8-6.7	6.25
P^4	1	7.7		1	7.5				
M^1	7	7.5-8.2	7.86	7	9.0-10.5	9.35	7	8.1-8.9	8.63
M^2	9	7.5-9.0	8.36	8	8.7-11.4	10.24	8	8.4-11.1	9.89
M^3	7	8.0-8.9	8.56	7	9.5-11.6	10.53			

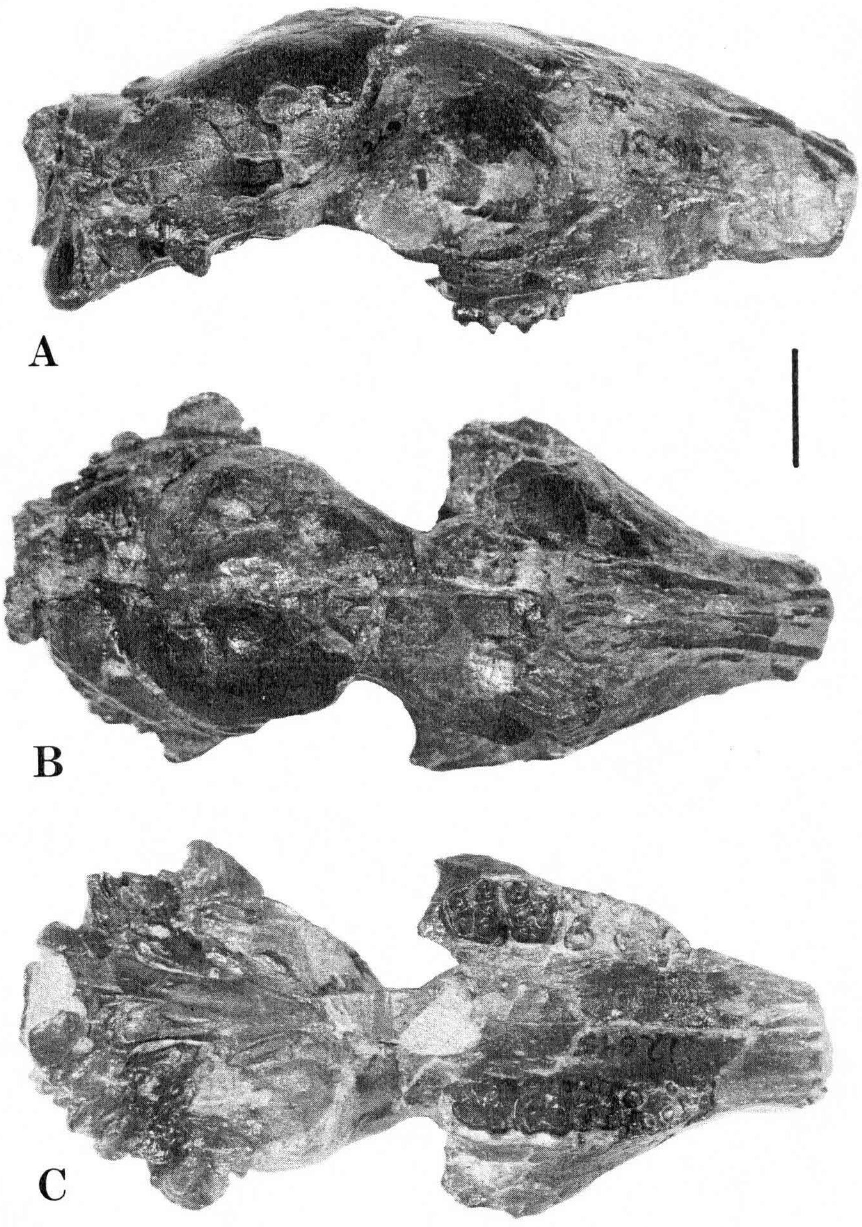


Fig. 15. Homacodon vagans *left mandible, MPM 6697.*
A. Right lateral view.
B. Dorsal view.
C. Ventral view.
Scale represents a length of 10 mm.

Fig. 16. Homacodon vagans *left mandible, MPM 6697.*
A. Occlusal, stereoscopic views, P_2, P_4-M_3.
B. Lateral view.
Scale represents a length of 10 mm.

men of which cannot be located in the American Museum) should be included within *Helohyus*. In size it is close to *H. lentus,* although the paraconid reduction and the presence of an external cingulum on the lower molars noted by Sinclair (1914, p. 279) may preclude its inclusion in that species. No material in the present collection appears referable to *"alticeps,"* so precise determination of its affinities is not possible.

The cranial anatomy of *Helohyus* is not as well known as that of either *Antiacodon* or *Homacodon*. Apart from the missing holotype of *Lophiohyus,* only a basicranium (AMNH 13079), thoroughly described by Coombs and Coombs (1982), tentatively is assigned to *Helohyus*. Materials in the present collection allow the initial asignment of postcranial materials to *Helohyus* on the basis of size.

Helohyus plicodon **Marsh 1872**
Figs. 17 & 18, Table 6

Holotype: YPM 11893, M^3, Bridger.
Diagnosis: Small species of *Helohyus*; M_1 length 7.4-9.1 mm. Includes *H. validus* of Marsh.

The species occurs through most of the thickness of the Bridger Formation. Although the available material is insufficient to serve as a statistical base, there seems to be a modest size increase through the Bridgerian, accompanied by gradual reduction in the size of the molar paraconid. Comparison of AMNH 12694 with *H. plicodon* (MPM 6807) from Loc. 2767 in the Bridger B suggests that *H. validus* can be synonymized with *H. plicodon.*

Several specimens include distal tibiae, which have a structure noticeably different from those of homacodontines. The area of distal fibula contact is clearly marked by a prominent triangular rugosity, but the fibula itself is not present. This suggests that either the fibula was reduced relative to its condition in the Homacodontinae or that it was so weakly fused that the two bones readily separated. Most of the tibia shaft is preserved in MPM 6706, and there is no suggestion of tibia-fibula contact proximal to the scar on the distal tibia. A similar condition is suggested by MPM 6708, although not nearly so much of the tibia remains.

The calcaneum tuber in *Helohyus plicodon* makes up well over 50% of the length of the bone, while the astragalus is virtually straight.

These postcranial characters taken together suggest that *H. plicodon* was still more cursorially specialized than were the species of homacodontines mentioned above, although there is no information on relative leg lengths.

Helohyus milleri Sinclair 1914
Table 7

Holotype: AMNH 12151, dentary and maxilla, C5 (Henry's Fork opposite mouth of Burnt Fork).

Diagnosis: Medium-sized species of *Helohyus*. Length of M_1 9.6-11.1 mm.

As pointed out by Sinclair in his description of the species, lower teeth differ from those of *H. plicodon* only in their slightly larger size. The new material extends the range of the species down into the Blacks Fork Member.

Table 7
Measurements, in millimeters, of teeth of *Helohyus milleri*

	N	L	$\bar{X}$	N	W_a	$\bar{X}$	N	W_p	$\bar{X}$
P_4	3	9.2-10.1	9.6	3	3.6-4.8	4.27			
M_1	3	9.6-11.1	10.23	3	5.7-7.1	6.43	3	6.2-7.6	6.97
M_2	3	10.7-11.5	11.20	3	6.5-8.2	7.57	3	7.3-8.2	7.83
P^4	1	7.8		1	8.0				
M^1	1	10.6							
M^2	2	10.6-11.0	10.8	2	12.6-14.8	13.7	2	12.0-13.7	12.85
M^3	2	9.4-11.5	10.45	2	12.2-15.0	13.6			

Helohyus lentus (Marsh) 1871
Figs. 2 and 19; Table 8

Holotype: YPM 11892, M_3, upper Bridger.

Diagnosis: Larger species of *Helohyus*. Average M_1 length is 12.1 mm.

This, the largest Bridger Formation artiodactyl, is found only in the upper part of the Twin Buttes Member, Bridger D. Material found during the present investigation, a single lower molar, does not contribute to understanding of *H. lentus*.

The holotype (YPM 11892) and three other specimens (USNM 17711, AMNH 12150 and 108122) are lower teeth or dentary fragments. Sinclair (1914) illustrated a maxillary fragment with M^1 and M^2 (PU 10084) and suggested that it may be referable to *H. lentus*. That specimen occludes effectively with USNM 17711, confirming Sinclair's suggestion based solely on isolated M_3s. The teeth of PU 10084 are typically helohyine in the avsence of a hypocone and the

Fig. 17. Helohyus plicodon *right mandible, stereoscopic views, AMNH 108123. Scale represents a length of 10 mm.*

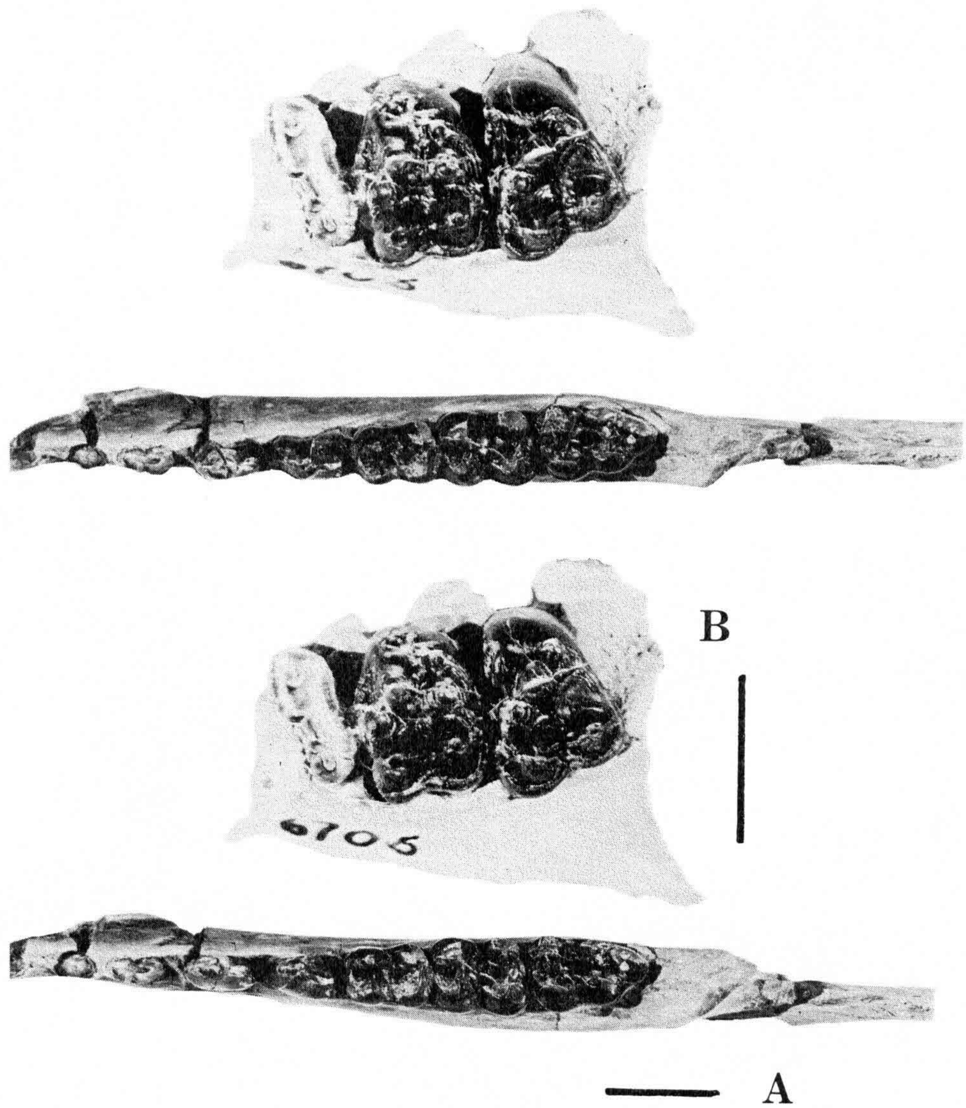


Fig. 18. Helohyus plicodon *dentitions, stereoscopic views.*
A. MPM 6707, left P_3-M_3.
B. MPM 6706, right M^2-M^3.
Scales represent a length of 10 mm.

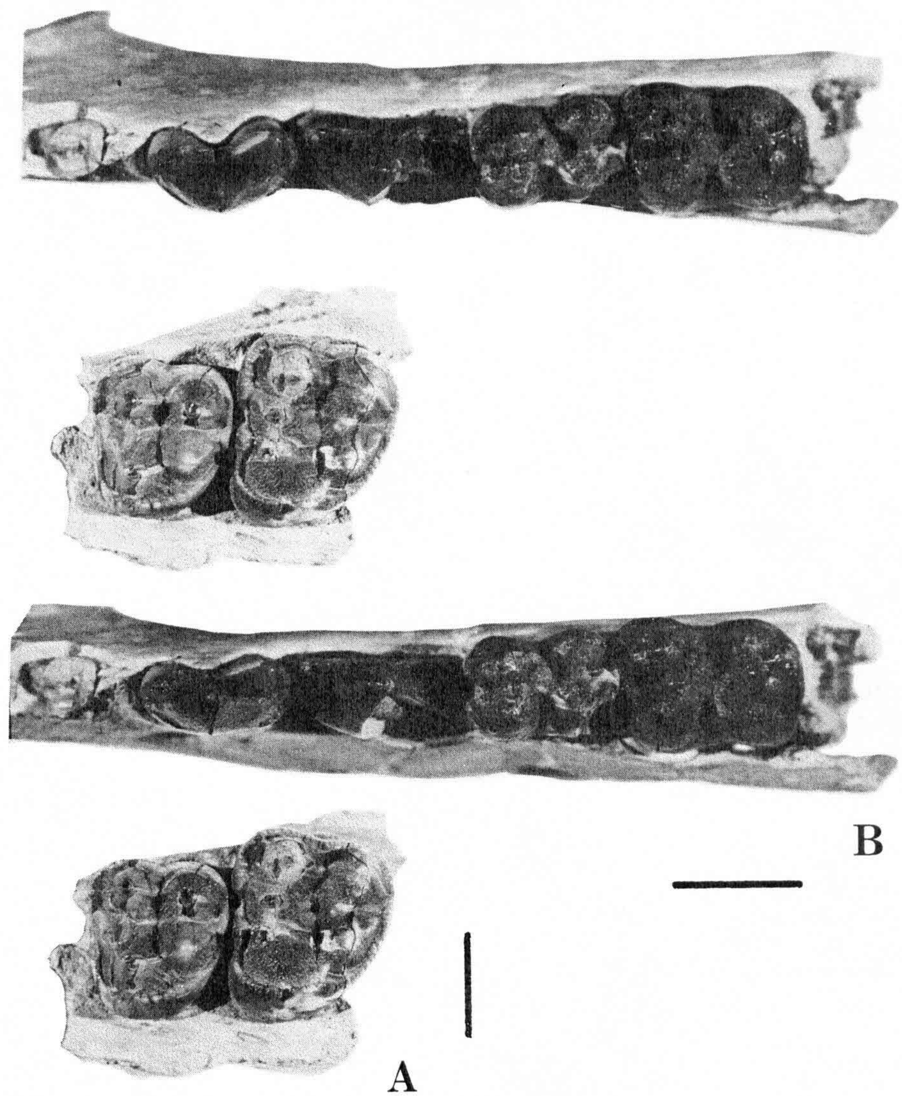


Fig. 19. Helohyus lentus *dentitions, stereoscopic views.*
A. PU 10084, left M^1-M^2.
B. USNM 17711, right P_3-M_2.
Scales represent a length of 10 mm.

Table 8

Measurements, in millimeters, of teeth of *Helohyus lentus*

	N	L	$\bar{X}$	N	W_a	$\bar{X}$	N	W_p	$\bar{X}$
P_4	1	13.3							
M_1	1	12.1							
M_2	2	13.5-14.4	13.95	2	10.3-10.9	10.6	2	10.2-10.8	10.5
M_3	3	18.4-19.7	19.20	3	10.9-11.7	11.37	3	10.6-10.8	10.7
M^1	2	12.2-13.2	12.7	2	13.3-15.2	14.25	2	12.5-13.6	13.05
M^2	1	15.5		1	18.5		1	16.5	

presence of a strong continuous cingulum. The cingulum is more pronounced than in smaller *Helohyus* species and the teeth are more squared.

Sinclair also illustrated the holotype (PU 10125) of Osborn's *Ithygrammadon cameloides,* speculating that because of the widely-spaced premolars it may be a helohyid. Currently available materials of *H. lentus* still do not permit this suggestion to be tested.

Helohyus lentus demonstrates the presence of a lineage characterized primarily by increasing size linking Bridgerian helohyines with late Eocene achaenodont artiodactyls. *Parahyus vagus,* an enigmatic Uintan species, occupies the temporal and morphological gap between *H. lentus* and *Achaenodon.* However, *Parahyus* is known from but two specimens, only one of which (TMM 42287-15; see West, 1982) has adequate data. The holotype is accompanied by ambiguous data. Lewis (1973) reported a *Parahyus* specimen from the Tepee Trail Formation but, since the specimen was missing at the time of description, he relied upon a photograph. McKenna (1980) located the specimen in the Yale collection, determined that the photograph was incorrectly scaled, and referred the specimen to *Achaenodon.*

Subfamily Diacodexinae Gazin 1955

Diagnosis: Upper molars with or without hypocone, but have conical protocone. P_4 lacks a metaconid. The hypoconulid of M_1 and M_2 is developed on the crest between the hypoconid and entoconid; lower molars have a broadly basined talonid.

Neodiacodexis Atkins 1970

Diagnosis: P^4 with two large sharp cusps; M^1 and M^2 tritubercular; paracone and metacone equal in size, conical sharp and high; conules well developed and relatively independent of major cusps; metaconule not hypertrophied; mesostyle present.

Neodiacodexis emryi Atkins 1970

Holotype: AMNH 56054, P^4-M^2, upper Bridger (Tabernacle Butte locality 5).

Diagnosis: As for genus.

No additional material referable to *N. emryi* was found during the course of this study, either in the field or in preexisting collections. It remains based upon a single maxillary fragment with P^4-M^2 recovered from late Bridgerian deposits at Tabernacle Butte (West and Atkins, 1970).

cf. *Neodiacodexis* sp.

Two isolated upper molars (CM 13232 and CM 13418) from the early Bridgerian Powder Wash locality (Green River Formation of northeastern Utah) are tentatively referred to *Neodiacodexis*. Both have rounded triangular outlines, lack a hypocone, have well-developed conules, subequal paracones and metacones, and conical protocones. The structure of the "wings" from the conules to the external cusps, varying mesostyle development, and differential structure of the internal cingular area preclude allocation of these teeth to *N. emryi*. Nonetheless the similarities are great enough to justify the queried generic assignment.

Discussion

Bridgerian artiodactyls quite clearly represent three distinct lineages within the Dichobunidae. Two, the Diacodexinae and the Homacodontinae have likely ancestral forms in older North American strata, while the Helohyinae appear for the first time in the North American middle Eocene.

The helohyines are the most generalized of the three. Their lower premolars are simple and trenchant, lacking any lateral cusps, the lower molars retain all three trigonid cusps, and the upper molars lack hypocones. The subfamily seems to continue onward into the late Eocene with a bifurcation into the achaenodonts on the one hand and smaller forms such as *Apriculus* on the other.

Coombs and Coombs (1977) used Helohyidae at the family level and placed them in the Anthracotherioidea. This followed their determination that all the close relatives of *Helohyus (Gobiohyus, Indohyus, Raoella, Kunmunella* and *Bunodentus)* are from southern or eastern Asia. I prefer retention of the subfamily rank, but the recognition of Asian affinities of *Helohyus* may be helpful in explaining its sudden occurrence in North America in the middle Eocene without apparent local ancestors. Coombs and Coombs' (1982) study of artiodactyl basicrania lent modest support to this contention, as *Helohyus* and *Gobiohyus* have somewhat more features in common than either shares with *Homacodon* or *Diacodexis*.

The Diacodexinae are commonly regarded as the "stem" subfamily of the Artiodactyla, as *Diacodexis* is the oldest known representative of the order. By middle Eocene they became extremely rare, although they did persist into the late Eocene as *Tapochoerus* (West and Atkins, 1970). Like the helohyines, they lack hypocone development, but their teeth never became as inflated and bulbous as *Helohyus*. Despite the primitive dentition, appendicular skeletal parts of *Diacodexis* (Rose, 1982) show a pronounced cursorial specialization.

The Diacodexinae probably gave rise to the Homacodontinae in the latter part of the early Eocene, as late Wasatchian *Hexacodus* is more clearly aligned with the homacodontines, with its rectangular upper molar outline. Middle Eocene homacodontines *(Microsus, Antiacodon* and *Homacodon)* are readily recognizable by the presence of a hypocone and well defined independent conules. The two smaller taxa, *Microsus* and *Antiacodon,* differ primarily in the degree of development of the paraconid and metaconid on the posterior molars and in the presence of a small mesostyle in *Antiacodon*. *Homacodon* is somewhat larger and has simpler premolars than do the others. The postcranial elements of *Antiacodon* described in this paper show it to be, like *Diacodexis,* highly specialized as a cursorial animal.

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Appendix

Below are complete listings of the fossil materials used in this study, arranged by species. The first part of each list is the newly collected material; following that is older material found in museum collections, listed by museum acronym. Alongside each museum number is a brief description of the nature of the material and the stratigraphic level and locality (if known). The asterisks indicate specimens not measured during this study.

Microsus cuspidatus

New Material				
MPM	6722	M_2	Bridger D	MPM loc. 2233
	6711	astragalus	C	MPM loc. 2406
	6709	M_3, astragalus, calcaneum, proximal tibia, distal femur.	B	MPM loc. 2801
AMNH	108128	astragalus	C	MPM loc. 1126
	108129	M_2	C	MPM loc. 1126
Older Material				
AMNH	12146*	Misc.	C_3	Henry's Fork, BFPO
	12145*	M_1-M_3	C_5	Henry's Fork Hill
USNM	336179	P^4-M^3	B	South of Church Buttes
	336178	P_4-M_3	B	Opposite Millersville
	336177	P_4-M_3	C	Dead Cow Buttes
YPM	37194	^{M}lower	?	Point Spring
	37190	M_3	Upper	Henry's Fork
	37193	^{M}lower	?	Point Gulch
	37191	M_1	Upper	Henry's Fork

Antiacodon pygmaeus

New Material				
MPM	5896	Skull and lower molars	B	MPM loc. 2934
	6721	Dentaries, maxilla, partial hind limb skeleton.	B	MPM loc. 3395
Older Material				
AMNH	5006*	M_1-M_2	Lower	Cottonwood Creek
	5007*	M_1-M_2	Lower	Cottonwood Creek
	12697*	dentary	B	Grizzly Buttes
	11427*	P_4, M_2-M_3	Lower	Grizzly Buttes West
	11426*	M_1-M_2	Lower	Grizzly Buttes West
	11974*	M_2-M_3	C_4	Henry's Fork, Lone Tree
	13127*	M_3	?B	Mouth of Summers Dry Creek
	13126*	P_4-M_2	B_2	Little Dry Creek

USNM	336176	P_4-M_3	B	Millersville
	18000	P_4	B	Eagle Buttes-Low Buttes North of Twin Buttes
	17707	P_4-M_2	B	NE extremity of Twin Buttes
	17706	M_1-M_3	B	NE extremity of Twin Buttes
	17709	M_3	B	NE extremity of Twin Buttes
	17708	P_4, M_2-M_3	B	Levitt Creek, Grizzly Buttes
	336202	frag. skeleton & skull	B	East of Black's Fork Bridge
YPM	13275	M_1-M_2	Lower	Black's Fork
	16865	P_4-M_1	?	Little Spring
	14660	M_1	Upper	Henry's Fork
	37192	M_1-M_2	Lower	Millersville
	37198	M_1	B	Dry Creek
	37195	M_2	?	Bridger

Antiacodon venustus

New material				
MPM	6717	M^1, M^2	C-D	MPM loc. 2900
Older material				
YPM	13274	M_1-M_3	B	Millersville
	13277	M_3	Upper	Lone Tree
	13271	M_3	Upper	Henry's Fork
	13273	M_1	?	Chalk Buttes
	13189	M^2-M^3	Upper	Lone Tree White Layer
	37188	M_2	Upper	Lone Tree, 4 miles down
	16861	M_1-M_3	Upper	Lone Tree White Fm.
	13272	P_4-M_2	Upper	Henry's Fork
	11765	M_3	Upper	Henry's Fork

Antiacodon sp.

New material				
MPM	6712	Astragalus	B	MPM loc. 2782
	6713	Astragalus	C	MPM loc. 2914
AMNH	108127	Astragalus	B	MPM loc. 2522

Homacodon vagans

New material				
MPM	6697	Dentary (P_2, P_4, M_3)	D	MPM loc. 2188
	6716	Astragalus	C	MPM loc. 2240

	6710	M^1	C	MPM loc. 3133
	6718	P_4	C	MPM loc. 1098
	6720	Astragalus	C	MPM loc. 1098
	6975	Astragalus	C	MPM loc. 2924
	6976	Astragalus	C	MPM loc. 1102
AMNH	108130	M_1	C	MPM loc. 2151
	108131	M^2	C	MPM loc. 2151
Older material				
AMNH	12140*	Maxilla	C_5	Henry's Fork Hill
	12141	M_3	C_4	Henry's Fork, L.T.
	12695	Skull	Upper	Henry's Fork, opposite mouth of Burnt Fork.
YPM	37199	M^2	Upper	Henry's Fork
	37197	M^3	Upper	Phil Mass Ranch
	37200	^{M}lower	?	Twin Buttes, Wyo., or White River, Utah
	37196	$_M$upper	Upper	Streaked Hill, Henry's Fork
	16862	M_3	Upper	Henry's Fork
	16867	M_1-M_2	Upper	Henry's Fork
	10012	Ankle	B	Millersville
	13129	Ankle	B	Millersville
	13129	Skull	Upper	Henry's Fork

?Homacodontine

USNM	336201	Hind limb parts	C	NE of Sage Creek Mt.

Helohyus plicodon

New Material				
MPM	6699	Lower dentition	C	MPM loc 2235
	6807	P_3-M_3 + P_4-M_3	B	MPM loc. 2767
	6700	M_1	C	MPM loc. 2909
	6698	upper teeth, calcaneum	C	MPM loc. 3138
	6706	M^2M^3, tibia proximal ulna	B	MPM loc. 2820
	6708	Astragalus, femur, distal tibia	B	MPM loc. 2801
AMNH	108123	P_4-M_3	D	MPM loc. 2403
	108125	M_3	B	MPM loc. 2522
	108124	M_1	C	MPM loc. 2187
	108137	Molar fragments	B	MPM loc. 1139
	108133	M^2	B	MPM loc. 1139
Older material				
AMNH	12148	M_1-M^3	?B	Summers Dry Creek
	12149	P_2-M_2	C_2	Henry's Fork, BFPO
	12147	P^4M^3	B_3	Middle Cottonwood Creek

	13128	M^1-M^2, M_1-M_2	B_3	Middle Cottonwood Creek
	92835	M_2-M_3	B_2	Grizzly Buttes
	5179	M_3(2)	B_3	Middle Cottonwood Creek
	56042	M_2-M_3	upper	Tabernacle Butte
	92844	Astragalus	C_3	Henry's Fork, BFPO
	11673	M^1-M^3	lower	Little Dry Creek
	12694	M_3	B_3	Middle Cottonwood Creek
	12141	M_3	C_4	Henry's Fork, Lonetree
USNM	17713	P_4-M_3	B	North of Twin Buttes, near conical butte
	17714	P_4-M_3	C_4	Sage Creek Basin
	17715	M_1	B	North of Cedar Mountain, NW 1/4 sec. 23, T15N, R111W
	17716	M_1	B	North of Cedar Mountain, NW 1/4 sec. 23, T15N, R111W
YPM	40276	M^2	Upper	Henry's Fork
	20679	P^3	?	Lone Spring
	40280	M_2	B	Sage Creek or Grizzly Butte
	40277	M_3	Upper	North of Henry's Fork Divide
	16868	^{M}lower	?	Dry Creek
	20696	M^3	Lower	Sage Creek
	40274	M^1	Upper	Henry's Fork Divide
	40275	M^1	Upper	Henry's Fork Divide
	40282	M_2	?	Lone Spring
	16860	P_3-M_1	?	no data
	40279	M_1	Upper	Henry's Fork
	40281	M^2	?	"Bridger"
	40278	M^2	?	"Bridger"
	16858	P_4	?	Birch Creek
	20698	M_2	?	Lone Spring
	16859	M_1-M_2	?	Bridger
	16857	P_2, M_2	?	Little Spring
	10216	M^1-M^3, P_4-M_1, M_3	?	Henry's Fork or Grizzly Buttes
	11893	M^3	?	Bridger

Helohyus milleri

New material				
MPM	6305	M_1	C	MPM loc. 2241
	6705	M_2	C-D	MPM loc. 2891
	78-363	Astragalus & calcaneum	B	MPM loc. 2814

81-38	Astragalus & distal tibia	B	MPM loc. 3400
6701	Astragalus & & calcaneum	B	MPM loc. 2919
6715	M_2	B	MPM loc. 2766
AMNH 208113	Astragalus	B	MPM loc. 2942
Older material			
AMNH 12151	Jaws & Maxilla	C_5	Henry's Fork, opposite mouth of Burnt Fork
1518	P_3-M_2, P_4	Upper	Twin Buttes
YPM 16819	M^2-M^3	C-D	Vicinity of Henry's Fork

Helohyus lentus

New material			
AMNH 108122	M_2	D	Twin Buttes
Older material			
AMNH 12150	M_3	D	Henry's Fork Hill
92865	Astragalus	Upper	Henry's Fork
USNM 11711	P_3-M_2	D	Twin Buttes, high above white layer
YPM 11892	M_3	Upper	Henry's Fork
40273	M^1	Upper	Henry's Fork
PU 10084	M^1-M^2	?	Bridger Basin

Neodiacodexis emryi

Older material			
AMNH 56054*	P^4-M^2	Upper	Tabernacle Butte, Loc. 5

cf. *Neodiacodexis* sp.

Older material			
CM 13232*	M^1	Lower	Powder Wash
13418*	M^1	Lower	Powder Wash