CONTRIBUTIONS FROM THE MUSEUM OF PALEONTOLOGY

THE UNIVERSITY OF MICHIGAN

Vol. 27, No. 8, p. 221–236

October 23, 1987

SYSTEMATIC REVISION OF THE GENUS *PROCHETODON* (PTILODONTIDAE, MULTITUBERCULATA) FROM THE LATE PALEOCENE AND EARLY EOCENE OF WESTERN NORTH AMERICA

ΒY

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SYSTEMATIC REVISION OF THE GENUS *PROCHETODON* (PTILODONTIDAE, MULTITUBERCULATA) FROM THE LATE PALEOCENE AND EARLY EOCENE OF WESTERN NORTH AMERICA

By

DAVID W. KRAUSE¹

Abstract.—Prochetodon is one of four valid genera in the multituberculate family Ptilodontidae. Although originally described from a single late Tiffanian locality, specimens of *Prochetodon* are now known from 33 localities ranging in age from middle Tiffanian to middle Clarkforkian distributed throughout the northern part of the Western Interior of North America. These additional specimens permit the identification of two new species, *Prochetodon foxi* and *P. taxus*, and revised diagnoses for both the genus and the type species, *P. cavus*.

INTRODUCTION

Prochetodon, a ptilodontid multituberculate, is an uncommon element in mammalian faunas from the late Paleocene and early Eocene of western North America. *Prochetodon* is the latest surviving genus of the Ptilodontidae. *Kimbetohia* (early Paleocene), *Baiotomeus* (middle Paleocene), and *Ptilodus* (early Paleocene to late Paleocene, possibly earliest Eocene) are the remaining members of the family (Krause, 1982, 1987). Prior to this study only one species of *Prochetodon*, *Pro. cavus*, had been described (Jepsen, 1940). *Prochetodon cavus* was first known from Princeton Quarry, a late Tiffanian (late Paleocene) locality in the Bighorn Basin of northwestern Wyoming (Jepsen, 1940). Since the description of this one species from a single locality, specimens of *Prochetodon* have been discovered from 32 additional localities geographically distributed in Alberta, Saskatchewan, Montana, North Dakota, and Wyoming and temporally distributed from the middle Tiffanian to the middle Clarkforkian (early Eocene), an interval of approximately 2.5 million years (Berggren et al., 1985). Not all of the new species of *Prochetodon*, *Pro. foxi* from the middle Tiffanian and *Pro. taxus* from the early and middle Clarkforkian, and provide revised diagnoses for the genus and for *Pro. cavus*.

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ABBREVIATIONS

Acronyms of institutions referred to in this paper are:

CM - Carnegie Museum of Natural History, Pittsburgh.

MCZ - Museum of Comparative Zoology, Harvard University, Cambridge.

MMMN - Manitoba Museum of Man and Nature, Winnipeg.

YPM-PU - Yale Peabody Museum, Yale University, New Haven - Museum of Natural History, Princeton University, Princeton.

SMM - Science Museum of Minnesota, St. Paul.

UA - The University of Alberta, Edmonton.

UM - Museum of Paleontology, The University of Michigan, Ann Arbor.

DENTAL MEASUREMENTS AND TERMINOLOGY

The terms employed in the description of the dentition of *Prochetodon*, and the measurements taken, are the same as those described in detail by Krause (1982, 1987). In referring to species of *Prochetodon*, the abbreviated *Pro*. is used to make the distinction from *Ptil*., the abbreviation employed for *Ptilodus*. The terminology of Archibald et al. (in press) is used in referring to the faunal zones that have been employed to subdivide the Tiffanian and Clarkforkian Land-Mammal Ages. The Tiffanian has five zones, which, from oldest to youngest are abbreviated as Ti1 to Ti5. The next youngest zone spans the Tiffanian-Clarkforkian boundary and is therefore divided into two subzones, Ti6 and Cf1, which in turn is followed by zones Cf2 and Cf3. Thus, as used here, early Tiffanian includes Ti1 and Ti2, middle Tiffanian includes Ti3 and Ti4, and late Tiffanian includes Ti5 and Ti6. Similarly, Cf1, Cf2, and Cf3 are referred to as early, middle, and late Clarkforkian, respectively.

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Class MAMMALIA Linnaeus, 1758 Subclass ALLOTHERIA Marsh, 1880 Order MULTITUBERCULATA Cope, 1884 Suborder PTILODONTOIDEA Sloan and Van Valen, 1965 Family PTILODONTIDAE Gregory and Simpson, 1926 *Prochetodon* Jepsen, 1940

Prochetodon Jepsen, 1940, p. 309.

Type species.—Prochetodon cavus Jepsen, 1940.

Included species.—Prochetodon cavus Jepsen, 1940; Pro. foxi, new species; and Pro. taxus, new species.

Distribution.—Early middle Tiffanian (Ti3) to middle Clarkforkian (Cf2) of western North America (Alberta, Saskatchewan, Montana, North Dakota, and Wyoming).

Revised diagnosis.—A genus of large ptilodontids, much larger than *Kimbetohia* and *Baiotomeus*, but equivalent in size to some species of *Ptilodus*. Differs from *Kimbetohia*, *Baiotomeus*, and *Ptilodus* in possession of lenticular, rather than conical, cusps buccally on P^{1-3} ; arcuate arrangement of mesial

and buccal cusps on P^2 (condition unknown in *Baiotomeus*): presence of 8 to 9 cusps on P^3 ; relatively long and narrow P^4 with persistent absence of cusps on mesiobuccal bulge: P_4 with broad, flat mesial face, reduced exodaenodont lobe, and distally canted shape in lateral view: and presence of shallow vertical grooves buccally on buccal cusps of M_1 .

Prochetodon foxi, new species Figure 1; Tables 1, 2

Ptilodus sp. (in part). Krishtalka. Black. and Riedel. 1975. p. 183, fig. 1. *Prochetodon* cf. *cavus* (in part). Krause. 1977. p. 13, Pl. 2: 8–13, Pl. 3: 1, 3–6. *Prochetodon* sp., Krause. 1977. p. 14, Pl. 3: 2: Holtzman. 1978. p. 25, figs. 3.6, 3.8, 3.9.

Holotype and locality.—YPM-PU 21223, right dentary with base of I₁ and P₃₋₄; from Long Draw Quarry in SE1/4, NE1/4, Sec. 24, T9S, R23E, Carbon Co., Bighorn Basin, Montana.

Hypodigm and localities.—Long Draw Quarry: Holotype only.

Roche Percée sites UAR2, UAR2a, and UAR2g, Williston Basin, Saskatchewan (Krause, 1977): UA 9753, 9796, 9825, 9830, 9919, 9960, 9975, 9979, 9991, 10017, 10036–10040, 10053, 10060, 10095, 10098, 10106, 10124, 10161, 10194, 10305, 10317, 10386, 10390, 10397, 10409, 10417, 10421, 10432, 10433, 10442, 10465, 10482, 10523, 10542, 10557, 10565, 10583, 10584, 10619, 10622, 10640, 10643, 10659, 10668, 10729, 10730, 10768, 11303–11306, 11317, 11326, 11418–11420, 11450, 11537–11539; MMMN 523.

Divide Quarry, Bighorn Basin, Wyoming (Gingerich, 1976): UM 77318.

Malcolm's Locality, Wind River Basin, Wyoming (Krishtalka et al., 1975): CM 12451, 12490, 16120, 16133, 16135, 16138, 23685, 23687.

Swan Hills Site 1, central Alberta (Russell, 1967): UA 11997, 11998.

Judson Locality, Williston Basin, North Dakota (Holtzman, 1978): SMM P77.7.55, P77.7.56. *Known distribution.*—Early middle Tiffanian (Ti3) of North Dakota (Williston Basin) and late middle Tiffanian (Ti4) of central Alberta, Saskatchewan (Williston Basin), Montana (Bighorn Basin), and Wyoming (Bighorn and Wind River basins).

Etymology.—Named for Professor Richard C. Fox of The University of Alberta, in recognition of his important contributions to the study of early mammals and in appreciation of his early profound influence upon me as a student.

Diagnosis.—Slightly larger (mean length of P_4 at Roche Percée = 8.10 mm) than *Pro. cavus* (mean length of P_4 at Princeton Quarry = 7.25 mm) and similar in size to *Pro. taxus* (length of P_4 of holotype = 8.0 mm). Buccal row of cusps on P^4 well-developed (extending well past mid-length) and with greater number of cusps (6.5–8) than in *Pro. cavus* (2.5–5) or *Pro. taxus* (1). Mesial part of crown of P^4 much lower than distal part and therefore relatively lower than in *Pro. cavus* and, particularly, *Pro. taxus*. Mesial margin of crown of P_4 evenly rounded in lateral profile and exodaenodont lobe indistinct. Crown of P_4 lower, relative to its length, than in *Pro. cavus* and *Pro. taxus*.

Description and discussion.—The largest sample of *Pro. foxi* is comprised entirely of isolated teeth and comes from the Roche Percée sites. A detailed description of the specimens in the Roche Percée sample has been given previously (Krause, 1977) and it is therefore necessary to describe only those details from other samples that augment the variability already observed, as well as those that further serve to distinguish *Pro. foxi* from *Pro. cavus* and *Pro. taxus*. Dental measurements of *Pro. foxi* are provided in Tables 1 and 2. The holotype is illustrated in Figure 1E, F. Illustrations of *Pro. foxi* from other localities are available in the following sources: Roche Percée - Krause, 1977, Pl. 2, figs. 8–13



FIG. 1— Prochetodon foxi, new species. 1 and 2, UA 10194, right P⁴ from Roche Percée Site UAR2a, stereophotographs of occlual and lingual views. 3 and 4, SMM P77.7.56, left P⁴ from the Judson Locality, stereophotographs of occlusal and lingual views. 5 and 6, YPM-PU 21223 (holotype), right dentary fragment with P₃₋₄ from Long Draw Quarry in buccal and lingual views. Approximately x5.

and Pl. 3, fig. 1; Malcolm's Locality -Krishtalka et al., 1975, fig. 1 and Krause, 1977, Pl. 3, figs. 3–6; Swan Hills Site 1 - Krause, 1977, Pl. 3, fig. 2; and the Judson Locality - Holtzman, 1978, figs. 3.6, 3.8, and 3.9.

 P_3 is present in the holotype of *Pro. foxi*. As in other ptilodontids, it is reduced to a long, slender, vertical peg that rests under the mesial part of the crown of P_4 .

 P_4 of *Pro. foxi* has a long, low crown and bears 15 to 16 servations. The exodaenodont lobe is not distinctly set off from the rest of the crown. In addition, the mesial margin of the crown is smoothly rounded and circular in outline. In these respects, P_4 's from Long Draw Quarry and Roche Percée bear closer resemblance to each other than either does to P_4 's from Malcolm's Locality. The P_4 's from Malcolm's Locality resemble, to some degree, those of *Pro. cavus* in having a weakly developed exodaenodont lobe and a less rounded mesial margin, perhaps indicating a relatively derived condition

Specimen			F	P ₄				M ₁	
1	L	W	LI	Н	D	S	L	W	С
Long Draw									
YPM-PU 21223	8.7	2.4	2.8	2.9	2.2	16			
UAR2									
MMMN 523	8.0			—		16			
UAR2a									
UA 10317	8.2	2.3	2.4	2.9	2.0	16			
UA 10397		2.2			_	16			
UA 10421	8.1	2.3	2.3	2.9	2.1	15			
UA 10095							3.5	1.6	6.5:5
UA 10124							4.2	1.9	8:5
UA 10622							4.1	1.8	8:5
UA 11326							3.9	1.8	7.5:5
UA 11418								1.7	
UA 11419							3.7		7:5

 TABLE 1— Measurements of the lower dentition of Prochetodon foxi, new species, from Long Draw Quarry and Roche

 Percée sites UAR2 and UAR2a.

and therefore a slightly younger age for Malcolm's Locality. The lateral profiles of P_4 in *Pro. foxi*, *Pro. cavus*, and *Pro. taxus* are compared in Fig. 2. Despite its greater length, P_4 of *Pro. foxi* has a relatively low crown.

In a previous paper I suggested that the specimens of *Prochetodon* from Roche Percée are different from those from Princeton Quarry "primarily in that they are slightly larger, the mesial margin of P_4 is more evenly curved . . . , the exodaenodont lobe of P_4 is less distinctly set off from the rest of the crown, P² has four, rather than three, cusps (YPM-PU 14434, a maxillary fragment from Princeton Quarry, bears a P^2 with an incipiently developed anterior cusp), and P^3 has, in the labial row, five, rather than four, cusps" (Krause, 1977, p. 15). It was also noted that specimens from Schaff and Fritz quarries show a mixture of characteristics: the size and shape of the P_4 's are more like those from Princeton Ouarry but the cusp number on P^{2-3} are more like those from Roche Percée. Unfortunately, all of the available samples from Princeton, Schaff, and Fritz guarries are small, particularly those from the latter two. Reanalysis of these samples, coupled with the study of specimens from isolated occurrences in the same general area, leads to the conclusion that the differences observed in the size and shape of P4 of Pro. foxi from Roche Percée and Pro. cavus from Princeton, Schaff and Fritz quarries are real, whereas the number of cusps on P^2 and P^3 is not a consistent and reliable taxonomic indicator. As noted in the quotation above, one of the Princeton Quarry P²'s has an incipient fourth cusp. Conversely, and not noted previously, two of the four cusps on a P² (UA 9960) from Roche Percée are fused at their bases and appear as one. Unfortunately, there are no upper premolars known from Fritz Quarry and there is only one specimen known from Schaff Quarry that retains P^2 and P^3 . A fragmentary P³ (YPM-PU 23950) from Princeton Quarry does have five cusps in the buccal row. A well-preserved and relatively complete specimen (MCZ 20039) from a locality (NE1/4, Sec. 22, T57N, R100W) at a level slightly higher than Princeton Quarry (and Schaff Quarry) (C. R. Schaff, pers. comm.) has a P^2 with four cusps and a P^3 with five cusps in the buccal row. Similarly, UM 73684 from UM locality SC-277, is a P³ with five cusps in the buccal row. In short, therefore, the known specimens indicate that *Pro. foxi* has a P^2 that usually has four cusps (but occasionally two of them are twinned) and a P^3 with five cusps in the buccal row. *Pro. cavus*, by contrast, has three to four cusps on P^2 and four to five cusps in the buccal row of P^3 . These differences may simply be correlated with size:

Specimen	F	5 1		P ²			P ³			P ⁴	
speemen	L	W	L	W	С	L	W	С	L	W	С
UAR2											
UA 9960			2.7	2.2	4						
UA 9975			2.8	2.1	4						
UAR2a											
UA 10390	2.1	1.8									
UA 10433	2.3	1.9									
UA 10465	2.2	1.8									
UA 10482	2.1	1.7									
UA 11420	2.2	1.9									
UA 9753			2.6	2.0	4						
UA 9825			2.8	2.2	4						
UA 10417			2.6	2.2	4						
UA 10432			2.6	2.1	4						
UA 10442			2.5	2.0	4						
UA 10523			2.7	2.2	4						
UA 10668			2.5	2.1	4						
UA 10557						3.7	2.2	5:4			
UA 10584						3.5	2.0	5:4			
UA 10730						3.5	2.0	5:4			
UA 11303						3.5	2.1	5:4			
UA 10194									5.5	1.8	(0)6.5:11:0
Malcolm's Locality											
CM 16138	2.3	1.8									
CM 16135						3.5	2.1	5:4			
Swan Hills Site 1											
UA 11998									_	2.0	(0)—::-
Iudson Locality											
SMM P77.7.55	2.3	1.9	4								
SMM P77.7.56									5.6	1.8	(0)8:12:0
Divide Quarry											
UM 77318						3.8	2.2	5:4			

 TABLE 2— Measurements of the upper dentition of Prochetodon foxi, new species, from Roche Percée sites UAR2 and UAR2a, Malcolm's Locality, Swan Hills Site 1, the Judson Locality, and Divide Quarry.

Pro. foxi is generally slightly larger than *Pro. cavus* and usually has the greater number of cusps on P^2 and P^3 .

Very small samples of *Prochetodon* from Swan Hills Site 1, the Judson Locality, and Divide Quarry are tentatively referred to *Pro. foxi*. The two fragments of P^4 from Swan Hills Site 1 show that the buccal row of cusps is well-developed and extends well past mid-length, as is characteristic of *Pro. foxi*. The single specimen, a P^3 (UM 77318), from Divide Quarry is identical to P^{3*} s of *Pro. foxi* from Roche Percée. Finally, although the P^2 (SMM P77.7.55) from the Judson Locality is identical to those of *Pro. foxi* from Roche Percée, the P^4 (SMM P77.7.56) has more cusps (eight) in the buccal row than in the only other complete P^4 (UA 10194) referred to *Pro. foxi*. As shown by the progressively lower number of cusps in this row in the progressively later species of *Prochetodon*, this trait appears to be primitive in the Judson Locality specimen. This apparent primitiveness is corroborated by the



FIG. 2— Camera lucida outline drawings of lateral profiles of all available unworn or only slightly worn lower fourth premolars of *Prochetodon. 1, Pro. foxi*: YPM-PU 21223 from Long Draw Quarry and UA 10421 from Roche Percée Site UAR2a. 2, *Pro. cavus*: YPM-PU 13362, 14436, 17923, 19015, 19099, 19121, 19492, 19848, and UM 73384 from Princeton, Schaff, and Fritz quarries and the surrounding vicinity. *3, Pro. taxus*: UM 71311 from UM locality SC-226 and YPM-PU 14542 from Paint Creek (=UM locality SC-143). *4,* Comparison of P₄ profiles of *Pro. foxi, Pro. cavus*, and *Pro. taxus* - see legends in *1, 2,* and *3.* All specimens were orientated about a baseline passing through the most mesial point above the mesiobasal concavity and along the base of the distobuccal ledge; they were registered about a point midway along the baseline.

presence in the Judson Local Fauna of primates which suggest that the Judson Local Fauna (Holtzman, 1978) is older than those at Long Draw (Gingerich, 1976), Malcolm's Locality (Gingerich, 1976), Roche Percée (Krause, 1978), and Swan Hills Site 1 (Krause, 1978). Additional specimens of *Prochetodon* from the Judson Locality may show that the sample should be referred to a new species but, for the present, these specimens are tentatively allocated to *Pro. foxi*.

Molars other than M_1 remain unknown for *Pro. foxi*. An isolated M^2 (CM 12454) from Malcolm's Locality referred by Krishtalka et al. (1975, Fig. 2) to *Ptilodus* sp. (=*Ptil. kummae* - see Krause, 1977, 1982) was later tentatively allocated to *Prochetodon* cf. *cavus* (now *Pro. foxi* - see above) by Krause (1977). Now that M^2 's are known for *Pro. cavus* and *Pro. taxus* it appears unlikely that CM 12454 is referable to either *Pro. foxi* or *Ptil. kummae*. Its large size (L=2.8 mm, W=2.8 mm) suggests that it belongs to a taxon that is otherwise unknown from Malcolm's Locality.

Prochetodon cavus Jepsen, 1940 Figure 3; Tables 3, 4

Ptilodus sp., Jepsen, 1930, p. 510, Pl. IX: 6. Prochetodon cavus Jepsen, 1940, p. 310, fig. 19, Pl. IV: 4–7; Krause, 1977, p. 15, Pl. 3: 10–11. Prochetodon cavus?, Krause, 1977, p. 15, Pl. 3: 7–9.

Holotype and locality.—YPM-PU 13925, right dentary with base of I_1 , P_3 , and mesial fragment of P_4 ; from Princeton Quarry in center of SE1/4, Sec. 21, T57N, R100W, Park Co., Bighorn Basin, Wyoming. (This specimen has been damaged considerably since first described by Jepsen in 1940, as is indicated by comparisons with his Pl. IV, fig. 4. At that time both I_1 and P_4 were relatively complete.)

Hypodigm and localities.—All of the localities listed below are in Park Co., Bighorn Basin, Wyoming.

Princeton Quarry: Holotype and YPM-PU 13362, 14034, 14336, 14433-14436, 14527, 23950-23952; UM 76858.

Schaff Quarry: YPM-PU 19369, 19492, 19503, 23953; MCZ 19441; UM 78893.

Fritz Quarry: YPM-PU 17922, 17923.

Hail Quarry: YPM-PU 23954.

NE1/4, Sec. 28, T58N, R101W: YPM-PU 23955.

SE1/4, Sec. 35, T58N, R101W: YPM-PU 23956.

UM locality SC-258: UM 73352, 73384.

Sec. 7, T57N, R100W: YPM-PU 19099.

North center, Sec. 7, T57N, R100W: YPM-PU 19015.

Sec. 18, T57N, R100W: YPM-PU 19090.

UM locality SC-266: UM 73511.

SE1/4, Sec. 17, T57N, R100W: YPM-PU 18949.

NW1/4, Sec. 21, T57N, R100W: YPM-PU 18979.

SW1/4, Sec. 22, T57N, R100W: YPM-PU 19848.

UM locality SC-277: UM 73684.

NE1/4, Sec. 22, T57N, R100W: MCZ 20039.

SW1/4, Sec. 22, T57N, R100W: MCZ 20018.

Sec. 22, T57N, R100W: YPM-PU 19121.

UM locality SC-198 (= YPM-PU Fossil Hollow Locality): YPM-PU 20512, 23957, 23958; UM 69242.

UM locality SC-165: UM 69256, 77930-77932.

UM locality SC-228: UM 71706.

Sec. 10, T56N, R99W: YPM-PU 18290.

Known distribution.-Early late Tiffanian (Ti5) of Wyoming (Bighorn Basin).

Revised diagnosis.—Smallest known species of the genus but only slightly smaller than *Pro. foxi* and *Pro. taxus* (compare measurements in Tables 1 to 6). Buccal row of cusps on P^4 extending to approximately mid-length and with greater number of cusps (2.5–5) than in *Pro. taxus* (1), but fewer than in *Pro. foxi* (6.5–8). Mesial part of crown of P^4 only slightly lower than distal part; it is therefore relatively lower than in *Pro. taxus* and relatively taller than in *Pro. foxi*. Exodaenodont lobe small but more distinctly set off from rest of crown than in other two species.

Description and discussion.—Pro. cavus is known only from localities in the Polecat Bench area of the northern Bighorn Basin. Jepsen (1940, p. 310–314) described the teeth then known of Pro. cavus

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FIG. 3— Prochetodon cavus. 1, MCZ 20039, partial skull with left P^{3.4} (not shown) and right P^{1.4}M^{1.2} from NE1/4, Sec. 22, T57N, R100W, Park Co., Wyoming, occlusal view. 2 and 3, MCZ 20039, left P⁴, stereophotographs of occlusal and lingual views. 4 and 5, YPM-PU 19099, right dentary fragment with P₄ from Sec. 7, T57N, R100W, Park Co., Wyoming, buccal and lingual views. Approximately x5.

in detail, including the long, slender (and now missing) I₁ of the holotype. At the time of Jepsen's writing, none of the molars were known and the allocation of P⁴ to *Pro. cavus* was not based on any direct association with other remains. YPM-PU 19369 and MCZ 20039 confirm Jepsen's identification of P⁴. MCZ 20039 is a partial skull with left P³⁻⁴ and right P¹⁻⁴M¹⁻², thus also providing the first record of M¹⁻² in this species (Figure 3). An isolated M² (YPM-PU 23953) from Schaff Quarry can therefore also be assigned to *Pro. cavus*.

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			F	4				M1	
Specimen	L	W	LI	Н	D	S	L	W	С
Princeton Quarry									
YPM-PU 13362	7.1	2.2	2.1	2.6		_			
YPM-PU 14436	7.4	2.4	2.3	2.7	2.5	13			
Schaff Quarry									
YPM-PU 19492	6.6	2.1	2.3	2.6	2.1	_	3.5	1.5	7:4.5
YPM-PU 19503	6.8	2.3	—	_	2.1	_			
Fritz Quarry									
YPM-PU 17922	7.5	2.5	2.3	3.0	2.4				
YPM-PU 17923	7.7	2.6	2.5	2.9	2.5	15			
UM loc. SC-258									
UM 73384	7.1	2.2	2.2	2.7	2.4				
Sec. 7, T57N, R100W									
YPM-PU 19099	7.3	2.3	2.4	2.7	2.6				
NC, Sec. 22, T57N, R1	00W								
YPM-PU 19015	7.5	2.4	2.5	2.7	2.3				
SW1/4, Sec. 22, T57N,	R100W								
YPM-PU 19848	7.3	2.4	2.5	2.6	2.2	_			
Sec. 22, T57N, R100W									
YPM-PU 19121	7.4	2.0	2.5	2.6	2.0	_			
UM loc. SC-165 UM 77931							3.5	1.6	7.5:4

TABLE 3— Measurements of the lower dentition of *Prochetodon cavus* from various localities in the northern Bighorn Basin, Wyoming.

 M^1 of *Pro. cavus* is similar to those of *Ptilodus* but the buccal row appears to be much narrower relative to the middle row and the mesial margin appears more rounded in occlusal view. Likewise, M^2 of *Pro. cavus* appears to differ from those of *Ptilodus* in having a less widely flaring buccal cusp, an incipient connection between the first and second cusps of the middle row, and a less evenly spaced lingual row of cusps (the second and third are more widely separated than the first and second). However, when these distinguishing criteria are applied to a mixed sample (i.e., one that probably contains both *Prochetodon* and *Ptilodus* - such as at Roche Percée) there appear to be intergradations that diminish the utility of the criteria despite the recognition of extremes. It remains to be seen if undoubted *Prochetodon* upper molars can be consistently separated from those of *Ptilodus*; additional molars of *Prochetodon* are required.

The lateral profiles of P_4 's of *Pro. cavus* are compared with those of *Pro. foxi* and *Pro. taxus* in Figure 2. P_4 's of *Pro. cavus* are generally shorter than those of *Pro. foxi* and *Pro. taxus* and have a more angled mesial margin and a more distinct exodaenodont lobe.

Illustrations of specimens of *Pro. cavus*, in addition to those presented in Figure 3, are available in Jepsen (1930, Pl. IX, fig. 6; 1940, fig. 19, and Pl. IV, figs. 4–7) and Krause (1977, Pl. 3, figs. 7–11).

Specimen	<u>а</u>	-		P ²			ь³			P4		Ā			M ²	
-	L	¥	L	¥	υ	L,	×	C	L	X	г с	≥	0	<u>ر</u>	≥	0
Princeton Quarry	- c	u -	ć	ז -	,	t c	-									
VPM-P[] 14336	7.1	<u>.</u>	6.2 4 C	/ 1	n u	9.7 7 2	۲.1 ۱.۷	4. 7. 7. 7								
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YPM-PU 23950						1	1	5:4*								
Schaff Quarry		, ,														
YPM-PU 19369 YPM-PU 23953	2.1	1.6	2.3	1.9	4	3.6	I	5:4	4.7	1.6	(0)5:10:0			2.0	2.0	1:3:3
NETIA_Sec_28_T58N_R101W																
YPM-PU 23955									1	1.7	-::(0)					
IIM Inc. SC.277																
UM 73684						3.6	2.1	5:4								
NE114. Sec. 22. T57N. R100W																
MCZ 20039(R)	2.0	1.5	2.4	1.8	4	3.6	2.2	5:4	4.9	1.7	(0)5:10:0 4.	5 2.0	7:10	2.0	1.9	1:3:3
MCZ 20039(L)						3.6	2.1	5:4	4.9	1.7	(0)3.5:10:0					
UM locality SC-198																
UM 69242	2.0	1.6														
UM locality SC-165																
UM 69256	2.4	1														
UM 77930						3.4	2.1	4:4								
*Estimated																

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Prochetodon taxus,, new species

Figure 4; Tables 5, 6

Prochetodon cavus (in part), Jepsen, 1940, p. 327. Prochetodon cf. P. cavus, Krause, 1980, p. 1165, Text-figs. 1–3. Prochetodon cf. cavus, Rose, 1981, p. 33.

Holotype and locality.—UM 71311, partial skull with $LP^{1-4}M^{1-2}$ and $RP^{2-4}M^{1-2}$, left dentary with root of $I_1P_3M_{1-2}$, right dentary with RP_4M_{1-2} ; from UM locality SC-226 at intersection of sections 15, 16, 21, and 22, T57N, R101W, Park Co., in Badger Basin area of northern Bighorn Basin, Wyoming.

Hypodigm and localities.---UM locality SC-226: Holotype only.

UM locality SC-143 (= YPM-PU Paint Creek Locality): YPM-PU 14542 (includes YPM-PU 13320).

UM locality FG-6: UM 72649-72651, 77555.

Known distribution.—Early to middle Clarkforkian (Cf1 to Cf2) of Wyoming (Bighorn Basin). *Etymology.*—Latin *taxus* (badger), in reference to Badger Basin, area of provenance of the holotype.

Diagnosis.—Slightly larger (approximately 10–15%) than *Pro. cavus* and similar in size to *Pro. foxi* (compare measurements in Tables 1 to 6). Buccal row of cusps on P^4 relatively poorly developed with only a single cuspule present mesially. Mesial and distal parts of P^4 of approximately equal height, the mesial part therefore being relatively taller than in *Pro. cavus* and, particularly, *Pro. foxi*. Exodaenodont lobe on P_4 not well set off from rest of crown.

Description and discussion.—Few specimens of *Pro. taxus* are known but the holotype (UM 71311) is remarkably complete. This specimen was described previously (Krause, 1980, text-figs. 2, 3) but further careful preparation has permitted the separation of upper and lower dentitions, thus revealing additional morphological detail (Figure 4).

 P_4 of *Pro. taxus* (also known in YPM-PU 14542 from UM locality SC-143 - see Krause, 1977, text-fig. 1) is generally larger than in *Pro. cavus* and is higher-crowned, particularly distally, than in *Pro. foxi*. In an earlier paper (Krause, 1980), I suggested that the teeth that are now assigned to *Pro. taxus* are more similar to those allocated to *Pro. foxi* from Roche Percée than to those of *Pro. cavus*. To some extent this is true, but many of these similarities (e.g., number of cusps on P² and P³) are probably correlated with size. However, the progressive loss of cusps in the buccal row of P⁴ from *Pro. foxi* to *Pro. taxus* is not size related. If these three species do comprise a single lineage, it appears that there was a reversal in size through time with a decrease from *Pro. foxi* to *Pro. foxi* and *Pro. taxus* to *Pro. taxus* to *Pro. taxus*. Correspondingly, *Pro. foxi* and *Pro. taxus* usually have more cusps on P² and P³ than does *Pro. cavus*.

Prochetodon sp.

Buckman Hollow (Green River Basin, Wyoming).—An isolated incisor (UM 68358) from Buckman Hollow may represent *Prochetodon* (Krause, 1980). UM 68358 is extremely long and slender as is typical of *Prochetodon* (Jepsen, 1940, Pl. IV, fig. 4). The Buckman Hollow Local Fauna is Clarkforkian in age (Dorr and Gingerich, 1980; Rose, 1981). The only species of *Prochetodon* currently known from Clarkforkian horizons is *Pro. taxus*.

SYSTEMATIC REVISION OF PROCHETODON



FIG. 4— Prochetodon taxus, new species. UM 71311 from UM locality SC-226. 1, skull fragment with left P¹⁻⁴M¹⁻² in left lateral view. 2 and 3, right dentary fragment with P₄M₁₋₂ in buccal and lingual views. Approximately x5.

Specimen			F	P ₄				M_1			M_2	
1	L	W	L1	Н	D	S	L	W	С	L	W	С
UM loc. SC-226												
UM 71311(R)	8.0	2.3	2.5	3.1	2.1	16	3.9	1.7	7:5	2.1	1.9	3:2
UM 71311(L)							3.8	1.7	7:5	2.1	—	-:2
UM loc. SC-143												
YPM-PU 14542	7.7	2.8	2.5	2.6	2.0	—						
UM loc. FG-6												
UM 72651										2.4*	1.9	4?:2
*Estimated												

TABLE 5— Measurements of the lower dentition of *Prochetodon taxus*, new species, from UM localities SC-226, SC-143, and FG-6 in the northern Bighorn Basin, Wyoming.

PHYLOGENY AND DISTRIBUTION OF PROCHETODON

Prochetodon, like *Kimbetohia* and *Baiotomeus*, is much less well represented in the early Cenozoic fossil record than is *Ptilodus*. It is known only from dental and gnathic remains and, until recently (Krause, 1977, 1980), none of its molars had been identified. *Prochetodon* appears to have been a component only of northern faunas. Although faunas of the same general age (middle Tiffanian to middle Clarkforkian) are known from more southerly areas, *Prochetodon* has not been found south of the Wind River Basin of south-central Wyoming. *Prochetodon* is the latest surviving member of the family Ptilodontidae.

None of the three known species of *Prochetodon* have ever been found to occur with any other species of the genus. As determined from available biostratigraphic information, *Pro. foxi* precedes *Pro. cavus*, which precedes *Pro. taxus*. Although there appears to have been a reversal in size trend (from larger to smaller to larger), a progressive trend can be discerned in the morphology of P^4 . In *Pro. foxi* the buccal row of cusps on P^4 is well-developed, extending distally to well past mid-length and possessing 6.5 to 8 cusps. Furthermore, the distal part of the crown of P^4 is distinctly higher than the mesial part. In *Pro. cavus* the buccal row of P^4 is shorter, possesses only 2.5 to 5 cusps in the known specimens and the distal part of the crown of P^4 is lower than in *Pro. foxi*. In *Pro. taxus* the buccal row of P^4 is extremely reduced and possesses only a single cusp, while the mesial and distal parts of the crown are of approximately equal height. It should be noted, however, that the trends described above are based on small samples and additional specimens will be required to clarify patterns.

The origin of *Prochetodon* remains elusive. Although probably derived from a Torrejonian or early Tiffanian species of *Ptilodus*, no species of *Ptilodus* has yet been identified that serves as a structural ancestor for *Prochetodon*.

ACKNOWLEDGMENTS

This paper represents a revised excerpt from my doctoral dissertation and I therefore thank the members of my dissertation committee for their reading of the original draft. The committee consisted of Drs. P. D. Gingerich (chairman), J. A. Dorr, Jr., D. C. Fisher, P. Myers, and G. R. Smith. I also thank Ms. M. C. Maas for her careful reading of the revised version. Specimens relevant to this study

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UM locality SC-226			2.9	2.2	4.5	4.5	2.4	5:4	5.8	1.7	0;11:1 (0)	5.3	2.3	8*:10	2.1	2.1	1:3:3
UM 71311(L)	2.6	1.8	3.0		4	4.3		5:4	5.9	1.8*	0:11:1 (0)	5.2	2.3	8:10	2.2	2.1	1:3:3
UM locality FG-6 UM 72649 UM 77555			2.6	2.0	4	3.9	2.2	5:4									

were loaned by Drs. D. Baird (PU), B. R. Erickson (SMM), R. C. Fox (UA), P. D. Gingerich (UM), F. A. Jenkins, Jr. and C. R. Schaff (MCZ), L. Krishtalka (CM), and G. E. Lammers (MMMN). This study was supported by National Science Foundation grant BSR-84–06707.

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