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A NEW ARCTOCYONID FROM THE PALEOCENE OF WYOMING

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Since 1959, the Department of Geology of the University of Wyoming and the Museum of Comparative Zoology, Harvard University, have been carrying on a joint program of field and laboratory work in the later Mesozoic and earlier Cenozoic vertebrate-bearing formations of Wyoming, paying special attention to those deposits amenable to washing techniques. Much of the work accomplished thus far has been done in the Shotgun member (Keefer, 1961) of the Fort Union formation in the northern part of the Wind River Basin.

Within this member is a bone bed, some twelve to twenty-four inches in thickness, that is extraordinarily rich in vertebrate remains, mostly single teeth of mammals, crocodiles and small sharks. The bed occurs at the base of a sandstone (unit 20 of Keefer's section at Twin Buttes) 217 feet above the base of the Shotgun member, which is 1265 feet in thickness at this locality. Keefer has shown that overlying the lower Fort Union in this region are two essentially contemporaneous, interfingering rock units, the lacustrine (or marine?) Waltman shale and the marginal Shotgun member. The mammalian fauna from the bone bed in the Shotgun is a rich one. From Keefer's sample collection, Gazin (in Keefer, 1961) has recorded : Ptilodus, Mimetodon, Ectupodus, Anconodon, Eucosmodon?, Catopsalis, Peradectes?, Gelastops, Diacodon?, possibly Aphronorus, Pentacodon, possibly Zanycteris, cf. Pronothodectes, Claenodon. Tricentes, Periptychus, Anisonchus, Promioclaenus, Litomylus?, Gidleyina and Pantolambda. Our extensive collections will add a number of forms as the work of identification proceeds. The Shotgun member at Twin Buttes has vielded very little in the way of vertebrate material outside of the bone bed.² Thus far we have found only a

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² During the 1961 season a concentration similar to but less rich than that of the bone bed was found some 90 feet lower in the member.

few fragments of a medium-sized pantodont. We propose that the assemblage be known as the Shotgun local fauna, from the name of the member in which it occurs. The age, so far as can be determined at present, appears to be early Tiffanian. At Shotgun Butte, the type locality, where the member has a thickness of 2,830 feet (Keefer, 1961), *Phenacodus* sp. and *Plesiadapis* sp. cf. *P. cookei*, have been found in the upper part of the sequence (Keefer and Troyer, 1956).

We are greatly obliged to Dr. William R. Keefer for his help in the field. For the opportunity to examine comparative material we are indebted to Dr. C. Lewis Gazin, U. S. National Museum, Dr. Malcolm C. McKenna, The American Museum of Natural History, and Dr. Craig C. Black, Carnegie Museum. During the field season of 1960 we were assisted by James A. Jensen, Lee A. Wooderson, John Zamecnik, Floyd Andrews, Clyde T. Williams, Richard P. Timmermeyer, Charles P. Lyman, Jr., and Robert F. Wallin. The photographs are the work of Miss Linda Loring. The following abbreviations are used: A.M.N.H., American Museum of Natural History; M.C.Z., Museum of Comparative Zoology; U.W., University of Wyoming.

ARCTOCYONIDAE ¹ Murray

OXYCLAENINAE Matthew

Colpoclaenus²gen. nov.

Type species: C. keeferi sp. nov.

Known distribution: Paleocene, early Tiffanian, Wyoming.

Diagnosis: Enamel of molars strongly wrinkled, all crests crenulated, accessory cuspules numerous. Principal cusps of upper M high, massive, tightly grouped; central basin small; protocone nearly central in position with long lingual slope; conules large, blunt, separated by grooves from principal cusps; hypocone small on M^{1-2} , rudimentary on M^3 ; cingula strong, not continuous around protocones; external cingulum interrupted by labial continuation of sharp cleft between paracone and metacone; upper M wide relative to length. Trigonids of lower M high, short; paraconid internal in position, closely appressed to metaconid, paraconid crest well developed; posterior crest connecting protoconid

¹ One of us (B.P.) proposes to transfer the Arctocyonidae from the Creodonta to the Condylarthra. This transfer and the various questions that it raises will be discussed in a later paper.

²Kolpos, a fold and *claenus*; in allusion to the wrinkled enamel of the molars and, in particular, to the curiously folded trigonids.

and metaconid present; protoconids and metaconids with short, centrally situated crests running lingually and labially, respectively, forming a third, transverse trigonid crest; deepest portion of talonid basin near lingual side; hypoconulid of M_3 long, broad, high, cuspidate.

Colpoclaenus keeferi¹ sp. nov.

Type: M.C.Z. no. 8355, LM₃.

Hypodigm: Type and U.W. nos. 1931, LM_3 ; 1932, RM_3 ; 1933, LM^1 ; 1934, RM^3 ; 1935, LM_2 ; M.C.Z. nos. 8356, RM_3 (much worn); 8357, LM^2 ; 8358, RM_2 .

Horizon and locality: Shotgun local fauna, Shotgun member of the Fort Union formation; NE¹/₄ SE¹/₂, sec. 31, T. 6 N., R. 3 E., ³/₄ mile SW of the more northerly of the Twin Buttes, Fremont County, Wyoming.

Diagnosis: Sole known species of the genus diagnosed above.

DESCRIPTION

Colpoclaenus keeferi is notable for the massive, high, principal cusps of the upper molars, the elevated trigonids and the extremely rugose enamel. The latter feature disappears after very little wear, as is demonstrated by a moderately worn M_2 (M.C.Z. no. 8358). There can be, we believe, no doubt that the various lower molars represent the same species, and their association with the uppers would appear to be demonstrated by excellent occlusion between M.C.Z. no. 8357, LM^2 , and U.W. no. 1935, LM_2 , as well as by the general structure.

The upper molars are considerably wider than long, M^{1-2} being essentially quadrangular, M^3 suboval in outline. The protocone is the largest of the three principal cusps; its apex is a little lingual to the center of each tooth of the series, and its lingual face is very long and gently sloping, rather shorter in M^3 than in M^{1-2} . The paracone is more labial in position than the metacone and is slightly larger and higher, being approximately the same height as the protocone. Paracone and metacone are grooved on their basinward faces and are separated by a well marked cleft. The large blunt proto- and metaconules are separated from the primary cusps by grooves and are united by crests to the anterior and posterior cingulum respectively; the protoconule is smaller

¹ For Dr. W. R. Keefer who discovered the Shotgun bone bed in the course of his work on the Fort Union of the Wind River Basin.

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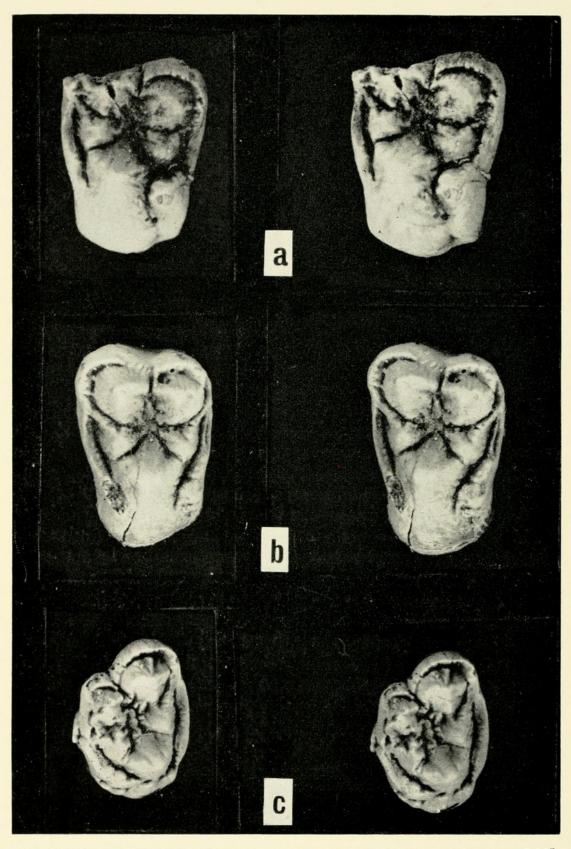
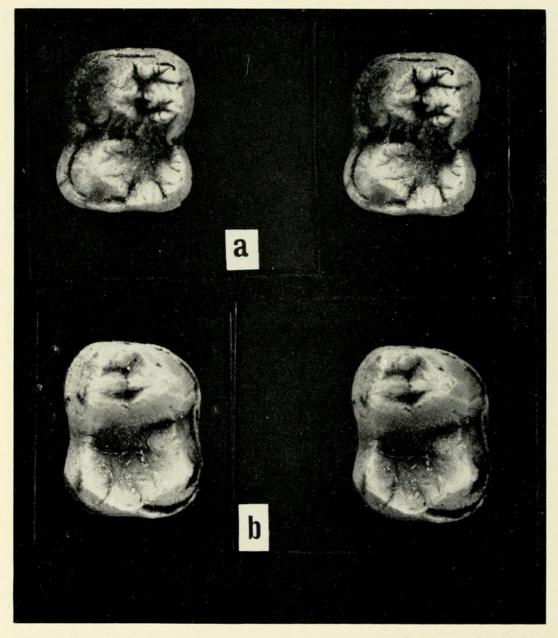


Figure 1. Colpoclaenus keeferi gen. et. sp. nov. Upper molars: a, LM², M.C.Z. no. 8357; b, LM¹, U.W. no. 1933; c, RM³, U.W. no. 1934. X3. Stereoscopic views.

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than the metaconule on M^{1-2} , about equal to it in size on M^3 . The rather shallow basin enclosed by these cusps and conules is situated in the labial half of the tooth and bears various poorly defined cuspules on its floor. A hypocone is differentiated on M¹⁻², on which it is considerably smaller than the conules, but is barely distinguishable on M³. Apart from an interruption on the external face, where the cleft between paracone and metacone continues on to the labial margin, a strong, crenulated cingulum runs from the hypocone around the tooth to the antero-internal corner, at which point the cingulum is broken in M^1 . M^2 shows no protostylar enlargement here and M³ a very slight one. With the exception of a slight rise in the cingulum at the parastylar site on M^3 , there is no indication of external styles. Anterior and posterior cingula extend farther lingually on M³ than on the preceding teeth and the two are almost united by a median lingual cuspule. Several cuspules are present on the posterior face of M³ above the cingulum.

M₂ is slightly constricted at the junction of trigonid and talonid but is otherwise nearly quadrangular in outline; the trigonid and talonid are approximately equal in length and width. The trigonid is somewhat higher than the talonid and narrows apically. The protoconid is a large massive cusp that forms nearly half of the trigonid. The heavy, cuspidate paraconid crest runs from the apex of the protoconid to the lingual side of the tooth, where the paraconid is poorly differentiated. The blunt metaconid is but little smaller than the protoconid and equal to it in height; the apices of the two cusps are connected by a papillate crest that is more lightly built than the paraconid crest. Blunt, wrinkled crests run directly lingually and labially down the facing slopes of the protoconid and metaconid. These abut (U.W. no. 1935) or fuse (M.C.Z. no. 8358) to form a third, central transverse crest. A sinuous, antero-posterior cleft partially separates the trigonid apex into labial and lingual halves. All this complicated structure is shallow and would rapidly be obliterated by wear. The posterior face of the trigonid is sloping and bears various small, papillate crests; that behind the metaconid is the most prominent but there is no trace on it of a metastylid. The very large, blunt hypoconid nearly equals the protoconid in size and makes up nearly half of the talonid. The cuspidate crista obliqua is low and fades away toward the base of the talonid. Two minor crests run forward from it to the trigonid base, isolating a very small fossette. The hypoconulid is low but relatively large, and in the



- Figure 2. *Colpoclaenus keeferi* gen. et sp. nov. M₂: *a*, U.W. no. 1935; *b*, M.C.Z. no. 8358. X3. Stereoscopic views.

unworn U.W. no. 1935 is tricuspidate and set off from the adjacent cusps by shallow grooves. As is shown by M.C.Z. no. 8358, it is obliterated as a distinct cusp after only a little wear. The entoconid is higher but scarcely larger than the hypoconulid and, like it, at least in U.W. no. 1935, is tricuspidate. From it a cuspidate ridge runs down to the base of the trigonid. The talonid basin is deepest in its anterolingual portion, and the floor bears a number of poorly defined cuspules. A strong, papillate cingulum runs from a point beneath the paraconid around the labial side of the tooth to the hypoconulid; in U.W. no. 1935, but not in 1962

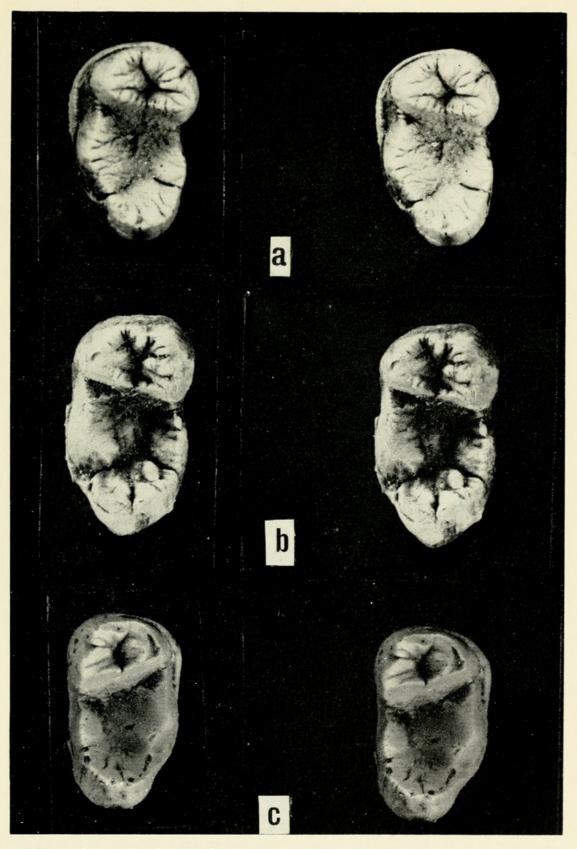


Figure 3. Colpoclaenus keeferi gen. et sp. nov. M₃: a, U.W. no. 1931; b, M.C.Z. no. 8355, type; c, U.W. no. 1932. X3. Stereoscopic views.

M.C.Z. no. 8358, this rises to a cuspule in the slight notch between trigonid and talonid.

The third molar is slightly narrower and rather longer than the second; it tapers bluntly toward the rear and, as in M₂, trigonid and talonid widths are approximately equal. The trigonid is shorter and conspicuously higher than the talonid, notably more so than in M_2 , tapers apically as on that tooth and is slightly oblique to the long axis, being longer on the lingual than on the labial side. The crown of the trigonid resembles that of M₂ in general, differing in the lesser development of the central transverse crest, which results in the formation of a shallow basin. The posterior face is nearly vertical, with wrinkled enamel. The hypoconid is the largest cusp of the tooth; it is low, blunt, elongate and bears a crest that is bowed laterally. The crista obliqua is lacking in U.W. no. 1931 and is represented only by vestigial, incomplete crestlets in the type and U.W. no. 1932; the hypoconid crest continues on to the base of the protoconid. The broad, flat-crowned hypoconulid is the highest of the talonid cusps and is almost as large as the hypoconid. It is set off by shallow grooves and is itself varyingly grooved and cuspidate. The entoconid resembles that of M_2 both in size and in structure. As on M_2 , the talonid basin is deepest antero-lingually and its floor is vaguely cuspidate; it is open anterior to the entoconid due to the absence of a crest on the posterior slope of the metaconid, which on the preceding tooth, together with the entoconid crest, forms a slight dam at this point. The external cingulum runs from the anterior face of the trigonid to the hypoconulid, showing some tendency toward formation of a cuspule between hypoconid and hypoconulid. The tooth is very slightly constricted at the junctions of the trigonid and talonid and of the hypoconulid with the adjacent cusps.

DISCUSSION

We have been able to compare the material referred to Colpoclaenus keeferi with specimens representing most of the described arctocyonids. Colpoclaenus is a very distinct genus; the combination of characters it presents — summed up in the diagnosis — separates it sharply from all other forms, although certain of them do approach it in one character or another. Anacodon resembles it in having accessory cuspules and strongly wrinkled enamel, and also in the possession of three transverse crests on the trigonid, as shown by an unworn M_2 of A. ursidens (A.M.N.H.

no. 92). Claenodon has moderately wrinkled enamel and comparable crests on the molar trigonids (Gazin, 1956, pl. 7, fig. 5). Other forms — Thryptacodon, Tricentes, Mimotricentes, Paradoxodon — have the enamel wrinkled to varving degrees but do not otherwise resemble Colpoclaenus. In Protogonodon the protocone has a fairly long lingual slope. The trigonid is high in Oxyclaenus, Chriacus, Spanoxyodon, Prothryptacodon, and Metachriacus. There is a tendency in some of these, especially in Prothryp*tacodon*, for the trigonid height to decrease from M_1 to M_3 ; in Colpoclaenus the trigonid is higher on M_3 than on M_2 . Colpoclaenus thus presents a curious combination of primitive characters, such as high principal cusps in the upper molars, high trigonids in the lowers, and advanced ones, such as a degree of wrinkling of the enamel and proliferation of accessory cuspules that is exceeded only in Anacodon. As the family is currently subdivided, Colpoclaenus must be placed in the Oxyclaeninae, but its acquisition of arctocyonine-like wrinkling perhaps gives added point to Simpson's suggestion (1937, p. 172) that the Arctocyoninae may be a partially artificial assemblage composed of several lines that were independently following similar adaptive trends.

The last lower molars of *Colpoclaenus* are quite primate-like in general appearance and in some structural details. When our knowledge of the animal was confined to these teeth and to the slightly worn M_2 we were persuaded that we were dealing with a primate astonishingly large for the Paleocene¹. Recognition of the upper molars rendered such an identification less likely and the finding of the unworn M_2 seems to us to have ended all possibility of it. We wryly sympathize with Cope and with Osborn and Earle who also at times believed an oxyclaenine (*Chriacus*) to be a primate.

			sicasurements	in min.		
		U.W. no. 1933	M.C.Z. no. 8357		U.W. no. 1934	
		M^1	M^2		M^3	
	L	7.1	8.0		6.4	
	W	11.2			8.8	
	U.W. no. 1935	M.C.Z. no. 8358	Type, M.C.Z. no. 8355	U.W. no. 1931	U.W. no. 1932	M.C.Z. no. 8356
	M_2	M_2	M_3	M_3	M_3	M_3
\mathbf{L}	8.8	9.1	11.2	10.5	10.4	10.9
W	7.0	7.6	6.4	6.3	6.2	6.3

Measurements in mm

¹ Unfortunately this enthusiasm found fleeting expression on page 9 of the Society of Vertebrate Paleontology News Bulletin No. 61, February, 1961.

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