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## PALEONTOLOGY AND GEOLOGY OF THE BADWATER CREEK AREA, CENTRAL WYOMING. PART 20. THE LATE EOCENE CREODONTA AND CARNIVORA

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### ABSTRACT

Though specimens of creodonts and carnivores are relatively rare in the Badwater Upper Eocene deposits, the six to eight taxa represented include a limnocyonid, several miacids, an amphicyonid, and a ?canid. The amphicyonid, *Daphoenus demilo*, new species, is the oldest known member of this family and retains some primitive, miacid-like characteristics.

### INTRODUCTION

Carnivores are one of the most incompletely represented groups of mammals in the Badwater Upper Eocene deposits. Only fifteen identifiable specimens of Carnivora and one of a creodont are known, representing six to eight taxa. The specimens include one nearly complete mandibular ramus, but for the most part consist of fragments of upper and lower jaws and isolated teeth. In many mammalian groups this record would provide no great detriment to determination of relationships, but in carnivores basicranial evidence has been found to provide fundamental clues to relationships (for example, Hunt, 1974:1039). This study of the Badwater carnivores, based almost entirely on dental evidence, cannot contribute the kind of information provided by the basicranium, but can give some indication of carnivore diversity during a faunally interesting interval. It also adds one family, the Amphicyonidae, to the North American Eocene record.

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Upper Eocene North American Creodonta and Carnivora have yet to be reviewed comprehensively. Most studies on Eocene carnivorous mammals still rely on Matthew (1909) for a comparative treatment, although Peterson's work (1919) on carnivores from the Upper Eocene of the Uinta Basin, Utah, and Stock's studies (1933, 1934, 1935) on carnivores from the Upper Eocene Sespe deposits of California contributed substantially to the record. Work now in progress (MacIntyre on miacids; Gustafson on Late Eocene to Oligocene carnivores and creodonts of the Vieja area, Texas; Hunt on Oligocene amphicyonids) can be expected to put the Upper Eocene in better perspective.

#### ACKNOWLEDGMENTS

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#### ABBREVIATIONS

Collections are identified by the following abbreviations: AMNH, American Museum of Natural History; CM, Carnegie Museum of Natural History; LACM, Los Angeles County Museum; TT, Museum of Texas Tech University; USNM, National Museum of Natural History.

#### LOCALITIES

Previous parts of this series (Black and Dawson, 1966; Black, 1974) provide information on the localities from which the mammals described here were collected.

#### SYSTEMATIC DESCRIPTIONS

Order Creodonta  
Family Limnocyonidae  
*Limnocyon* ?sp.

*Specimen*.—USNM 21088, maxillary fragment with P<sup>4</sup>.

*Locality*.—5. Uintan.

*Discussion*.—This, the only creodont known from the Badwater Eocene deposits, was described by Gazin (1956:9). It is smaller than *Limnocyon potens* (= *L. douglassi*) from the early Uintan (Washakie B, Uinta B). The Badwater specimen is inadequate to serve as more than a record of the occurrence of a creodont in the faunas.

Order Carnivora  
Family Miacidae  
*Tapocyon* cf. *T. robustus*

*Specimens*.—CM 17500, right maxillary fragment with P<sup>4</sup>–M<sup>1</sup>; USNM 21087, left jaw with P<sub>4</sub>–M<sub>2</sub>; CM 16894, left P<sub>2</sub>; CM 15991, left P<sub>4</sub>; CM 16776, right M<sub>1</sub> trigonid.



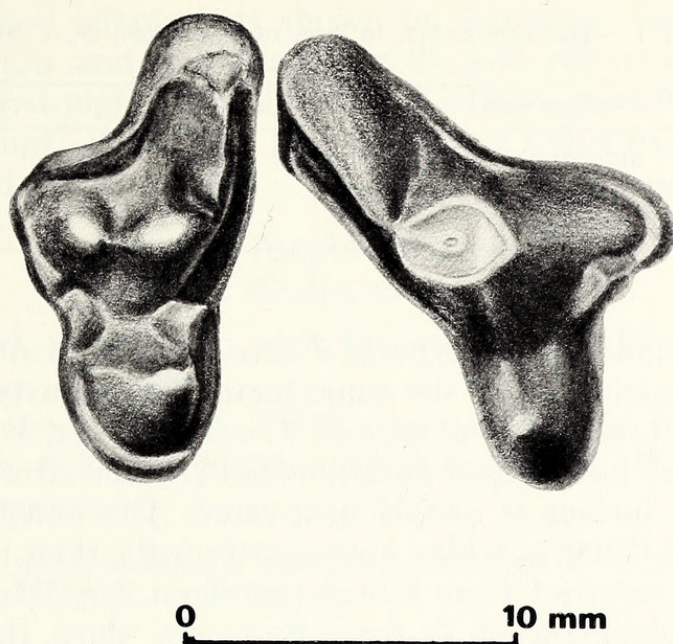


Fig. 1.—*Tapocyon* cf. *T. robustus*, CM 17500, right P<sup>4</sup>–M<sup>1</sup>, occlusal view.

*Localities*.—5, 6, 7. Uintan.

*Descriptions and comparisons*.—Of the five specimens referred to *Tapocyon* from the localities in the Badwater Upper Eocene, no two were associated, but similarity to the better sample of *Tapocyon occidentalis* from the Tapo Ranch fauna, in the Upper Eocene Sespe Formation (Stock, 1934), supports their reference to this genus. Size agreement within the Badwater sample suggests that one species is present.

Known species of *Tapocyon* include *Tapocyon occidentalis* Stock, 1934, from the Sespe, and *Tapocyon robustus* (Peterson, 1919), based on a lower jaw with P<sub>4</sub>–M<sub>2</sub> and associated partial postcranial skeleton from the Myton member, Uinta Formation of Utah. Peterson (1919:50–52) referred the latter questionably to *Prodaphoenus*, pointing out that a new genus may be represented. Stock (1934:425–426) referred *P.* (?) *robustus* to *Tapocyon*, showing that *T. occidentalis* and *T. robustus* are very similar, the main differences being that the former is slightly smaller in overall size and has a wider posterointernal expansion on P<sub>4</sub>.

The specimens of *Tapocyon* from Badwater differ in a few features from those of *T. occidentalis* and *T. robustus* but there is no great morphological gap between the California, Utah, and Wyoming samples. The jaw from Badwater, USNM 21087, referred to by Gazin (1956:9) as *Miacis* cf. *robustus* (Peterson, 1919) is less deep than in *T. occidentalis* and *T. robustus*. The maxillary fragment with P<sup>4</sup>–M<sup>1</sup>, CM 17500, the teeth complete except for the paracone tip on P<sup>4</sup> (Fig. 1),



Table 1.—*Measurements, in mm, of Tapocyon cf. T. robustus.*

Measurements	CM 17500
P <sup>4</sup> anteroposterior	16.5
M <sup>1</sup> anteroposterior	6.8
M <sup>1</sup> transverse	14.4

is generally similar to the type of *T. occidentalis*, LACM (CIT) 1654, a maxillary fragment with the same teeth. The parastylar region of P<sup>4</sup> in CM 17500, broken in the type of *T. occidentalis*, is well developed and has a small but distinct anteromedial cuspule. Between P<sup>4</sup> and M<sup>1</sup> the maxillary surface is deeply excavated. The parastylar projection of M<sup>1</sup> in CM 17500 is wider anteroposteriorly than in LACM (CIT) 1654 and in a referred Tapo Ranch specimen, LACM (CIT) 1651.

The two specimens of P<sub>4</sub> from Badwater show that this tooth is somewhat variable. In USNM 21087, P<sub>4</sub> is less expanded posterointernally than in CM 15991. *Tapocyon occidentalis*, LACM (CIT) 1650, is between the two Badwater specimens in amount of posterointernal expansion of P<sub>4</sub>. Stock (1934:425) used the narrower posterior part of P<sub>4</sub> in *T. robustus* as a feature to differentiate this specimen from *T. occidentalis*. Variation in this character within the Badwater sample suggests that it may not be reliable. The paraconid of P<sub>4</sub> in both Badwater specimens and *T. robustus* is more anteroposteriorly oriented, less transverse, than in *T. occidentalis*.

*Tapocyon* is characterized by a reduced talonid of M<sub>1</sub> and a small M<sub>2</sub>. *Tapocyon occidentalis* has the greatest reduction, with a narrow, somewhat elongated M<sub>1</sub> talonid, and the smallest M<sub>2</sub>, especially reduced in the talonid. In USNM 21087 the talonid of M<sub>1</sub> has a broken surface but its outline appears transversely wider than in *T. occidentalis*; in the Badwater specimen M<sub>2</sub> is larger than in *T. occidentalis*. *T. robustus* is at the large end of the spectrum, with a transversely wider, anteroposteriorly shorter talonid of M<sub>1</sub> and largest M<sub>2</sub>.

*Relationships.*—The samples of *Tapocyon* from Wyoming, Utah, and California appear to form a closely related group, all occurring in the Late Uintan. The Wyoming sample seems slightly closer to that from Utah than to that from California, mostly on the basis of the better development of the talonid of M<sub>1</sub> and of M<sub>2</sub> in the former two. More complete material from Wyoming and Utah may show that *Tapocyon* from these two geographic areas are distinct specifically, but at present no specific distinction is recognized. The Badwater material yields no new information on the position of *Tapocyon* within the Miacidae. Stock (1934) emphasized its rather aberrant position within the family. The aberrant features appear to be mostly in the direction



of some "cat-like" adaptations shown by *Tapocyon* including some premolar reduction, and the structure of the jaw, robust anteriorly and with a relatively straight ventral border (Galiano, personal communication, 1979; Hunt, 1974:1039, for *Uintacyon robustus* = *Tapocyon robustus* as used here).

#### Family Amphicyonidae

##### *Daphoenus demilo*, new species

*Type specimen*.—CM 15596, right jaw with  $P_1$ ,  $P_3$ – $M_1$ , Wood locality. Duchesnean.

*Referred specimens*.—CM 35871, right maxillary fragment with  $M^{1-2}$ ; CM 35872, right jaw fragment with broken  $P_3$ ,  $P_4$ – $M_2$ ; both locality 20. Duchesnean.

*Etymology*.—The name, a classical allusion, is dedicated to our volunteer worker, Lee Schiffer, and her timeless brand of humor.

*Specific characters*.—Small species of *Daphoenus*. Lower teeth closely spaced except  $P_1$ , which has diastemata anterior and posterior to it.  $M_1$  trigonid less open than in other species of genus.  $M_2$  with well developed paraconid.  $M^1$  with buccal shelf well developed.

*Description*.—The jaw of the type specimen, CM 15596 (Fig. 2), is slender with a gently curved ventral border. One mental foramen occurs in a line below the diastema behind  $P_1$  and the second, smaller foramen is higher on the jaw in a line below the talonid of  $P_2$ . The teeth preserved in this specimen,  $P_1$ ,  $P_3$ ,  $P_4$ , and  $M_1$ , are well worn; the lower canine,  $P_2$ ,  $M_2$ , and  $M_3$  are broken off but their position and approximate size can be determined. The lower canine is represented only by the large root.  $P_1$  is a stubby, single rooted tooth with the worn crown elongated anteroposteriorly; it is separated from the canine and  $P_2$  by diastemata.  $P_2$  appears to have been closely appressed to  $P_3$ , and the worn  $P_3$  to  $P_4$ .  $P_4$ , a larger tooth than  $P_3$ , has a tiny anterior cuspule and a well developed posterior accessory cusp situated posterobuccal to the main cusp; the talonid is bordered by a cingulum and bisected by a longitudinal crest.  $M_1$ , the largest tooth, has at this stage of wear the metaconid worn lower than the paraconid; the basined talonid is slightly narrower than the trigonid. The alveoli show that  $M_2$  was two rooted and the trigonid alveolus is slightly wider than that of the talonid.  $M_3$  was also two rooted; the trigonid alveolus is about as wide as the talonid alveolus of  $M_2$ ; the talonid alveolus is shorter anteroposteriorly than the trigonid alveolus.

The referred incomplete jaw, CM 35872, has less worn teeth. The very incomplete  $P_3$  suggests that a posterior accessory cusp was present. The talonid of  $P_4$  is wider than in the type due to its expansion both buccally and lingually. At this stage of wear the metaconid of  $M_1$  is higher than the paraconid.  $M_2$  is well developed, with the paraconid only slightly smaller than the metaconid and an elongated, basined talonid nearly as wide as the trigonid.

With such a small sample, one jaw from Wood locality and one from locality 20, it is difficult to determine whether the dental differences between these specimens represent variation or a specific difference. The specimens are treated here as representing one species. Other faunal evidence suggests that the specimens from Wood locality and locality 20, though not exactly the same in age, are younger than those from the other Badwater Upper Eocene localities.

In the maxillary fragment, CM 35871 (Fig. 3),  $M^1$  is slightly worn with wear facets



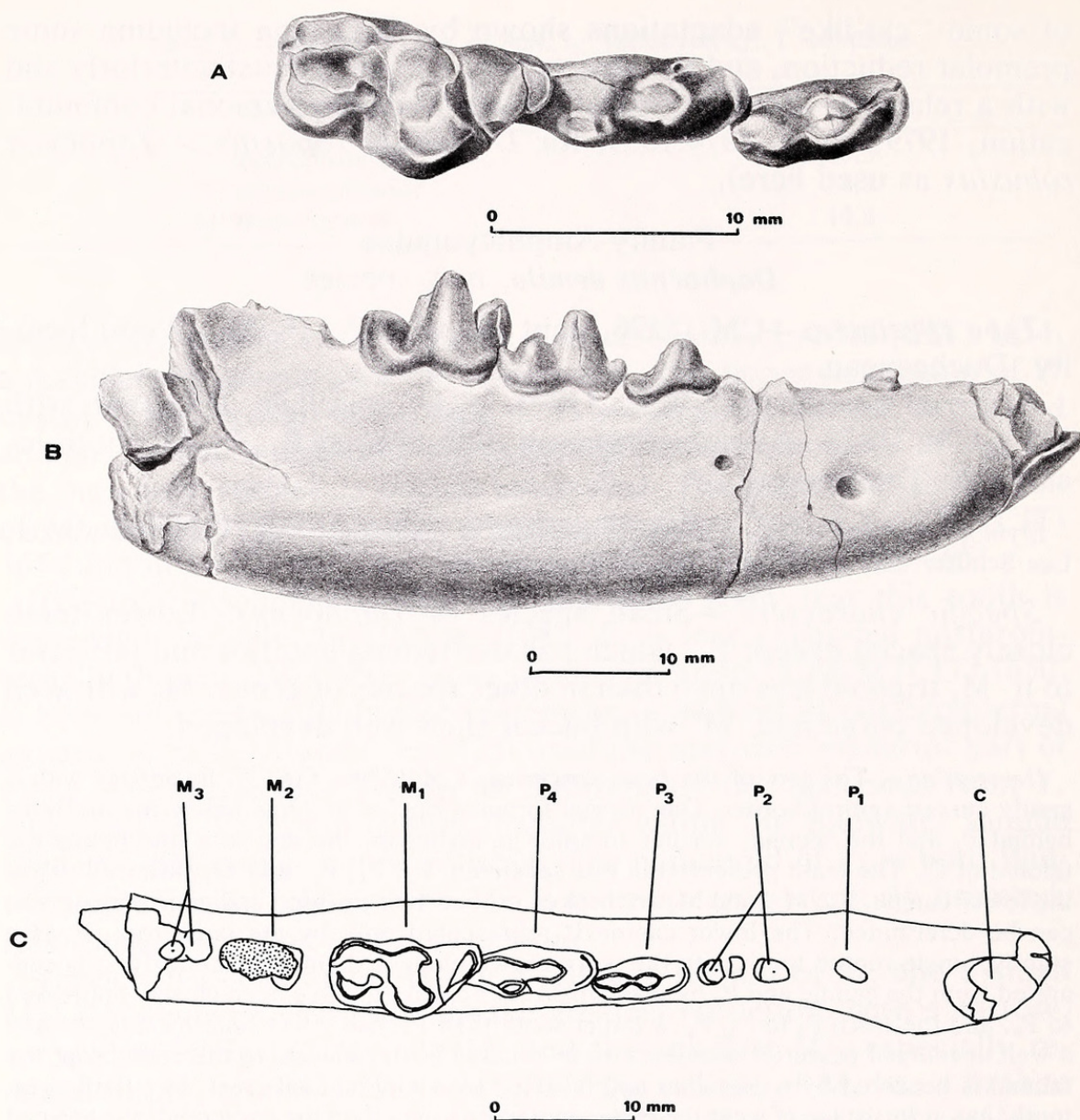


Fig. 2.—*Daphoenus demilo*, CM 15596, holotype. A) Occlusal view of P<sub>3</sub>–M<sub>1</sub>; B) Lateral view of jaw; C) Occlusal view of jaw; broken M<sub>2</sub> stippled.

present on the anterior surface between paracone and parastyle, the posterior slope of the paracone, and the top of the metacone. M<sup>1</sup> has a distinct shelf buccal to the paracone and metacone, on which a ridge extends from the paracone to the rounded anteroexternal parastyle, and with a raised anteroposterior crest near the buccal border. The protocone is situated at the apex of a V-shaped basin. The paraconule is distinct, the metaconule somewhat less so. The internal cingulum is well developed, especially posterolingually, and extends as a narrower shelf around anterior and posterior sides of the tooth, at least to a line with the conules. The buccal part of M<sup>2</sup> is broken away, but the more lingual part preserved shows a V-shaped basin buccal to the protocone, a well developed internal cingular shelf that is relatively better developed anterolingually than on M<sub>1</sub>, and with anterior and posterior extensions along the sides of the tooth. The specimen is too incomplete to give any indication of M<sup>3</sup>.



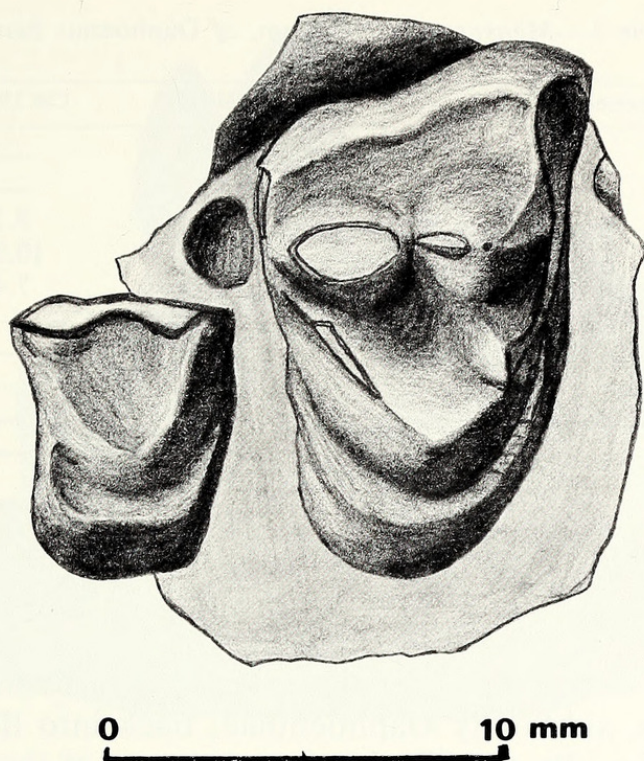


Fig. 3.—*Daphoenus demilo*, CM 35871, occlusal view of right maxilla with  $M^{1-2}$ .

*Comparisons and relationships.*—Reference of this Late Eocene species to the genus *Daphoenus* is based on the following combination of characters: robustly developed  $M^1$  and  $M^2$  (so far as known);  $M^1$  with well-developed cingulum across entire lingual wall; spacing of lower premolars with some gaps anteriorly, crowding posteriorly;  $P_4$  with well-developed posterior accessory cusp posteroexternal to the main cusp; structure of  $M_{1-2}$  with wide basined talonid on both,  $M_2$  relatively well developed. *Daphoenus demilo* is more primitive than other species of *Daphoenus* in the well-developed buccal shelf on  $M^1$ , a feature characteristic of miacids, the less open trigonid of  $M_1$ , and the better developed paraconid of  $M_2$ . Other species of *Daphoenus* usually show more spacing of the anterior premolars than in *D. demilo* with a diastema posterior to  $P_2$ .

*Daphoenus demilo* is less like the other daphoenines, *Daphoenocyon* and *Daphoenictis*. *D. demilo* differs from *Daphoenocyon* in having a more slender jaw, lower premolar spacing, and less bulbous  $P_4$ – $M_2$ . The referred specimen of *D. demilo* from locality 20 does show some suggestion of *Daphoenocyon* in the expanded talonid of  $P_4$ , although the expansion is only slightly greater than in other species of *Daphoenus*. The peculiar cat-like *Daphoenictis* is very unlike *D. demilo* in its elevated  $P_3$ , emphasis on the posterior accessory cusp on  $P_{3-4}$ , and the reduced, shearing structure of  $M_1$ .



Table 2.—*Measurements, in mm, of Daphoenus demilo.*

Measurements	CM 15596	CM 35872	CM 35871
P <sub>1</sub> anteroposterior	2.9	—	—
P <sub>3</sub> anteroposterior	7.0	—	—
P <sub>4</sub> anteroposterior	9.5	9.1	—
M <sub>1</sub> anteroposterior	11.0	10.9	—
M <sub>2</sub> anteroposterior (alveolar)	5.4	7.4	—
M <sub>3</sub> anteroposterior (alveolar)	3.4	—	—
P <sub>1</sub> –M <sub>3</sub> anteroposterior (alveolus of M <sub>3</sub> )	50.1	—	—
P <sub>1</sub> –P <sub>4</sub> anteroposterior	30.0	—	—
M <sub>1–3</sub> anteroposterior (alveolus of M <sub>3</sub> )	21.8	—	—
Depth jaw at M <sub>1</sub>	17.0	—	—
M <sup>1</sup> anteroposterior	—	—	7.5
M <sup>1</sup> transverse	—	—	12.5

*Discussion.*—*Daphoenus demilo* extends the record of the family Amphicyonidae, subfamily Daphoeninae, back into the Late Eocene in North America. By the Chadronian presence of three distinct lines of daphoenine development shows considerable divergence of the group in North America, from the relatively conservative *Daphoenus* (Russell, 1972) to *Daphoenocyon* (Hough, 1948) and the cat-like *Daphoenictis* (Hunt, 1974). So far as known only *Daphoenus* continued throughout the Oligocene. (The entire complex and the apparently closely related amphicyonids of Europe are under review by Hunt.)

Family ?Canidae  
*Procynodictis vulpiceps*

*Specimen.*—CM 37480, right jaw fragment with M<sub>1–2</sub>.

*Locality.*—1. Uintan.

*Discussion.*—The only specimen of this taxon from the Badwater deposits (Fig. 4) generally resembles the type of *Procynodictis vulpiceps*, AMNH 2514 (“*Diplacodon* beds”), and referred specimens, AMNH 1995 and 2506, both from the base of Uinta C. The main differences of CM 37480 from the type are in the former the trigonid of M<sub>1</sub> is somewhat more closed and M<sub>2</sub> is smaller, especially in the talonid. M<sub>2</sub> in AMNH 2506 is closer in size to that of the Badwater specimen, so size of M<sub>2</sub> appears variable and is not considered a character to prevent reference of the Badwater specimen to *P. vulpiceps*.

The fortunate occurrence of a forelimb with the jaw of the type of *P. vulpiceps* (Wortman and Matthew, 1899) showed that this form had technically become a canid by having a carpus with fused scapholunar bone. There is no basicranial evidence on the affinities of *Procynodictis* and certainly no sharp dental differences separate *P. vulpiceps* from



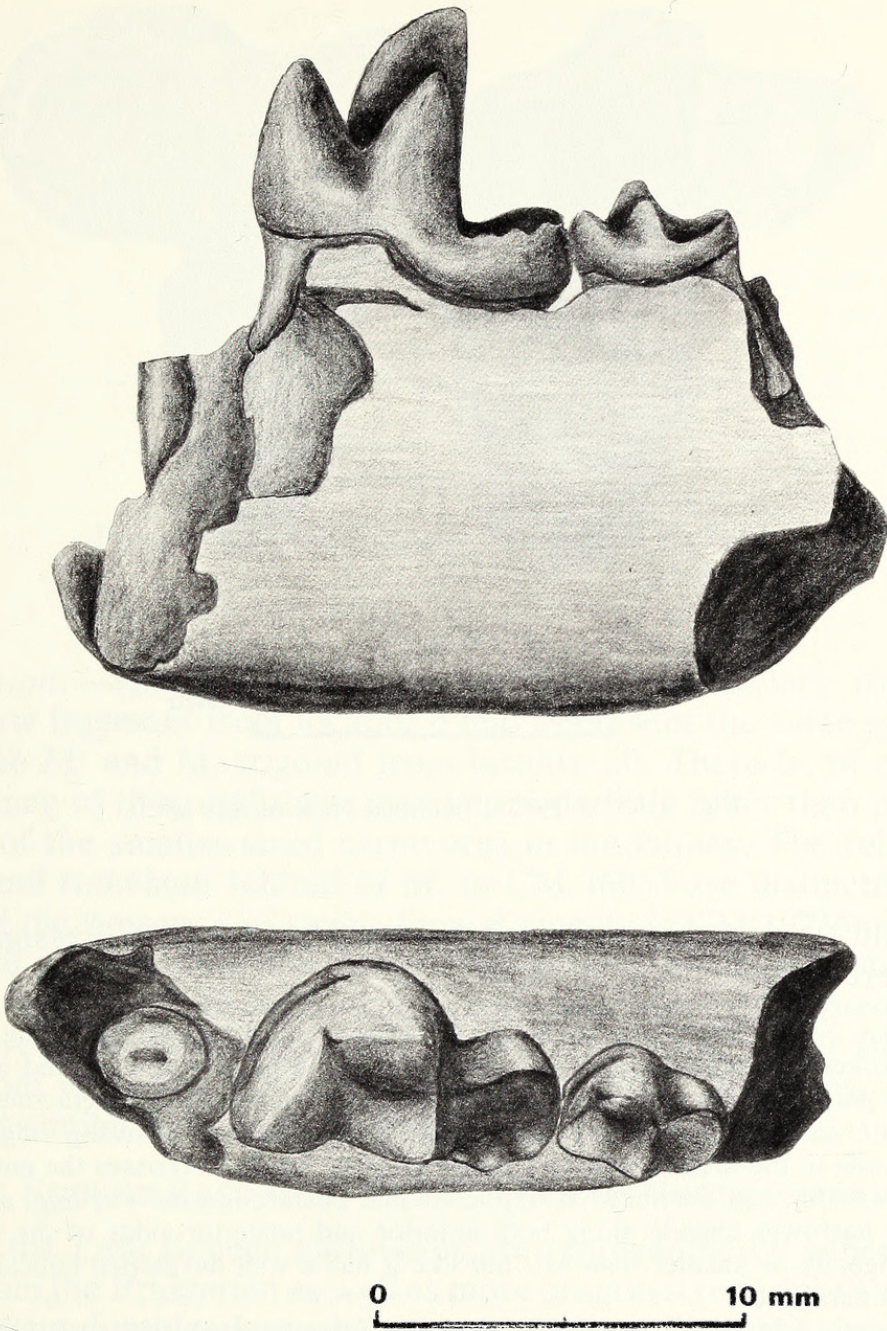


Fig. 4.—*Procynodictis vulpiceps*, CM 37480. Top, medial view of jaw fragment; bottom, occlusal view with  $M_{1-2}$ .

miacids. *Procynodictis*, as well as the possibly closely related *Miacis gracilis* Clark, 1939, and *Plesiomiakis* Stock, 1935, illustrate not only the progressive nature of some Uintan carnivores but also the difficulties of determining relationships in the group.

#### Family Indet.

Five incomplete specimens cannot be referred with assurance to any genus. Their dental characters are suggestive of the miacid-canid-am-



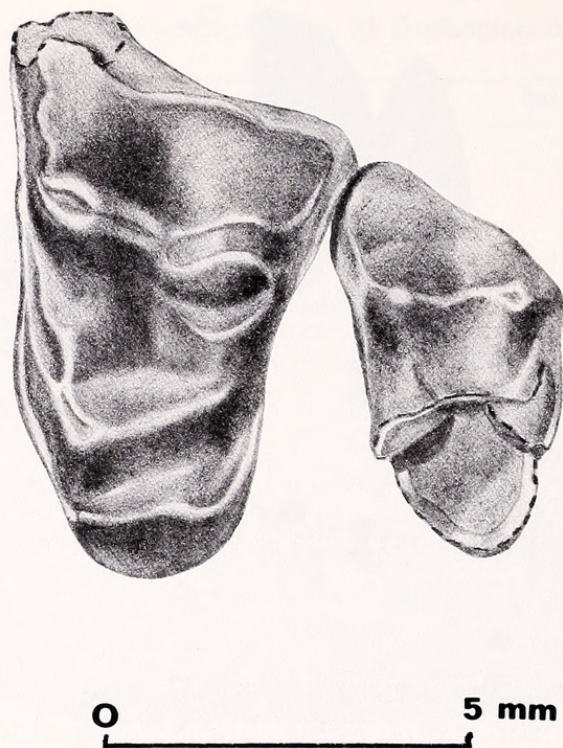


Fig. 5.—CM 19735, occlusal view of left  $M^{1-2}$ .

phicyonid type of carnivore development but no family assignment is given here.

*Specimen*.—CM 19735, locality 6, left maxillary fragment with  $M^{1-2}$  (Fig. 5).  $M^1$  is slightly broken buccally but appears to have had a wide buccal shelf and a distinctly projecting parastyle; the paracone is much more prominent than the metacone, and both protoconule and metaconule are present; the protocone has a strong ridge from its posterior side to the metaconule; the strong internal cingulum crosses the entire lingual side of the tooth, has a somewhat hypocone-like posterointernal swelling, and is continued by narrower cingula along both anterior and posterior sides of the tooth.  $M^2$ , broken lingually, is smaller than  $M^1$ , but like it has a well developed buccal shelf and prominent paracone.

*Specimens*.—CM 16053, locality 6, right jaw fragment with broken  $P_4$ – $M_1$  (Fig. 6), and CM 15583, locality 5A, trigonid of left  $M_1$ . On  $P_4$  anterior and posterior accessory cusps are distinct; a ridge extends from the posterior surface of the posterior cusp to end in a small cuspule; the talonid is wider lingually than buccally and is surrounded by a cingular shelf. The trigonid of  $M_1$  in CM 16053 is broken but that of CM 15583, probably the same species, is distinctly triangular. The talonid of  $M_1$  has a buccal cingulum; the hypoconid crest is thus not buccally situated and the heel is trenchant, somewhat as in *Uintacyon*. Perhaps the most striking feature of CM 16053 is the large size of  $P_4$  relative to  $M_1$  (see table of measurements).

*Specimen*.—CM 29063, locality 20, left  $M^1$ , broken buccally. This specimen is smaller than CM 19735 but resembles it in having a well developed lingual cingulum that extends along the entire lingual wall and connects to a narrower shelf along the anterior wall of the tooth.

*Specimen*.—TT 5955, locality 20, trigonid of left  $M_1$ .



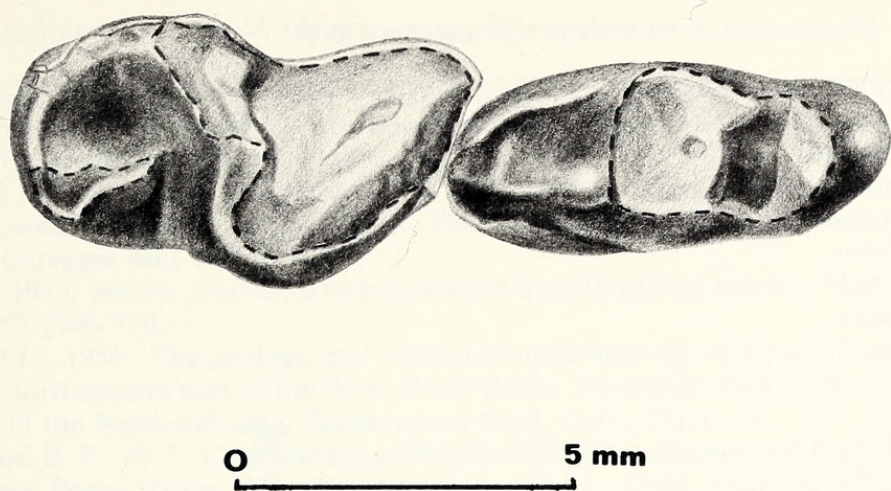


Fig. 6.—CM 16053, occlusal view of right P<sub>4</sub>–M<sub>1</sub>.

*Discussion.*—Size similarity suggests that the maxillary fragment and the jaw fragment from locality 6 may represent the same species, as may the M<sup>1</sup> and M<sub>1</sub> trigonid from locality 20. There is, of course, no assurance of this, and these specimens do little other than provide a record of the smaller-sized carnivores in the faunas. The relatively large P<sub>4</sub> and trenchant talonid of M<sub>1</sub> in CM 16053 are distinctive features, and the presence of strong lingual cingula in CM 19735 and CM 29063 lend a somewhat daphoenine appearance to these specimens. That this type of upper molar morphology was more widespread than has been recognized is suggested by some specimens, under study by Emry, from the early Chadronian of Bates Hole, Wyoming, with a somewhat similar development of M<sup>1</sup>.

LATE EOCENE RECORD OF CARNIVORES IN NORTH AMERICA

During the Late Eocene carnivores are represented by genera continuing from the Bridgerian as well as more progressive forms (Table 4). The hyaenodontids show the greatest generic diversity during the entire interval, although this can be broken into the Uintan survival of

Table 3.—Measurements, in mm, of CM 16053.

Measurements	
P <sub>4</sub> anteroposterior	6.7
P <sub>4</sub> transverse	2.9
M <sub>1</sub> anteroposterior	6.8
M <sub>1</sub> transverse	3.9
Depth jaw at M <sub>1</sub>	12.8



Table 4.—*Distribution of named carnivore genera in the North American Late Eocene.*

Taxa	Early Uintan <sup>1</sup>	Late Uintan <sup>2</sup>	Duchesnean <sup>3</sup>
<b>Hyaenodontidae</b>			
<i>Limnocyon</i> <sup>4</sup>	×	×	
<i>Oxyaenodon</i>	×		
<i>Apataelurus</i>	×		
<i>Proviverra</i> <sup>4,5</sup>		×	
<i>Hyaenodon</i>			×
<i>Pterodon</i>			×
<b>Miacidae</b>			
<i>Miacis</i> <sup>4</sup>	×	×	
<i>Uintacyon</i> <sup>4</sup>	×	×	
<i>Tapocyon</i>		×	
<i>Plesiomiacis</i> <sup>6</sup>		×	
<b>Canidae?</b>			
<i>Procynodictis</i>		×	
<b>Amphicyonidae</b>			
<i>Daphoenus</i>			×
<b>Family Indet.</b>			
<i>Eosictis</i>		×	

<sup>1</sup> Washakie B, Wagonhound, Poway.<sup>2</sup> Myton, Halfway, Tapo Ranch, Badwater localities 5, 6, 7.<sup>3</sup> Lapoint, Pearson Ranch, Badwater localities Wood, 20.<sup>4</sup> Occurs also in Bridgerian.<sup>5</sup> *Mimocyon longipes* Peterson, 1919, appears referable to *Proviverra*.<sup>6</sup> Possibly closely allied to *Procynodictis*.

two Bridgerian genera and presence of two new forms, and the Duchesnean appearance, apparently following immigration from Eurasia, of *Hyaenodon* and *Pterodon*. Miacids are well represented and include progressive forms, such as *Miacis gracilis*, showing some canid-like features. Basicranial evidence is not available for the Late Eocene miacids, except *M. gracilis*. Although *Procynodictis* has been referred to the Canidae, this is based on postcranial evidence, and in the absence of basicranial evidence relationships among the Late Eocene miacids and *Procynodictis* and between these and later carnivores are not clearly established.

No felids or machairodontids are known. Somewhat cat-like dental adaptations are shown, however, by the hyaenodontid *Apataelurus*, the miacid *Tapocyon*, and *Eosictis*, a form of uncertain familial allocation.



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