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**A New Subfamily, Conacodontinae,
and New Species,
Conacodon kohlbergeri, of the
Periptychidae (Condylarthra, Mammalia)**

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(Received 1 October 1982)

Abstract

An associated palate and dentaries from the early Paleocene (Puercan), San Juan Basin, New Mexico, are the type of a new species, *Conacodon kohlbergeri*. This species is cladistically most closely related to *C. entoconus*. Both species lack the paracoid on P₃₋₄ and have a more complete precingulum on the upper molars. Both *Conacodon* and *Oxyacodon* have a lingually expanded hypocone and lack the protocone on P³. These two genera are included in a new subfamily, Conacodontinae. A trichotomy between this subfamily, the Anisonchinae, and Periptychinae cannot be resolved at present.

Key Words

Mammalia, Condylarthra, Periptychidae, Conacodontinae, *Conacodon*, *Conacodon kohlbergeri*, systematics, cladistics, Paleocene of western North America.

Introduction

During the summer of 1981 a joint Yale-U.S. Bureau of Land Management group examined the stratigraphic position of localities in the lower Paleocene portion of the Nacimiento Formation, San Juan Basin, New Mexico. The study concentrated on the stratigraphic intervals in Betonie-Tsosie, Kimbetoh, and Barrel Springs (De-na-zin Wash) arroyos that have classically yielded Puercan mammals. Although the study was primarily stratigraphic, fossil vertebrates were also collected. One of the specimens recovered from Kimbetoh Arroyo was a palate with associated dentaries. In this paper the specimen is described and designated as the holotype of a new species of the periptychid *Conacodon*. A new subfamily, the Conacodontinae, is also recognized for *Conacodon* and *Oxyacodon*.

Methodology

Measurements

The measurements of all specimens described and discussed in this paper were done on an Ehrenreich Photo Optical Shopscope. The various dimensions were measured to the nearest one-hundredth millimeter and rounded to the nearest one-tenth millimeter. The measurements in Table 1 follow definitions given in Archibald

(1982) and utilized in Archibald et al. (1983) with one exception. In Archibald (1982) the anterior width and posterior width of upper molars were measured from the lingualmost point of the protocone to the anterolabial and posterolabial corners of the tooth, respectively. In the measurement of specimens of *Oxyacodon* in Archibald et al. (1983), the more lingually placed hypocone served as the lingualmost point for both the anterior and posterior width. In order to indicate the lingually expanded hypocone found in a number of periptychids, we have measured the anterior width from the lingualmost point of the protocone (as in Archibald 1982) and the posterior width from the lingualmost point of the crown. In this instance, the hypocone is decidedly more lingual, but in some other periptychid taxa the protocone is more lingual. Thus *H* in Table 1 is the distance from the lingualmost point of the hypocone to the lingualmost point of the protocone measured normal to length.

Systematics

Cladistic methodology was employed in this study to help discern phylogenetic relationships (Eldredge and Cracraft 1980; Nelson and Platnick 1981; Wiley 1981). For cladistics, as for any systematic methodology, there are many opinions regarding its application. We have been admittedly less cladistic in our approach to classification than in our approach to phylogenetic reconstruction. For example, we have given formal designation to non-monophyletic taxa (e.g., the genus *Oxyacodon*) and have not named each dichotomous branching (e.g., the clades within the genus *Conacodon*). This may be an anathema to some cladists, but there is no single accepted method of cladistic classification and we are far more interested in the baby (phylogenetic reconstruction) than the bath water (classification). Similarly, there is no single cladistic approach to phylogenetic reconstruction beyond grouping taxa on

the basis of shared-derived character-states.

Most of our approach is self-explanatory, but a few points should be made explicitly. No formal weighting technique was employed in the character analysis. However, by simply choosing the 19 characters used in this study, weighting of a sort has been imposed. Further, derived states of certain characters (e.g., lingually expanded hypocone, character 7) were deemed more important because they can be interpreted to be structurally more complex and were rarer occurrences among the taxa considered. Characters that were more poorly understood, however complex they might be (e.g., the region of the postmetacnule wing, meta- and postcingulum, character 12), were given less weight. Polychotomous branchings were not resolved if our present knowledge did not seem to warrant such a step.

The polarity of morphoclines was assessed by comparison with a single out-group species, *Protungulatum donnae*, and with what appears to be the most primitive periptychid, *Mimatuta morgoth*. This is not meant to imply that out-group comparison is the best or only way to assess polarity. Rather limits must be set on the group to be analyzed and the choice of *P. donnae* is reasonable. The basis for assessing that *P. donnae* is primitive for all 19 characters used in this study is more speculative, but is a justifiable starting point. (See "Discussion" for further comments.)

Material and Provenience Data

The type specimen of *Conacodon kohlbergi*, UNM B1700, along with other specimens of typical Puercan mammals, was found weathering out of the top of a 20-to-25 cm dark gray (carbonaceous) mudstone by R. M. Schoch, 21 June 1981. This "lower black streak" (BLM loc. 1711) is a thin but well-exposed bed occurring in the southeast wall of Kimbetoh Arroyo low in the Nacimiento Formation. Based upon

our measurements the bed is approximately 10.7 m above the underlying local contact with Ojo Alamo Sandstone.

The three referred specimens of *Conacodon kohlbergeri* were located in the AMNH collections. All three are from the San Juan Basin, New Mexico (see Hypodigm). Two of the specimens, AMNH 16525 and 58346, had been identified as *Conacodon cophater* and the other, AMNH 58347, as *Anisonchus gillianus*.

The specimens of *Conacodon cophater* and *C. entoconus* used in this study are also from the AMNH San Juan Basin collection. The measurements of these specimens as well as those of other taxa noted in the text are available from the senior author.

Exact locality data, when known, should be obtained from the institutions housing the specimens.

Systematic Paleontology

Order Condylarthra Cope, 1881
 Family Periptychidae Cope, 1882b
 Subfamily Conacodontinae, new subfamily

Type genus

Conacodon Matthew, 1897.

Included genera

Conacodon Matthew, 1897 and
Oxyacodon Osborn and Earle, 1895.

Distribution

Early Paleocene (Puercan) of New Mexico, Utah, and Montana.

Diagnosis

Periptychids with hypocone on M¹⁻³ large and lingually expanded, and protocone on P³ absent.

Discussion

Based on a cladistic analysis of the characters noted in the diagnosis and which are discussed later in this paper, *Conacodon* and *Oxyacodon* constitute a monophyletic group relative to other periptychids. (Archibald et al. 1983; Rigby 1981; Van Valen 1978). In order to indicate this relationship we propose the recognition of a new subfamily, the Conacodontinae.

Genus *Conacodon* Matthew, 1897

Conacodon kohlbergeri, new species
 (Figs. 1, 2, 3 and Table 1)

Holotype

UNM B1700, palate with right P⁴, M¹⁻², left P³⁻⁴, M¹⁻², isolated right P², bone fragment with right P³, right dentary with P₄, M₁₋₃, left dentary with P₃₋₄, M₁, isolated right P₂, and bone fragments, Nacimiento Formation, BLM loc. 1711, "lower black streak" locality, Kimbetoh Arroyo, San Juan Basin, San Juan County, New Mexico.

Hypodigm

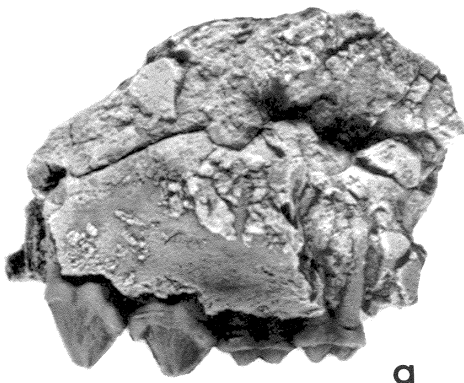
AMNH 58346, left maxilla with P⁴, M¹⁻²; probably AMNH 16525, palate with right P³⁻⁴, M¹ fragment, M²⁻³, and left P⁴, M¹⁻²; AMNH 58347, left dentary with M₂₋₃. Labels indicate AMNH 58346 and 58347 are from the 1958 expedition to Tsosie while AMNH 16525 was collected "3 mi. E. of Kimbetoh" in 1913. All are, or probably are from the Nacimiento Formation, Betonie-Tsosie Arroyo, San Juan Basin, San Juan County, New Mexico.

Distribution

Early Paleocene (Puercan) of New Mexico.

Etymology

For William (Bill) Kohlberger — good friend, young colleague, and budding scientist. We will miss him.



a

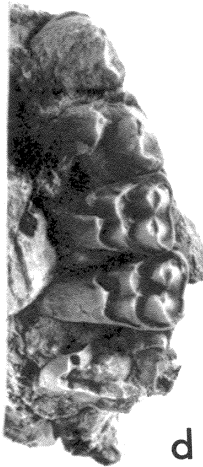


b

5 mm



c



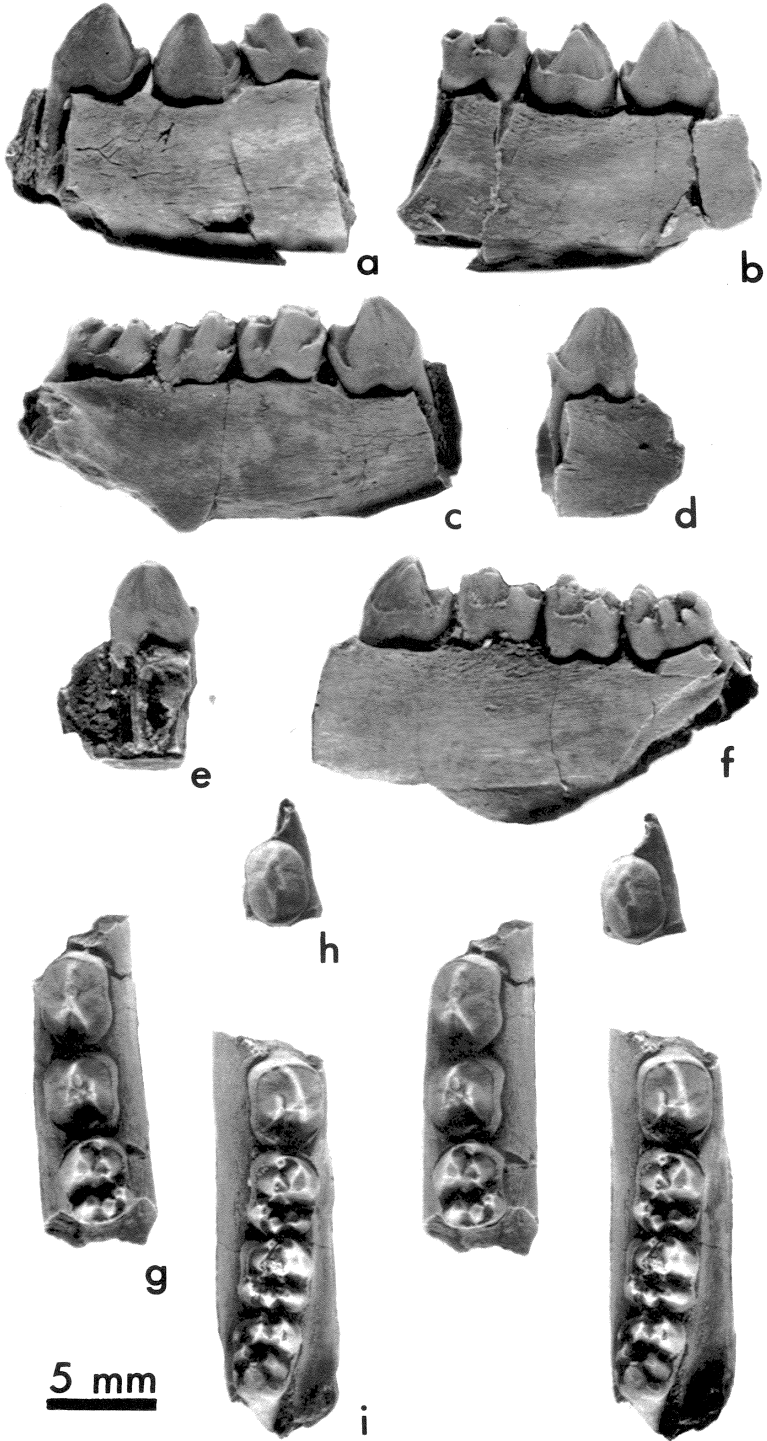
d

Fig. 1 ▲

Conacodon kohlbergeri, n. sp. Upper dentition of type, UNM B1700: a, labial view of left maxilla with P³⁻⁴, M¹⁻²; b, posterior view showing displacement of left and right maxillae; c, stereophotograph in occlusal view of right isolated P², isolated P³ in bone fragment, P⁴, M¹⁻²; d, stereophotograph in occlusal view of left P³⁻⁴, M¹⁻², M³ fragment.

Fig. 2 ►

Conacodon kohlbergeri, n. sp. Lower dentition of type, UNM B1700: a, labial view of left P₃₋₄, M₁; b, lingual view of left P₃₋₄, M₁; c, labial view of right P₄, M₁₋₃; d, labial view of right P₂; e, lingual view of right P₂; f, lingual view of right P₄, M₁₋₃; g, stereophotograph in occlusal view of left P₃₋₄, M₁; h, stereophotograph in occlusal view of right P₂; i, stereophotograph in occlusal view of right P₄, M₁₋₃.



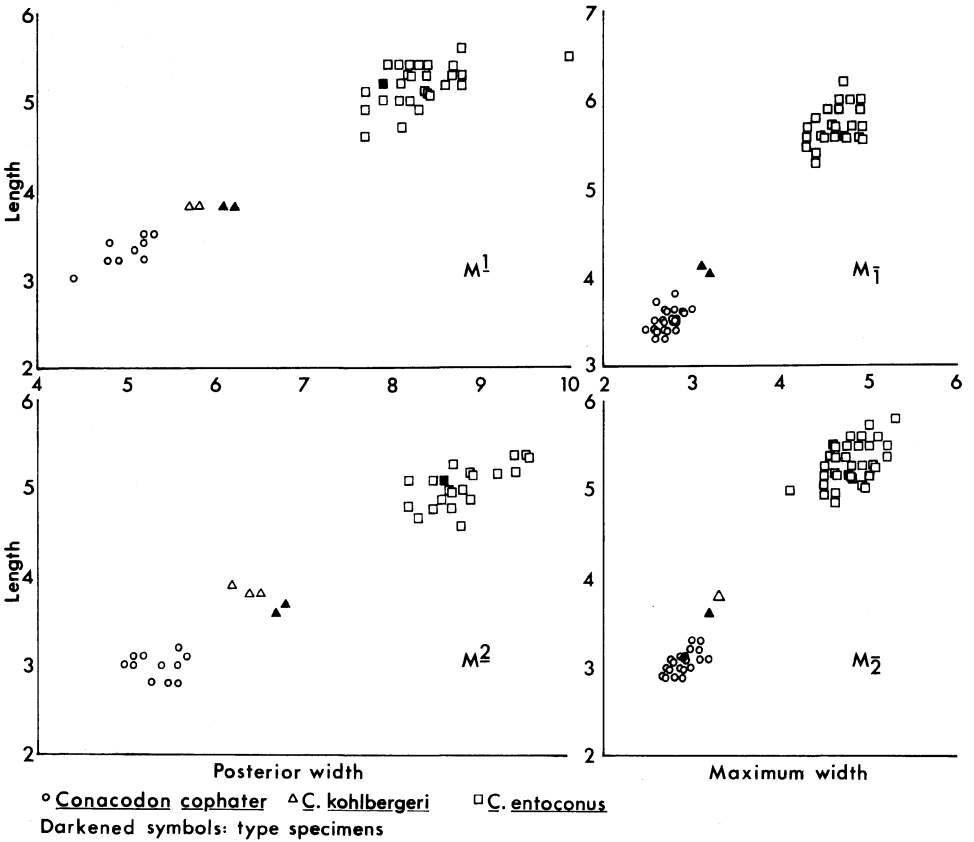


Fig. 3
 Bivariate plots of length versus posterior width of M₁ and M₂, and length versus maximum width of M₁ and M₂ for species of *Conacodon*. Measurements of *C. kohlbergi* given in Table 1. Measurements of *C. entoconus* and *C. cophater* based on specimens from the AMNH and are available from the senior author. Scales are in mm.

Table 1

Measurements of the dentition of *Conacodon kohlbergeri* n. sp., San Juan Basin, New Mexico. Abbreviations: *L* = anteroposterior length; *W* = labiolingual width; *L - TR* = trigonid length; *L - TA* = talonid length; *W - TR* = trigonid width; *W - TA* = talonid width; *W - A* = anterior width; *W - P* = posterior width; *H* = hypocone width; \bar{x} = mean; *a* = approximate measurement. See text for further discussion of some measurements. Measurements in mm.

Specimen number	P ₂		P ₃		P ₄		M ₁				M ₂				M ₃							
	L	W	L	W	L	W	L	L-TR	L-TA	W-TR	W-TA	L	L-TR	L-TA	W-TR	W-TA	L	L-TR	L-TA	W-TR	W-TA	
UNM B1700 (type)																						
right	4.0	2.8			4.1	3.4	4.1	2.3	1.8	3.1	2.9	3.6	1.9	1.8	3.2	3.2	4.1	1.8	2.3	3.1	2.8	
left			4.5	3.2	4.1	3.4	4.0	2.3	1.7	3.2	3.0											
AMNH 58347					4.1	3.4	4.1	2.3	1.8	3.2	3.0	3.8	2.2	1.7	3.3	3.2	4.4	1.9	2.5	3.1	2.7	
\bar{x}					4.1	3.4	4.1	2.3	1.8	3.2	3.0	3.7	2.1	1.8	3.3	3.2	4.3	1.9	2.4	3.1	2.8	

Specimen number	p ²		p ³		p ⁴		M ¹			M ²			M ³						
	L	W	L	W	L	W	L	W-A	W-P	H	L	W-A	W-P	H	L	W-A	W-P	H	
UNM B1700 (type)																			
right	3.7	3.7	4.0	4.4	4.2	6.2	3.8	4.9	6.2	1.2a	3.7	5.0	6.8	1.9a					
left			4.2	4.7	4.2	5.9a	3.8	4.9	6.1	1.3a	3.6	5.1	6.7	1.7a					
AMNH 16525																			
right			4.3	5.3	4.5	6.8	3.9a	—	—	—	3.9	4.8	6.2	1.6a	3.3	4.5	5.0	1.1	
left					4.5	6.1	3.8	4.8	5.8	0.9a	3.8	5.1	6.4	1.3					
AMNH 58346					4.1	6.0	3.8	4.7	5.7	1.1	3.8	4.8	6.5	1.9					
\bar{x}			4.2	4.8	4.3	6.2	3.8	4.8	6.0	1.1	3.8	5.0	6.5	1.7					

Diagnosis

Size about 20% larger than *Conacodon cophater* (Cope, 1884) and about 40% smaller than *C. entoconus* (Cope, 1882a); parastyle on P⁴ present as in *C. cophater* (absent in *C. entoconus*); paraconid on P₃₋₄ absent as in most specimens of *C. entoconus* (present in *C. cophater*); molar metacingulum and postmetaconule wing form continuous shelf or postcingulum slightly contacts metacingulum but in both conditions labial termination of postcingulum more dorsal (meta- and postcingulum continuous but interrupted by postmetaconule wing on M³ and metacingulum and postmetaconule wing continuous but meta- and postcingulum in same dorsoventral plane on M¹⁻² in *C. entoconus*, meta- and postcingulum continuous and in same dorsoventral plane and not interrupted by postmetaconule wing on M¹⁻³ of *C. cophater*); metaconule on M¹⁻³ slightly larger and more distinct and columnar than in *C. entoconus* and *C. cophater*; metaconid on P₄ distinct but small and positioned high on protoconid (metaconid small or possibly lacking on P₄ of *C. cophater* and *C. entoconus*); talonid of P₄ trenchant (basined in *C. cophater* and *C. entoconus*); metacristid present on M₁ and slight on M₂₋₃ (metacristid absent on molars of *C. cophater* and *C. entoconus*); paraconid on molars more lingual than in *C. cophater* and *C. entoconus*; lingual cingulid on M₃ bears small cuspsules below metaconid and hypoconulid or cristid between entoconid and hypoconulid (such cuspsules or cristids lacking in *C. cophater* and *C. entoconus*).

Description

The left side of the type palate has more teeth in place than the right, P³⁻⁴, M¹⁻², and the roots of M³ (Fig. 1a, b, and d). The anterior portion of the maxillary process of the zygomatic arch and the anterior border of the orbit lie dorsal to P⁴ (Fig. 1a). An opening dorsal to the anterior root of P³ may be the

infraorbital foramen. The posterior end of the right side of the palate has been displaced ventrally about one centimeter relative to the left side (Fig. 1b). The right maxilla preserves P⁴, M¹⁻², and what is probably the right P³ is preserved in a fragment of bone (Fig. 1c). Because of distortion the P³ cannot be matched to the right maxilla. What is probably the isolated right P² can be matched confidently to the bone fragment bearing the P³ (Fig. 1c), although lingually displaced relative to P³ when matched to the fragment. The following description of the upper dentition is based on the type specimen (UNM B1700) and the two referred specimens (AMNH 16525 and 58346). Figure 1 of the type upper dentition (plus Fig. 4) will help clarify this description.

The P²⁻³ are triangular in occlusal view, have an inflated base, and are each dominated by a single prominent paracone(?). The P² and P³ are very similar except for the smaller size of P². Each premolar expands in the protoconal region, but this cusp is not present. This lingual region on P²⁻³ is supported by one root and the labial half of each premolar is supported by two roots. Cingula and a styler shelf are lacking except near the anterolabial corner of P² and the antero- and posterolabial corners of the P³. The anterolabial parastylar region on P²⁻³ is represented by a narrow cingulum. The slightly larger posterolabial "metastylar" region on P²⁻³ bears a crista running to the paraconal(?) apex. A narrow cingulum lies below (dorsal to) this crista on P³.

The P⁴ is notably more transversely widened than P²⁻³ because of the presence of a distinct protocone. However, the lingual margins of P²⁻³, P⁴, and M¹⁻³ are approximately aligned because of the progressively more lingual placement of the more anterior cheek teeth. The base of the P⁴ is inflated and the crown is dominated by a paracone and protocone. The labial aspect of the crown is supported by two roots and the protocone by one. Like the P²⁻³, the P⁴ lacks a styler shelf, but the parastylar and "metastylar" regions are better developed.

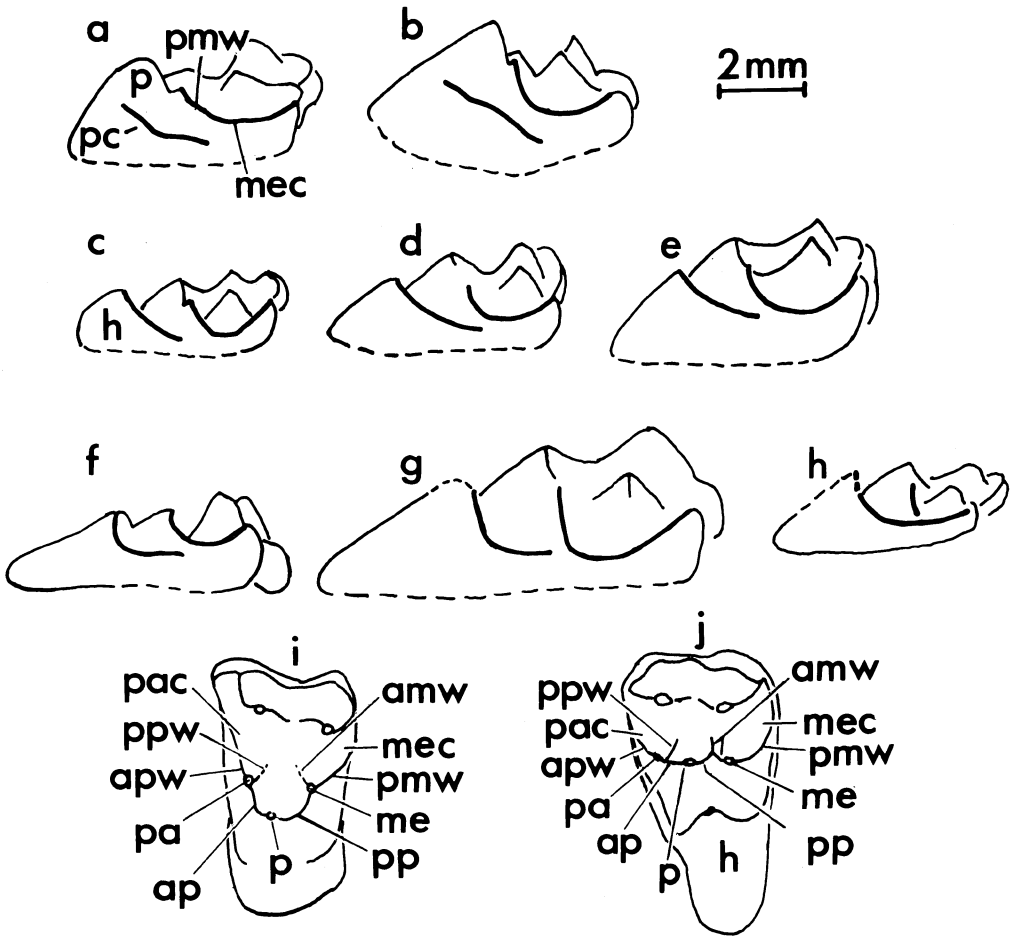


Fig. 4

Approximately posterior views of left (or reversed right) M²s showing relationships of metacingulum, postmetaconule wing, and postcingulum: *a*, *Protungulatum donnae*, YPM 38220 (cast of UCMP 105007); *b*, *Mimatuta morgoth*, cast of UMVP 1560, type (reversed); *c*, *Oxyacodon agapetillus*, UCMP 89690; *d*, *O. priscilla*, UCMP 36640; *e*, *O. apiculatus*, AMNH 3550 (reversed); *f*, *Conacodon kohlbergeri*, UNM B1700; *g*, *C. entoconus*, AMNH 16418; *h*, *C. cophater*, AMNH 16435. Occlusal views of left M²s showing relationships of structures surrounding lingual side of

protofossa: *i*, *Protungulatum donnae*, YPM 38221 (cast of UCMP 112111); *j*, *Conacodon kohlbergeri*; slightly modified after AMNH 58346 to show unworn condition. See text for explanation. Abbreviations: *amw* = premetaconule wing; *ap* = preprotocrista; *apw* = preparaconule wing; *h* = hypocone; *me* = metaconule; *mec* = metacingulum; *p* = protocone; *pa* = paraconule; *pac* = paracingulum; *pc* = postcingulum; *pmw* = postmetaconule wing; *pp* = postprotocrista; *ppw* = postparaconule wing.

The parastyle is an isolated cusp set low on (dorsal to) the anterior face of the paracone. The more expanded "metastylar" region bears a crista (and sometimes a cuspule) directed towards the paraconal apex. In occlusal view, the parastyle, paracone, and "metastyle" are in approximate alignment. A narrow, discontinuous precingulum runs from the parastyle to the anterior face of the protocone. A narrow, continuous postcingulum runs from the "metastyle" to the posterior face of the protocone. The large protocone, set lower than (dorsal to) the paracone, has a slightly labiolingually compressed apex bearing small anterior and posterior cristae and sometimes a small labial crista. The lingual face of the protocone is set at a moderately low angle due to the considerable lingual expansion of the base and the probable labial shift of the apex. The P^4 is equal to or exceeds the size of M^1 .

The upper molars are triangular in occlusal outline with the hypocone forming the very lingually extended apex, especially on M^2 . The hypocone and protocone are supported by a large transversely widened root and the labial third of the crown is supported by two smaller roots. The stylar shelf is narrow but continuous, except labial to the metacone on the one known M^3 (AMNH 16525). Anteriorly the stylar shelf continues around the base of the paracone to join the paracingulum, interrupted only by a slight parastylar swelling and paracrista. Posteriorly the stylar shelf is interrupted by a metacrista and a narrow metacingulum continues posterolingually from the slightly expanded metastylar region. Posterior to the metacone, the metacingulum is beveled off in early stages of wear. The metacingulum continues lingually as the postmetaconule wing. There is a narrow but continuous postcingulum running from the hypoconal apex towards the metacingulum. In two specimens (UNM B1700 and AMNH 58346) the labial termination of the postcingulum lies below (dorsal to) the metacingulum and in the other (AMNH

16525) it barely contacts the metacingulum. On all molars a narrow but continuous precingulum begins slightly below (dorsal to) or level with the paracingulum and runs lingual. On M^1 the precingulum stops on the lingual surface of the protocone, but on M^{2-3} it encircles the base of the protocone continuing towards the hypoconal apex. On M^{1-2} the paracone and metacone are similar in height and size. On M^3 the metacone is smaller. On all upper molars a distinct centrocrista is present. The various cristae and cuspules surrounding the protofossa on M^{1-3} of *Conacodon kohlbergeri* are somewhat unusual in their placement, although the arrangement is not unique for peripitychids. Therefore, the following identifications of some cristae are interpretive relative to their possible homologues in such taxa as *Protungulatum donnae*. (Compare Figures 4i and j for clarification.) The paraconule is usually absent, but when present as on the M^2 of AMNH 58346, it is a small cuspule positioned close to and almost directly anterior of the protoconal apex. On the basis of this specimen it can be argued that the crista emanating from the anterior aspect of the protocone is a combined preprotocrista and preparaconule wing. The postparaconule wing contacts the protocone just anterior to the apex of the protocone. On the basis of the M^2 of AMNH 58346, this wing contacts the preprotocrista not the paraconule as is usually the case. The metaconule is a fairly large, sometimes columnar cusp, situated posterior to the protoconal apex. What is presumed to be an abbreviated postprotocrista contacts the premetaconule wing, rather than contacting the metaconule as is usual. A more typical postmetaconule wing joins the metaconule to the metacingulum. The lingual face of both the protocone, and particularly the hypocone, are set at a low angle. The base of the hypocone is greatly expanded lingually, especially on M^2 . The hypocone becomes somewhat more lingual in position relative to the protocone going from M^1 to M^3 .

The associated dentaries of the type dentition, UNM B1700, include the left P_{3-4} , M_1 (Fig. 2a, b, and g) and the right P_4 , M_{1-3} (Fig. 2c, f, and i). The ventral surface of the left dentary is intact below P_4 , but is lacking on the right dentary. An associated premolar in a bone fragment is slightly smaller than the left P_3 , and is probably P_2 (Fig. 2d, e, and h). In occlusal view the anterior ridge of the P_2 is slightly convex to the right, while the posterior ridge is left of the midline, both of which suggest this is a right P_2 . A small opening, probably a mental foramen, is also preserved on the right side of the dentary (Fig. 2d) anteroventral to the anterior root of the premolar, again suggesting it is a right P_2 . The following description of the lower dentition is based on the type specimen (UNM B1700) and the referred specimen (AMNH 58347). Figure 2 of the type lower dentition will clarify this description.

The size of the premolars gradually increases from P_2 through P_4 . Like the lower molars, they are all supported by two roots. The P_2 is a simple, slightly anteroposteriorly elongate cusp bearing a small posterior heel. The P_3 is only slightly more complex. Its posterior heel is larger and bears a small anteroposteriorly directed cristid. Two muted cristids run down the posterolingual and -labial sides of the single large cusp. There is no sign of a paraconid or metaconid on P_3 (or P_2). The P_4 is wider, but not longer than the P_3 (Table 1). Like the P_3 it lacks a paraconid, but a small distinct metaconid is present high on the flank of the protoconid. The heel or talonid of the P_4 has a sharp, steep-sided, anteroposteriorly directed cristid. All the premolars are noticeably inflated relative to the molars and the P_4 is equal to or exceeds the size of M_1 .

In the lower molars, the trigonid is low relative to the talonid. The protoconid is the largest trigonid cusp, but it is only slightly taller than the paraconid and metaconid. The paraconid is slightly lingual of the anteroposterior midline of the molars. It is connected to the metaconid by a

metacristid, but the metacristid lessens from M_{1-3} as the paraconid becomes smaller and more closely appressed to the metaconid. The hypoconid is only slightly larger than the other talonid cusps. On the M_{1-2} talonids, the cusp apices appear to be "closed" or closely appressed due to the shortening of the talonid basin and the inflation of the bases of cusps. This condition is not as marked on M_3 because of the posterior elongation of the hypoconulid. Discontinuous to continuous cristids obliqua, postcristids, and entocristids join the talonid cusps one to another and to the posterior aspect of the trigonid. In addition, the talonid cusps sometimes bear small muted cristids directed towards the center of the talonid basin. All three molars have narrow, but distinct anterior basal cingulids and internal cingulids running from below the paraconid to below the entoconid. The M_3 of the type bears two cuspsules on the internal cingulid, one below the metaconid and another below the hypoconulid (Fig. 2f, i). AMNH 58347 bears neither of the cuspsules, but a distinct cristid runs from between the entoconid and hypoconulid towards the talonid basin.

Discussion

In order to understand the relationships of *Conacodon kohlbergeri*, this species was compared cladistically to other species of *Conacodon* and *Oxyacodon*, *Mimatuta morgoth*, other periptychids, and the arctocyonid *Protungulatum donnae*. The resulting cladogram is shown in Figure 5 and the 19 characters that were considered in this analysis are listed in Table 3 and are discussed below. A key to the various conventions used in Figure 5 can be found in the explanation for that figure.

Since one of the main purposes of this paper is to interpret the relationships of *Conacodon kohlbergeri*, the other taxa within the Conacodontinae are treated in some detail. Similarly, the morphologically most primitive periptychid and condylarth,

Mimatuta morgoth and *Protungulatum donnae*, respectively, are treated in equal detail. These species provide the basis for assessing the polarity and degree of change in the 19 characters analyzed.

Mimatuta morgoth is more fully discussed by Archibald (1982) and Van Valen (1978). *Protungulatum donnae* serves as the out-group (of periptychids) for this analysis. Although *P. donnae* appears to be the morphologically most primitive condylarth (Archibald 1982; Van Valen 1978; Sloan and Van Valen 1965), it is not clear that it is the closest sister taxon to the Periptychidae. Such an assessment will come only when the early evolution of condylarthrans is better understood. For now, *P. donnae* can be viewed as representing the sister taxon for all other condylarthrans, or maybe more appropriately, the primitive condylarthran morphotype.

Other periptychids are not discussed in detail in the following analysis. Thus the use of the term "other periptychids" in Figure 5 is intentionally nebulous for several reasons. First, this analysis centers on the Conacodontinae and the inclusion of equally derived periptychids is done only to show the overall relationship of subfamilies within the Periptychidae and to point out some notable parallelisms between taxa within the Conacodontinae and taxa from other subfamilies. Second, the family is currently being reviewed by the senior author and the inclusion of other periptychids reflects only preliminary conclusions at approximately the subfamilial level.

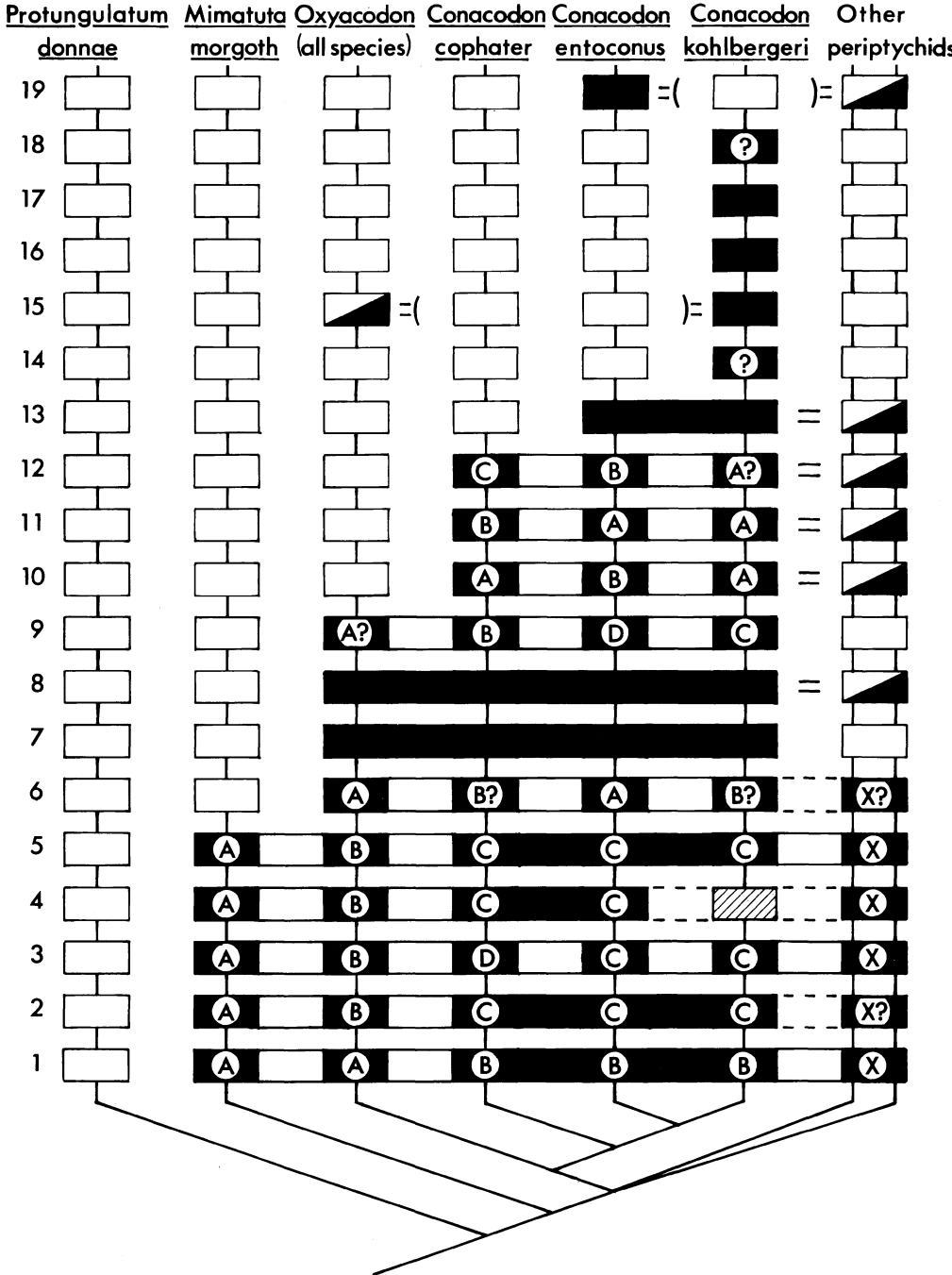
These preliminary conclusions suggest an as yet unresolved trichotomy among the Conacodontinae (*Oxyacodon* and *Conacodon*), the Periptychinae (*Hemithlaeus*, *Ectoconus*, and *Periptychus*), and the Anisonchinae (*Haploconus*, *Anisonchus*, plus *Gillisonchus* and other unnamed genera). For purposes of this analysis, the Periptychinae and Anisonchinae are considered as a single clade (the two lines

under "other periptychids" in Figure 5). The only interpretations offered for this combined clade are whether the clade is primitive for a character (open rectangles in Figure 5), whether the clade shares a derived character-state with other taxa (X within a blackened rectangle in Figure 5 representing an undivided morphocline), or whether certain taxa within the clade display a derived character-state in parallel with taxa from other clades (half-shaded rectangle and = in Fig. 5). Some of the taxa that are interpreted to have evolved various character-states in parallel are discussed below.

Some of the taxa named and included in the Periptychidae by Van Valen (1978) are not included here because the material has not been studied in detail by the authors. However, one genus *Fimbrethil* Van Valen,

Fig. 5 ►

Cladogram for species of *Conacodon* and other periptychids compared to *Protungulatum donnae* based on characters (1–19) of the dentition discussed sequentially in the text. Character-states are represented as follows: open rectangles, primitive; black rectangles, derived (with question mark, questionably derived); black rectangle with letter, derived but part of morphocline (with question mark, character-state uncertain); half-shaded rectangles, derived for only some members of a clade; diagonal lines, uniquely derived. For morphoclines: A is the least derived condition; X represents several derived character-states that have not been subdivided within a clade; solid lines connect various levels of derived character-states within a morphocline (dashed lines when morphocline is uncertain or uniquely derived character-state occurs within morphocline). Black-rectangles joining clades represent shared-derived character-state or most derived condition within morphocline. Parallelisms between clades represented by equal signs (with parentheses when clades not contiguous on cladogram).



1978 is considered to be a junior synonym of *Oxyacodon* (Archibald et al. 1983). The conclusions offered in the present analysis regarding the unresolved trichotomy among the Conacodontinae, the Periptychinae, and the Anisonchinae were made independently using a different methodology, but they are in general accord with three of the five lineages recognized in the provisional phylogeny of Van Valen (1978, fig. 6).

In the following analysis, the 19 characters are discussed sequentially (see Table 3). The reader is referred to Figure 5 for the cladogram constructed from this analysis.

Character 1 The base of the protocone is expanded lingually and the apex is shifted labially in *Mimatuta morgoth* and *Oxyacodon* (1A) relative to *Protungulatum donnae* and the apex is shifted even more labially in *Conacodon* (1B) (see Figure 4). Similar trends occur in other periptychids (1X).

Character 2 A discontinuous, narrow internal cingulid develops below the paraconid particularly on M_2 in *Mimatuta morgoth* (2A) and Archibald et al. (1983) noted in the rediagnosis of *Oxyacodon* that an internal cingulid is usually absent in this genus. Although it is weak, it is better developed than in *M. morgoth*, often reaching to below the metaconid (2B). A continuous internal cingulid occurs from below the paraconid to the base of the entoconid on M_{2-3} in species of *Conacodon* (2C). As indicated by the dashed lines and question mark in Figure 5 it is not certain whether all other periptychids can be united by this character.

Character 3 Periptychids tend to have a shorter lower molar length relative to width (length/width ratios for M_{1-2} , Table 2), the apices of the cusps are more closely appressed, and the talonid basin (but not necessarily the whole talonid) is shorter (3A–D,X). The extreme of this trend is found in *Conacodon cophater* where the three talonid cusps on M_2 are arranged in an almost labiolingual line (3D).

Character 4 Similarly, almost all periptychids tend to shift the paraconid from a lingual position to the midline (anteroposterior) of the molar (4A–C,X). The one notable exception is *C. kohlbergeri*, which has a lingually placed paraconid (symbolized by diagonal lines in Figure 5). This is interpreted to be a reversal of the trend found in periptychids and is consequently regarded as a uniquely derived character-state.

Character 5 Among periptychids there is a general trend to enlarge and inflate the posterior premolars (5A–C,X). Even in the structurally most primitive species, in *Mimatuta morgoth*, the base of the P_4 talonid shows some inflation (5A) relative to that seen in the P_4 of *Protungulatum donnae*. (Associated upper molars and P^4 have not been reported for *M. morgoth*.) In species of *Oxyacodon* this inflation is more pronounced in the posterior premolars (5B) and in species of *Conacodon* the trend continues, plus the P^4_4 reach or exceed the size of M^1_1 (5C) (see Table 2). In other subfamilies, such as the Periptychinae, some representatives such as *Periptychus* also show a considerable inflation of the posterior premolars. However, this more derived condition in both *Periptychus* and *Conacodon* probably evolved in parallel. This is suggested because the primitive members interpreted to belong to the clades represented by *Periptychus* and *Conacodon* (*Hemithlaeus* and *Oxyacodon*, respectively) show less premolar inflation.

Character 6 The paraconid tends to become appressed to the metaconid in all periptychids, except possibly in the most primitive taxa such as *Mimatuta morgoth* (6A–B?, X?). The analysis (and thus distribution) of this morphocline remains uncertain as indicated by the question marks for character six. Thus, the questionably more derived condition (6B?) found in *Conacodon cophater* and *C. kohlbergeri* is not used to suggest a closer affinity of these two species.

Character 7 The shared-derived

character-state we deem most important in uniting species of *Oxyacodon* and *Conacodon* is the great size and lingual expansion of the hypocone. As shown in Figure 5, other periptychids are considered to be primitive in lacking this character-state. However, it should be noted that all periptychids show a trend from increasing the postcingulum in primitive forms such as *Mimatuta morgoth* (a small hypocone can be present) to having a well-developed hypocone as in all other periptychids. Thus, *Oxyacodon* and *Conacodon* can be viewed as sharing an exclusively derived character-state for the condition of the hypocone (as we have done), or as the extreme in a trend to enlarge the hypocone.

Character 8 In all species of *Oxyacodon* and *Conacodon* where a P^3 is known, the protocone on this tooth is absent and we consider this to be shared-derived. The only other species of periptychid that reduced the P^3 protocone belong to *Haploconus*. Based on unpublished research of the senior author, we regard this as a parallel trend (8=).

Character 9 A somewhat variably derived character-state found in species of *Conacodon* and *Oxyacodon* is the development of a precingulum encircling the base of the protocone and contacting the hypocone (see M^2 's in Fig. 1c, d). Our interpretation is that this complete precingulum apparently started on the M^3 (phylogenetically) and shifted anteriorly along the molar series to M^1 . Small samples of the four species of *Oxyacodon* known from upper dentitions (*O. agapetillus*, *O. ferronensis*, *O. priscilla*, and *O. apiculatus*) and slightly larger samples of the three species of *Conacodon* were examined. For *Oxyacodon*, none of the M^{1-3} 's for any species show the derived condition. The two known M^3 's of *O. agapetillus* (both in UCMP 89690) show the derived condition. The only known damaged M^3 of *O. ferronensis* (BYU 3825) may be derived. Neither of two M^3 's referred to *O. priscilla* (UCMP 36640 and AMNH 58555) are derived. The only M^3 of *O. apiculatus*

(AMNH 3550) is not derived, but the precingulum almost contacts the hypocone. For *C. cophater*, the derived condition is found on 5 of 6 (83%) M^3 's, 7 of 12 (58%) M^2 's, and 0 of 11 (0%) M^1 's. For *C. kohlbergeri* only one M^3 is tentatively referable and it shows the derived condition, while 5 of 5 (100%) M^2 's are derived, and 0 of 5 (0%) M^1 's are derived. In *C. entoconus* the derived condition occurs as follows: 11 of 11 (100%) M^3 's, 15 of 15 M^2 's (100%), and 11 of 15 (80%) M^1 's.

Assuming the morphocline for this character has been correctly interpreted, species of *Conacodon* can be linked in a straightforward manner. *C. kohlbergeri* (9C) and *C. entoconus* (9D) would be closest, with *C. cophater* (9B) more primitive. The variable condition seen in species of *Oxyacodon* is more difficult to interpret. If the known samples of the various species of *Oxyacodon* cited above are taken as representative, the derived condition seen in the M^3 of *O. agapetillus* (and possibly *O. ferronensis*) would link this (these) species with *Conacodon*. *O. apiculatus* would be next with *O. priscilla* as primitive. However, it must be recalled that individuals assigned to the three species of *Conacodon* show variation in the development of the complete precingulum, and thus individuals assigned to species of *Oxyacodon* also might be expected to show variation. Therefore, it is predicted that some individuals of all species of *Oxyacodon* will have the derived condition (a complete precingulum) on M^3 . If this is the case, the genus as a whole questionably (indicated by the question mark for 9A) shows the least derived condition. If this prediction is corroborated by future discoveries, this character can be added to the list of diagnostic features for the Conacodontinae. If the prediction is incorrect, it may help to align certain species of *Oxyacodon* with *Conacodon* and break apart the presently nonmonophyletic genus *Oxyacodon* (see later comments). Finally, not all representatives of the Periptychidae have been examined in great

Table 2

Various ratios of dental measurements for *Protungulatum donnae*, *Mimatuta morgoth*, and species of *Oxyacodon* and *Conacodon*. Ratios involving more than one tooth site are based on associated teeth. Measurements are taken from the following sources or are summarized in these sources: *Protungulatum donnae* and *Mimatuta morgoth*, Archibald 1982; species of *Oxyacodon*, Archibald et al. 1983; *Conacodon kohlbergeri*, Table 1; *C. cophater* and *C. entoconus*, measurements of AMNH specimens by senior author. Abbreviations: \bar{x} = mean; OR = ordered range; *N* = sample size; *max. W* = maximum width; see Table 1 for others. See text for discussion.

		<i>Protungulatum donnae</i>	<i>Mimatuta morgoth</i>	<i>Oxyacodon agapetillus</i>	<i>O. priscilla</i>
	\bar{x}	0.95	0.89	0.97	0.99
<u>L P₄</u>	OR	0.92 0.97	0.88 0.90	0.93 1.00	0.90 1.08
L M ₁	N	2	2	2	13
	\bar{x}	0.78	0.85	0.95	0.93
<u>W P₄</u>	OR	0.75 0.81	0.81 0.89	0.90 1.00	0.89 1.00
W M ₁	N	2	2	2	13
	\bar{x}			0.97	1.01
<u>L P⁴</u>	OR			0.93 1.00	1.00 1.03
L M ¹	N			2	3
	\bar{x}			0.94	0.88
<u>W P⁴</u>	OR			0.93 0.95	0.81 0.93
W M ¹	N			2	3
	\bar{x}	1.36	1.42	1.32	1.33
<u>L M₁</u>	OR	1.34 1.38	1.39 1.46	1.26 1.43	1.21 1.44
max. W M ₁	N	6	4	5	25
	\bar{x}	1.24	1.27	1.17	1.14
<u>L M₂</u>	OR	1.17 1.37	1.21 1.29	1.08 1.24	1.03 1.29
max. W M ₂	N	9	4	9	26

*P₄ lacks paraconid.

<i>O. apiculatus</i>	<i>Conacodon cophater</i>	<i>C. kohlbergi</i>	<i>C. entoconus</i>
1.03	1.16	1.02*	1.12*
0.98	1.06	1.00	1.00
1.07	1.26	1.03	1.18
11	19	2	19
0.89	1.03	1.08	1.11
0.79	0.96	1.06	1.04
0.97	1.12	1.10	1.21
10	19	2	19
0.98	1.23	1.13	1.17
0.86	1.13	1.09	1.04
1.08	1.26	1.18	1.29
3	9	5	20
0.81	1.06	1.02	1.05
0.74	0.96	0.96	0.95
0.88	1.17	1.06	1.12
2	8	4	20
1.35	1.29	1.29	1.23
1.21	1.20	1.25	1.14
1.59	1.42	1.32	1.33
13	23	2	25
1.18	1.05	1.15	1.11
1.14	0.97	1.14	1.04
1.29	1.11	1.15	1.24
10	21	2	34

Table 3

Character-states of the dentition discussed in the text and used in the cladogram (Fig. 5). For morphoclines, the most derived state is given below.

Primitive	Derived
19 Parastyle present on P ⁴ .	19 Parastyle absent on P ⁴ .
18 Metaconule on M ¹⁻² not larger, and more distinct, nor columnar.	18 Metaconule on M ¹⁻² is larger, more distinct, and columnar.
17 Internal cingulid on M ₃ lacks cuspules or cristids.	17 Internal cingulid on M ₃ has cuspules or cristids.
16 Talonid of P ₄ basined or at least nontrenchant.	16 Talonid of P ₄ trenchant.
15 Metacristid lacking on some or all lower molars.	15 Metacristid present on some or all lower molars.
14 Metaconid small or absent.	14 Metaconid small, distinct, and high on flank of P ₄ protoconid.*
13 Paraconid present on P ₃₋₄ .	13 Paraconid absent on P ₃₋₄ .
12 Metacingulum and postmetaconule wing on M ¹⁻³ form continuous shelf with labial termination of postcingulum dorsal to shelf.	12 Metacingulum and postcingulum on M ¹⁻³ form continuous shelf with postmetaconule wing at most contacting the shelf.
11 Paraconid on M ₁₋₃ not reduced.	11 Paraconid on posterior lower molars reduced.
10 Styler shelf wide or moderately wide and continuous.	10 Styler shelf narrow and sometimes discontinuous.
9 Precingulum does not encircle protocone and does not contact hypocone on any upper molars.	9 Precingulum encircles protocone and contacts hypocone on some or all upper molars.
8 Protocone present on P ³ .	8 Protocone absent on P ³ .
7 Hypocone on M ¹⁻³ not large nor situated lingually.	7 Hypocone on M ¹⁻³ large and situated very lingually.
6 Paraconid not appressed to metaconid on lower molars.	6 Paraconid appressed to metaconid on lower molars.
5 Posterior premolars not large nor inflated.	5 Posterior premolars large and inflated.
4 Paraconid lingual of antero-posterior midline of lower molars.	4 Paraconid on or near antero-posterior midline of lower molars.†
3 Lower molar (and talonid) length not short relative to width and molar cusps not appressed.	3 Lower molar (and talonid) length short relative to width with molar cusps appressed.
2 Internal cingulid absent on lower molars.	2 Internal cingulid present on lower molars.
1 Protocone base not expanded lingually and apex not shifted labially on M ¹⁻³ .	1 Protocone base expanded lingually and apex shifted labially on M ¹⁻³ .

* This is interpreted as uniquely derived for *Conacodon kohlbergeri* relative to other species of *Conacodon*, but other species considered in analysis have P₄ metaconid (see text).

† Paraconid is lingual of midline in *Conacodon kohlbergeri*, which is interpreted as reversal of morphocline in Periplychidae (see text).

enough detail to be certain that none possesses this complete precingulum.

Character 10 The styler shelf tends to be reduced in periptychids. This probably occurred in parallel in several lineages, because within the *Oxyacodon* - *Conacodon* clade the styler shelf is not reduced (or very little) in *Oxyacodon* but is in *Conacodon* (10A-B). *C. entoconus* shows the greatest reduction (10B) in possessing a discontinuous styler shelf labial to the paraconid on M¹.

Character 11 In addition to shifting the paraconid labially towards the midline and appressing it more closely to the metaconid most periptychids tend to reduce the size of this cusp. In *Conacodon kohlbergi* and *C. entoconus* the M₃ paraconid is reduced to a small cusp or ridge (11A) and in *C. cophater* this reduction extends to the M₂ paraconid (11B). This occurs in parallel in other periptychids such as derived species of *Haploconus* (11=).

Character 12 *Protungulatum donnae*, *Mimatuta morgoth*, all species of *Oxyacodon*, and two specimens of *Conacodon kohlbergi* (the type, UNM B1700 and AMNH 58346) have a meta-cingulum forming a continuous shelf with the postmetaconule wing. In these forms, the labial termination of the postcingulum lies dorsally (toward the roots) to the postmetaconule wing (Fig. 4a-f). Archibald et al. (1983) noted that in *C. entoconus* the meta- and postcingulum form a continuous shelf that is interrupted by the postmetaconule wing. This seems to be an appropriate description for the M³ of this species. However, for M¹⁻² it is more correct to say that in *C. entoconus* the postmetaconule wing and metacingulum still form a continuous shelf but that the meta- and postcingulum now lie in nearly the same dorsoventral plane (Fig. 4g) and the postcingulum may contact the postmetaconule wing. One specimen, AMNH 16525, tentatively referred to *C. kohlbergi*, displays a similar morphology. If this specimen is correctly referred to this species, then *C. kohlbergi* is more variable than either *C. entoconus* or *C. cophater* in this character. In *C.*

cophater the meta- and postcingulum lie in the same dorsoventral plane and form a continuous shelf that is not, or is only slightly interrupted by the postmetaconule wing (Fig. 4h). This could represent a morphocline with the variable *C. kohlbergi* showing the beginnings of the trend (12A?), *C. entoconus* being intermediate (12B), and *C. cophater* the most derived (12C). If true, it could be used to argue for a more recent common ancestry for *C. entoconus* and *C. cophater*. However, the next character to be discussed suggests that *C. entoconus* and *C. kohlbergi* are more closely related and thus the more derived condition found in *C. cophater* may not be indicative of a closer relationship to *C. entoconus*. This same trend occurs in parallel in other clades (12=) such as in *Anisonchus* and allied genera (Van Valen 1978; Rigby 1981).

Character 13 The type and only known P₃₋₄ of *Conacodon kohlbergi* lack paraconids. This condition is also found in almost all specimens of *C. entoconus*. A few specimens examined (AMNH 3503D, 23199ah, 27611) do have a small or incipient paraconid just lingual to the midline on P₄. In contrast, *C. cophater*, most specimens belonging to species of *Oxyacodon* (see Archibald et al. 1983, for exceptions), *Mimatuta morgoth*, and *Protungulatum donnae* possess a distinct paraconid on P₃₋₄. We regard the lack of the P₃₋₄ paraconid as a shared-derived character-state for *C. kohlbergi* and *C. entoconus*. The *Hemithlaeus* - *Ectoconus* - *Periptychus* clade (the Periptychinae) reduces and loses the P₃ paraconid in parallel (13=).

Character 14 *Conacodon kohlbergi* has a small, but distinct metaconid situated high on the flank and appressed to the P₄ protoconid (Fig. 2b and f). Unlike the type of *C. kohlbergi*, most P₄'s referable to *C. cophater* and particularly *C. entoconus* show wear on the apex of the protoconid. Some unworn P₄'s of *C. cophater* (e.g., AMNH 16435) suggest this species has at most a small swelling in the region of the metaconid. The condition cannot be established with certainty for *C. entoconus*, but

a metaconid may be lacking. *Protungulatum donnae*, *Mimatuta morgoth*, and species of *Oxyacodon* all show some development of a metaconid on P_4 , although its size decreases through this series of taxa. The condition seen in *C. kohlbergeri* could be interpreted to be primitive with *C. cophater* and *C. entoconus* sharing the condition of a more reduced P_4 metaconid. This must remain a possibility, but the lack of well-preserved relevant regions on the P_4 's of the two latter species renders this a moot alternative. Further, in *C. kohlbergeri* the position of the metaconid high on the flank of the protoconid is qualitatively different than the lower positioned metaconid on the P_4 's of the previously noted species. The tentative conclusion is that the condition in *C. kohlbergeri* is uniquely derived (14?).

Character 15 A metacristid is present on M_1 and less distinctly on M_{2-3} in *Conacodon kohlbergeri*. This presumably is a unique development. An M_2 of *Oxyacodon ferronensis* (Archibald et al. 1983) and the type M_2 of *O. marshater* (Van Valen 1978) possess a metacristid. This presumably was a parallel development in these species of *Oxyacodon* and in *C. kohlbergeri*.

Character 16 *Conacodon kohlbergeri* appears to be unique in the possession of a distinctly trenchant P_4 talonid, with a sharp, steeply sided cristid running from the back of the talonid to below the protoconid. In many P_4 's of *Protungulatum donnae* a similarly located cristid is found on the talonid, although it is far more subdued. It could be argued that the condition found in *C. kohlbergeri* is directly modified from that in *P. donnae*; however, all the other derived character-states shared by other periptychids and *C. kohlbergeri* [except possibly the presence of a P_4 metaconid (14) and the more lingual placement of the molar paraconids (4)] strongly counter this possibility. In going from *P. donnae* to *Mimatuta morgoth* and species of *Oxyacodon* the P_4 talonid (especially the width) shows increase in size and the talo-

nid becomes basined. In *C. entoconus* and *C. cophater*, the P_4 talonid is still basined, but the size trend seems to reverse partly due to an absolute decrease in size of the talonid and partly due to the greater inflation of the P_4 trigonid. These same size relationships are found in the P_4 talonid of *C. kohlbergeri* although it is trenchant. Such derived similarity argues for modification from the *Conacodon*-type P_4 talonid rather than from the *P. donnae*-type P_4 talonid.

Character 17 The two known M_3 's of *C. kohlbergeri* are unique in either bearing cuspsules on the internal cingulid below the metaconid and hypoconulid (UNM B1700) or in bearing a cristid between the entoconid and hypoconulid (AMNH 58347).

Character 18 As noted in the diagnosis and description, the metaconule on M^{1-2} of *C. kohlbergeri* appears to be slightly larger, more distinct and columnar relative to its condition in *C. entoconus* and *C. cophater*. At least for the present, this character-state is rather difficult to evaluate. Therefore, we treat its possibly unique status in *C. kohlbergeri* as questionable (18?).

Character 19 Finally, *Conacodon entoconus* is unique in its lack of the parastyle on P^4 . Other periptychids, such as some specimens of *Haploconus angustus*, have reduced or lost the P^4 parastyle in parallel.

On the basis of the foregoing analysis, we feel *Conacodon kohlbergeri* is most closely related to *C. entoconus*. Both share the loss of the paraconid on P_{3-4} (13) and the more advanced conditions in the development of the precingulum on the upper molars (9C,D). The possibility that *C. kohlbergeri* and *C. cophater* are more closely related can be confidently eliminated. The only derived character-state these two species might share exclusively is a closer appression of the paraconid and metaconid on the lower molars (6B?). As discussed earlier, the distribution of this character is difficult to assess and thus the likelihood of a correct assessment is low.

Another and somewhat more likely alternative is that *C. entoconus* and *C. cophater* are more closely related. If two uniquely derived character-states for *C. kohlbergeri* [lingual position of the paraconid (4) and presence of a metaconid high on the flank of the P₄ protoconid (14?)] were instead regarded as primitive, *C. entoconus* and *C. cophater* would share a more labial position of the paraconid (4C) and a reduction of the P₄ metaconid (14). However, as noted earlier the presence or absence of a metaconid on the P₄ of either *C. entoconus* or *C. cophater* is not certain, thus eliminating for now this character-state as a possible basis for associating these two species. If the more lingual position of the paraconid on lower molars of *C. kohlbergeri* were truly primitive, most or all periptychid affinities for this species would have to represent rampant homoplasy. The one derived character-state found in both *C. entoconus* and *C. cophater* that deserves further attention is the more continuous postcingulum-metacingulum on the upper molars (12B,C). However, because of the uncertainties regarding the state of this character in *C. kohlbergeri* (as discussed earlier) and the two derived character-states that appear to unite *C. kohlbergeri* and *C. entoconus*, we reject for the time being, a close *C. entoconus* - *C. cophater* tie.

Following a strictly "nested" approach to classification, one might wish to retain *Conacodon kohlbergeri* along with the genotypic species, *C. entoconus*, in *Conacodon* while recognizing a new genus for *C. cophater*. An approach based more on overall morphological divergence might place the rather distinctive *C. kohlbergeri* in a new genus. However, unless *C. entoconus* and *C. cophater* were also recognized as separate genera, this solution should be rejected on cladistic grounds. A third choice, which we have followed, is to retain all three species in *Conacodon*. This decision is admittedly arbitrary, but it seems to be warranted by the range of species variation seen in other currently recog-

nized periptychid genera. As study on this family continues, the first option noted in this paragraph may become warranted.

At the next higher level of relationship, a number of derived character-states (1B; 2C; 3C,D; 5C; 9B-D; 10A,B; 11A,B; 12A?-C) unite the preceding three species within *Conacodon* relative to species belonging to *Oxyacodon*. This means that *Conacodon* is monophyletic with respect to *Oxyacodon*; however, the reverse is not the case. Archibald et al. (1983) could not find any unambiguous polarities for species within *Oxyacodon*. The present study has not been able to resolve any of these ambiguities with any certainty and further, no shared-derived character-states can be clearly demonstrated to unite the species of *Oxyacodon*. Thus all species of *Oxyacodon* and the monophyletic genus *Conacodon* form a polychotomous branching. The possibility remains open that one or more species of *Oxyacodon* are more closely related to species within *Conacodon*, which would of course make the latter genus nonmonophyletic as presently constituted.

Conacodon and *Oxyacodon* are united by at least two, and possibly three shared-derived character-states relative to other periptychids (7; 8; and possibly 9A?-D). It was based upon this separation of *Conacodon* and *Oxyacodon* from other periptychids that we recognize the subfamily Conacodontinae. We feel this best expresses the current understanding of the phylogenetic relationships among the three clades of advanced periptychids. If the trichotomy of the Conacodontinae, the Anisonchinae, and the Periptychinae can be resolved, the classification should be modified to show this resolution.

Acknowledgments

We thank the editorial board of *Postilla* (Drs. R. S. Miller, J. H. Ostrom, C. G. Sibley, and B. H. Tiffney), Dr. M. Novacek, and Dr. K. Rose for reviewing the manuscript. Discussions with Drs. M. Novacek and B. H. Tiffney were particularly helpful, but any errors of observation, interpretation, or methodology are the responsibility of the authors. We thank Dr. Barry Kues, University of New Mexico (UNM), and Drs. Richard Tedford and Malcolm McKenna, American Museum of Natural History (AMNH) for allowing us to use specimens in their institutions. Other specimens or casts of specimens noted in this study are from Brigham Young University (BYU), University of Kansas Museum of Natural History (KU), University of California Museum of Paleontology (UCMP), University of Minnesota Museum of Paleontology (UMVP), and Yale Peabody Museum of Natural History (YPM). Acknowledgment is made to the Donors of The Petroleum Research Fund, administered by the American Chemical Society (Grant No. PRF 12143-G2 to J.D.A.), for support of this research. Additional support was provided by the U. S. Bureau of Land Management (BLM).

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