

## “South American” Marsupials from the Late Cretaceous of North America and the Origin of Marsupial Cohorts<sup>1</sup>

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Newly described marsupial specimens of Judithian (late Campanian) and Lancian (Maastrichtian) age in the western interior of North America (Wyoming to Alberta) have dental morphologies consistent with those expected in comparably aged sediments in South America (yet to be found). Three new Lancian species are referable to the didelphimorphian Herpetotheriidae, which suggests that the ameridelphian radiation was well under way by this time. The presence of a polydolopimorphian from Lancian deposits with a relatively plesiomorphic dental morphology and an additional polydolopimorphian taxon from Judithian deposits with a more derived molar form indicate that this lineage of typically South American marsupials was diversifying in the Late Cretaceous of North America. This study indicates that typical South American lineages (e.g. didelphimorphians and polydolopimorphians) are not the result of North American peradectian progenitors dispersing into South America at the end of the Cretaceous (Lancian), or at the beginning of the Paleocene (Puercan), and giving rise to the ameridelphian marsupials. Instead, these lineages, and predictably others as well, had their origins in North America (probably in more southerly latitudes) and then dispersed into South America by the end of the Cretaceous. Geophysical evidence concerning the connections between North and South America in the Late Cretaceous is summarized as to the potential for overland mammalian dispersal between these places at those times. Paleoclimatic reconstructions are considered, as is the dispersal history of hadrosaurine dinosaurs and boid snakes, as to their contribution to an appraisal of mammalian dispersals in the Late Cretaceous. In addition, we present a revision of the South American component of the Marsupialia. One major outcome of this process is that the Polydolopimorphia is placed as Supercohort Marsupialia *incertae sedis* because no characteristics currently known from this clade securely place it within one of the three named marsupial cohorts.

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**KEY WORDS:** Ameridelphia, Didelphimorphia, Polydolopimorphia, Judithian, Lancian, marsupial phylogeny, biogeography.

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<sup>1</sup>This article contains corrections to the text and a new Figure 11 not incorporated in the originally published version in Vol. 11, Nos. 3/4. For purposes of future citation, the present version (Vol. 12 and Nos. 3/4) should be used.

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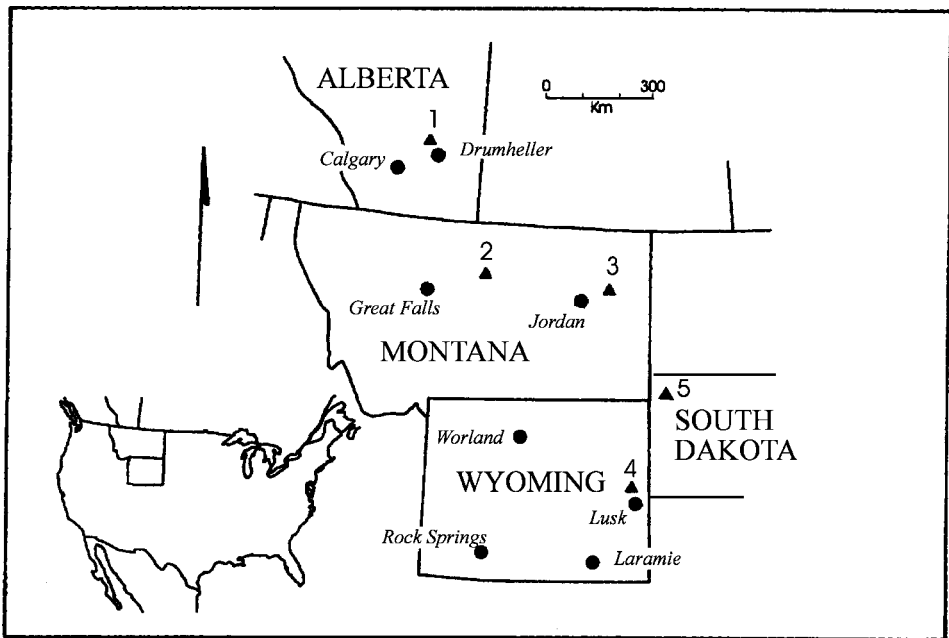
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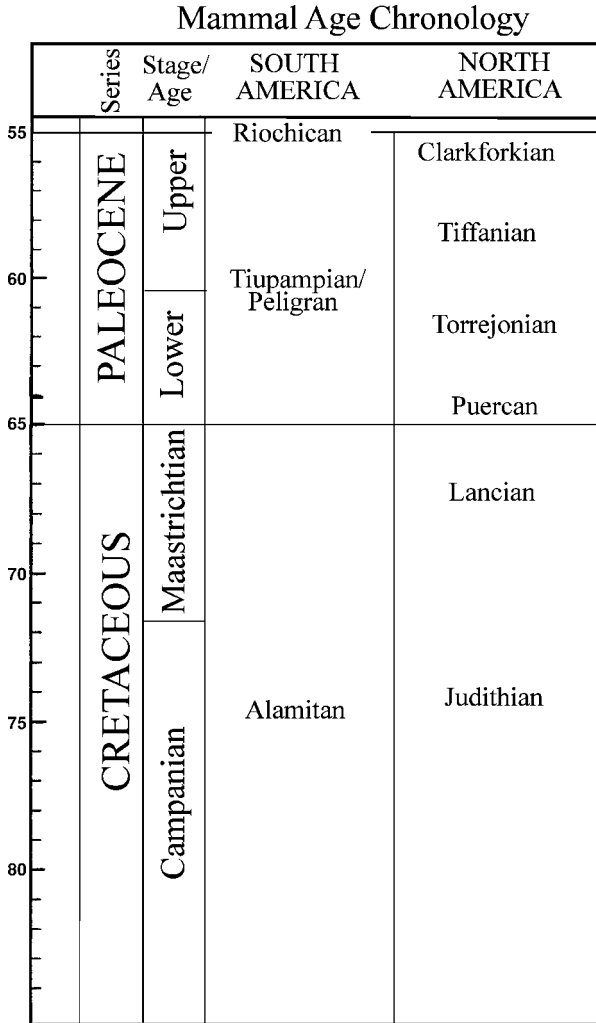
## INTRODUCTION

This paper describes four new species of fossil marsupials from Judithian and Lancian (nominally late Campanian to Maastrichtian) age deposits in the western interior of North America (Figs. 1 and 2). In addition, it advocates placing a fifth marsupial taxon, *Ectocentrocristus foxi* (Rigby and Wolberg, 1987), previously described as a new subfamily of Didelphidae, in the Order Polydolopimorphia. These fossils suggest the prior presence of lineages typically found in the Paleogene of South America in North America. Among the implications of this work is that the early didelphimorphian and polydolopimorphian marsupials should have been present in equatorial North America and South America during these Late Cretaceous times, as well, but have not yet been discovered. Thus far the poorly known Campanian–Maastrichtian record of South America (mostly restricted to the southern tip of this continent) has yielded only nontherian mammalian taxa, possibly increasing the likelihood that the origination, as well as early dispersal of the above marsupial taxa was centered in tropical North America. Thus, the specimens we describe herein, plausibly were immigrants from a more equatorial latitude in the Americas.

Simpson (1945) considered the basic insectivorous to carnivorous American marsupials as members of the Didelphoidea, whereas the Australian forms were placed in the



**Fig. 1.** Locality map of site of Late Cretaceous didelphimorphian (*Nortedelphys*) and polydolopimorphian (*Hatcheritherium*, *Ectocentrocristus*) taxa in the western interior of North America: (1) Scollard Formation, near Scollard, Alberta, Canada (*N. magnus*); (2) Judith River Formation, Choteau County, Montana (*E. foxi*); (3) Hell Creek Formation, McCone County, Montana (*N. intermedius*, *N. minutus*); (4) Lance Formation, Niobrara County, Wyoming (*H. alpha*, *N. magnus*, *N. intermedius*, *N. minutus*) and (5) Lower Hell Creek Fm., Harding County, South Dakota, USA (*N. intermedius*).



**Fig. 2.** Late Cretaceous to Eocene fossil mammal chronology of North America and South America illustrating the approximate time frames for the various South American and North American Land Mammal Ages in this time period, after Woodburne and Swisher (1995) and Flynn and Swisher (1995).

Dasyuroidea. However, marsupials were recognized as a group of mammals comparable in ecological diversity to placental mammals (Ride, 1964, 1970) and raised to an equivalent taxonomic rank, the higher level taxonomy within the Marsupialia consisted of four orders: the Marsupicarnivora, which included all the insectivorous to carnivorous taxa of North America, South America, and Australia, such as the didelphids, stagodontids, pediomyids, borhyaenids, thylacynids, and dasyurids; the Paucituberculata, the South American caenolestids, polydolopids, groeberiids, and argyrolagids; the Peramelina (Australian

faunivores), the peramelids, and thylacomyids; and the Diprotodontia, which includes all the Australian herbivore families (e.g., macropodids, phascolarctids, vombatids, phalangerids, pseudocheirids, etc.). The phylogenetic arrangement of these ordinal taxa was in a more or less progressive fashion from marsupicarnivores to peramelinans to diprotodontians (e.g., Ride, 1964, 1970) with paucituberculatans being independently derived from the marsupicarnivores as well. The origin of the Marsupicarnivora was inferred to have been from the North American Late Cretaceous marsupials (such as *Alphadon*), with most of these taxa assigned to the Didelphidae. The Didelphidae were considered to contain the ancestry of all marsupicarnivores. Subsequently, Crochet (1979) distinguished between the predominantly South American Didelphidae, a Cenozoic family, identified by the V-shaped centrocrista on the upper molars (a derived or apomorphic state) and the predominantly North American Peradectidae, which is most diverse in the latest Cretaceous and has a linear centrocrista between the paracone and the metacone (the ancestral or plesiomorphic state).

In addition, the work of Szalay (1982a,b, 1994) focused on the ankle joint articulation pattern in marsupials, and in particular on the articular facets between the astragalus and the calcaneus. Szalay (1982a,b) proposed that all Australian marsupials and the South American microbiotheres shared the derived state of a single, continuous calcaneoastragalar facet rather than the more plesiomorphic condition of two separate facets, the calcaneoastragalar facet and the sustentaculoastragalar facet, as characteristic of the American marsupials. This resulted in a geographic partitioning of marsupials, with the Australian taxa and the South American microbiotheres assigned to the marsupial cohort Australidelphia, whereas all the other American marsupials were placed in the Ameridelphia. The classification of Szalay (1982a,b) was further refined by Aplin and Archer (1987) as more biochemical and fossil data became available. A variety of biochemical and molecular data (e.g., Kirsch *et al.*, 1991) generally supported the contentions of Szalay (1982a,b), with the additional complexity that there was a close relationship between the South American microbiothere, *Dromiciops*, and living members of the Australian Diprotodontia (Springer *et al.*, 1998).

Marshall *et al.* (1990) suggested that a third marsupial cohort was necessary to define the three major clades of marsupials, which also corresponded to the three major radiations of marsupials, the Alphadelphia in North America, the Ameridelphia in South America, and the Australidelphia in Australia. The Alphadelphia was considered to be a paraphyletic stem group giving rise to both the ameridelphian and australidelphian cohorts via different phyletic lineages.

The classification of Kirsch *et al.* (1997) is generally comparable to that of Marshall *et al.* (1990), with Boreometatheria replacing Alphadelphia, Notometatheria the Ameridelphia, and Eometatheria the Australidelphia. In all classifications, the Peramelina are related to Dasyuromorphia within the Australidelphia, and Microbiotheria are linked at different places, but still within the Australidelphia.

Biogeographically, it appeared that alphadelphian marsupials dispersed to South America and then gave rise to the Ameridelphia (Case and Woodburne, 1986). However, the species described here indicate a different biogeographic pattern. In the present study, South American marsupials are considered to be present in the latest Cretaceous of North America and then disperse to South America. Plate reconstructions of the Caribbean region (e.g., Pindell, 1994; Villamil and Pindell, 1998) support the potential of overland mammal dispersal in the Late Cretaceous from North to South America (or

Table I. *Nortedelphys* Measurements

Species	Specimen no.		Length	Ant. width	Post. width
<i>N. magnus</i>	UA 2846 <sup>a</sup>	LM1	2.70	2.70	2.90
		LM2	2.85	3.30	3.30
		LM3	2.55	3.40	3.35
		LM4	1.75	3.05	2.10
		Lp3	1.80	1.15	
		Lm1	2.30	1.50	1.60 <sup>b</sup>
		Lm2	2.65	1.90	2.00
		Lm3	2.75	1.90	1.70
		Lm4	2.50	1.60 <sup>b</sup>	1.20
		<i>N. intermedius</i>	UCMP 45601	LM1	2.77
LM3	2.46			2.22	2.37
UCMP 134776	LM3		2.46	2.22	2.37
	RM3		2.40	2.32	2.72
UCMP 53097	RM3		2.06	2.40	2.49
	RM3		2.06	2.40	2.49
UCMP 54479	RM3		2.06	2.40	2.49
	RM3		2.06	2.40	2.49
UCMP 51427	LM1		1.82	—	2.17
	LM2		2.07	2.17	2.49
UCMP 51385	RM1		2.11	2.25	2.40
	RM2		2.47	2.32	2.65
UCR 20885	LM3		2.13	2.37	2.43
	LM3		2.13	2.37	2.43
UCMP 46994	LM1		2.29	1.92	2.36
	LM1	2.29	1.92	2.36	
UCMP 47464	LM1	2.27	1.85	2.33	
	LM1	2.27	1.85	2.33	
UCMP 132625	LM1	2.14	1.79	2.10	
	LM1	2.14	1.79	2.10	
UCMP 47588	Lm1	2.22	1.03	1.20	
	Lm1	2.22	1.03	1.20	
UCMP 52660	Lm2	2.54	1.36	1.46	
	Lm2	2.54	1.36	1.46	
UCMP 46319	Lm3	2.30	1.46	1.38	
	Lm3	2.30	1.46	1.38	
UCMP 137350	Rm3	2.20	1.39	1.34	
	Rm3	2.20	1.39	1.34	
<i>N. minimus</i>	UCMP 72211	LM3	1.64	1.80	2.03
		LM3	1.64	1.80	2.03
		LM3	1.64	1.80	2.03
UCMP 52715	RM2	1.89	1.75	2.02	
	RM2	1.89	1.75	2.02	
UCMP 137351	RM1	1.49	1.40	1.68	
	RM1	1.49	1.40	1.68	

<sup>a</sup>From Lillegraven (1969).

<sup>b</sup>Estimated measurement.

vice versa), but this is progressively less likely from the Paleocene to the late Paleogene (see below).

## MATERIALS AND METHODS

### Definitions and Measurements

*Nortedelphys* measurements are listed in Table I. Unless otherwise noted the classification for marsupials follows that of Marshall *et al.* (1990), with certain innovations presented in Table II.

Dental nomenclature is illustrated in Fig. 3 and follows Luckett (1993) where premolars (P—upper and p—lower) are numbered 1–3 and molar designation is M1–4 (upper molars) and m1–4 (lower molars). Anatomical directions are L (left) and R (right). Measurements are in millimeters.

Terms for Cenozoic mammal ages in North America follow Woodburne and Swisher (1995) and for the Cretaceous, Lillegraven and McKenna (1986). South American Mammal Age terms follow Flynn and Swisher (1995). Calibration of the Mesozoic systems follows Gradstein *et al.* (1995).

**Table II.** Revised Classification of the Marsupialia<sup>d</sup>


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Supercohort Marsupialia  
 Cohort Alphadelphia  
 Order Peradectia  
   Family Peradectidae  
   Family Pediomyidae  
   Family Stagodontidae  
   Family Caroloameghiniidae  
 Cohort Ameridelphia  
 Order Didelphimorphia  
   Superfamily Didelphoidea  
     Family Pucadelphidae  
       *Incadelphys*; early Paleocene, S.A.1, 2  
       *Mizquedelphys*; medial Paleocene, S.A.1, 2  
       *Pucadelphys*; medial Paleocene, S.A.1, 2  
     Family "Didelphidae"  
       *Itaboraidelphys*; late Paleocene, S.A.1  
       *Marmosopsis*; late Paleocene, S.A.1  
       *Carolopaulacoutoia*; late Paleocene, S.A.1  
       *Tiulordia*; early Paleocene, S.A. 2  
       *Jaskhadelphys*; early Paleocene, S.A. 2  
     Family Caluromyidae<sup>1</sup>  
     Family Herpetheriidae  
       *Nortedelphys*; Lancian, N.A.2  
       *Swaindelphys*; Tiffanian, N.A.2  
       *Peratherium*; early Eocene-? medial Miocene,  
       Eur; early Oligocene, Af; ?As. 1  
     Subfamily Eobrasilinae<sup>1</sup>  
     Family Derorhynchidae  
       *Derorhynchus*; late Paleocene, S.A. 2  
     Family Protodidelphidae  
 Order Sparassodonta  
   Superfamily Borhyaenoidea  
     Family Mayulestidae  
       *Mayulestes*; early Paleocene, S.A. 2  
     Family Hondadelphidae<sup>1</sup>  
     Family Hathliacynidae<sup>1</sup>  
       *Allqokirus*; early Paleocene, S.A. 2  
     Family Borhyaenidae<sup>1</sup>  
     Family Proborhyaenidae<sup>1</sup>  
     Family Thylacosmilidae<sup>1</sup>  
 Order Paucituberculata<sup>1</sup>  
 Ameridelphia, *incertae sedis*  
   *Andinodelphys*; early Paleocene, S.A.2  
 Cohort Australidelphia  
 Order Microbiotheria  
   Family Microbiotheriidae  
     *Mirandatherium*; late Paleocene, S.A.  
 Order Peramelina<sup>1</sup>  
 Order Dasyuromorpha<sup>1</sup>  
 Order Notoryctemorphia<sup>1</sup>  
 Order Diprotodontia<sup>1</sup>  
 Marsupialia *inertae sedis*  
   Order Polydolopimorphia<sup>1</sup>  
     Suborder Hatcheriformes  
       Hatcheriformes, *incertae sedis*  
       *Hatcheritherium*; Lancian, N.A.2  
       *Palangania*; late Paleocene, S.A.2  
       *Glasbius*; Lancian, N.A.2  
     Suborder Bonaparteriiformes

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Table II. Continued

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Superfamily Bonapartherioidea
Family Prepidolopidae <sup>1</sup>
Family Bonapartheriidae <sup>1</sup>
Subfamily Bonapartheriinae
Subfamily Epidolopinae <sup>1</sup>
<i>Epidolops</i> ; late Paleocene, S.A.2
Family Gashterniidae <sup>1</sup>
Superfamily Argyrolagoidea
Family Groeberiidae <sup>1</sup>
Family Patagoniidae <sup>1</sup>
Family Argyrolagidae <sup>1</sup>
Suborder Polydolopiformes
Family Polydolopidae
Subfamily Polydolopinae <sup>1</sup>
Polydolopiformes, <i>incertae sedis</i>
<i>Ectocentrocristus</i> ; Judithian, N.A.2
<i>Roberthoffstetteria</i> ; medial Paleocene, S.A.2

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<sup>a</sup>Classification is discussed in the text. Taxa indicated by 1 are not changed from Marshall *et al.* (1990), except that *Carolopaulacoutoia* McKenna and Bell (1997) replaces *Sternbergia* Paula Couto (1970). The arrangement of the two major clades of polydolopimorphians, Bonapartheriiformes and Polydolopiformes, follows Goin (2003 and literature cited therein). Peradectian affinities of caroloameghiniids were supported by Goin *et al.* (1998a,b). Genera discussed in the text are indicated by 2.

### NOMENCLATURE

AMNH	American Museum of Natural History, New York
UA	University of Alberta, Edmonton, Alberta, Canada
UCMP	University of California Museum of Paleontology, Berkeley
UCR	University of California, Riverside (now housed at UCMP)
UNM-B	University of New Mexico (U.S. Bureau of Land Management collections), Albuquerque, New Mexico
UW	University of Wyoming, Laramie, Wyoming
YPM	Yale University Peabody Museum, New Haven, Connecticut

### SYSTEMATIC PALEONTOLOGY

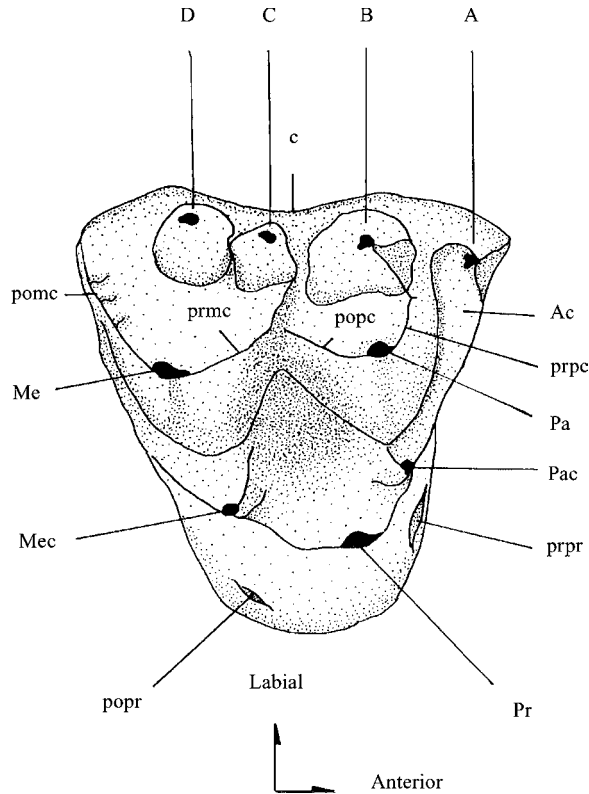
Supercohort MARSUPIALIA (Illiger, 1811) *incertae sedis*  
 Order POLYDOLOPIMORPHIA (Ameghino, 1897)  
 Suborder POLYDOLOPIFORMES Goin and Candela (1996)  
 POLYDOLOPIFORMES *incertae sedis*

*Ectocentrocristus foxi* Rigby and Wolberg, 1987  
 (Figure 3, Rigby and Wolberg, 1987)  
 (Fig. 4A–C herein)

*Holotype*. AMNH 77372, an isolated left upper molar, probably an LM3.

*Measurements*. Length: 3.90 mm; Width: 3.35 mm.

*Referred Specimens*. AMNH 77371, m1; UNM-B5485 upper molar fragment.



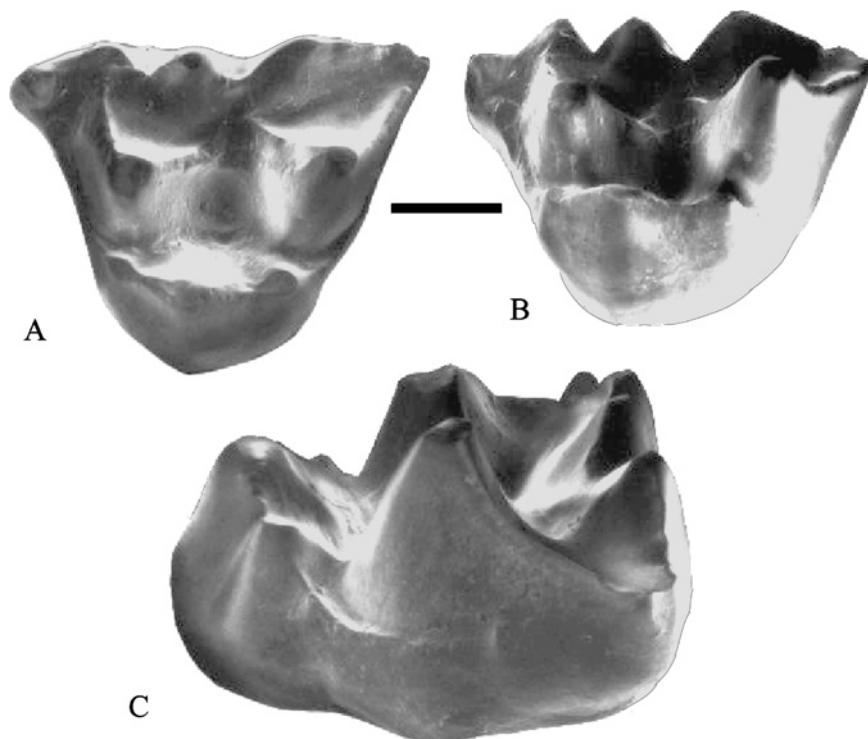
**Fig. 3.** Diagram of an upper left molar of a marsupial (based on the new genus *Hatcheritherium*) to illustrate the dental terminology used herein: A–D refer to stylar cusps A through D; Ac—anterior cingulum; e—ectoflexus; Me—Metacone; Mec—metaconule; Pa—paracone; Pac—paraconule; pomc—postmetacrista; popc—postparacrista; popr—postprotoconal cingulum; Pr—protocone; prmc—premetacrista; prpc—preparacrista; prpr—preprotoconal cingulum. Note that the postparacrista (popc) and the premetacrista (prmc) form the centrocrista between the paracone (Pa) and the metacone (Me).

*Age and Locality.* Judithian (late Campanian). Holotype and referred specimen, AMNH 77371, are Judithian (late Campanian) in age, from Clambank Hollow, upper part of the Judith River Formation, Choteau County, Montana (see Sahn, 1972: 339). Referred specimen UNM-B5485 derives from Fossil Forrest Quarry 1, lowermost Kirkland Shale, New Mexico, which probably is late Campanian (=Judithian) in age (see Rigby and Wolberg, 1987: 66).

*Revised Diagnosis.* Linearly placed stylar cusps along the labial margin with flattened lingual face; stylar cusps increasing rapidly in size from A to D; wide and deep trigon basin; para- and metaconules lingually placed and incipiently aligned with the protocone.

*Revised Description.* This is intended to supersede that of Rigby and Wolberg (1987) and focuses on the holotype. The prior description of the lower molar is considered





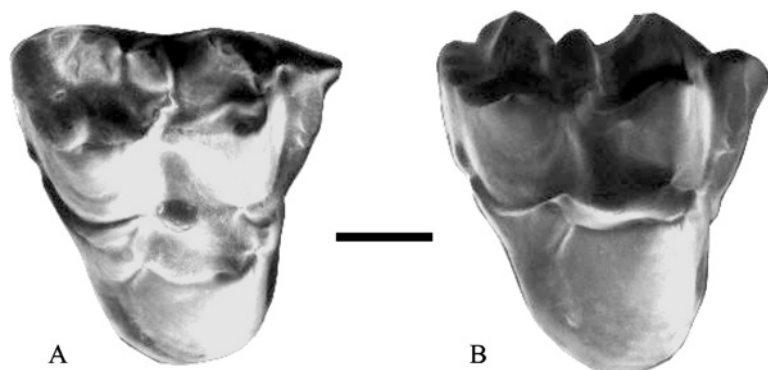
**Fig. 4.** A–C, *Ectocentrocristus foxi* Rigby and Wolberg, 1987, Holotype—AMNH 77372, an isolated left upper molar, probably a M3. Originally illustrated in a line drawing by Rigby and Wolberg (1987; Fig. 3). A—occlusal view; B—lingual view, and C—anterior view. Scale bar = 1.0 mm.

sufficient. The occlusal outline of the holotype is basically triangular, but the antero-posterior length is greater than the transverse width (from labial margin to lingual side of protocone). There is no ectoflexus along the labial margin. The metastyle is somewhat elongated posteriorly. Five styler cusps, A–E, are present with  $A < B < C < D$  and the E cusp is minute. Styler cusps A and B are conical and are connected by a low, notched crest, whereas styler cusps C and D are bladed with prominent anteroposterior crests. The preparacrista connects to styler cusp B and is shorter than the postmetacrista. The paracone is subequal to the metacone in area, but lower than the metacone, and the two cusps are widely separated and are most strongly developed at their respective anterior and posterior margins. A narrow anterior cingulum extends from styler cusp A to the paraconule and a very narrow posterior cingulum extends from the metaconule to near the end of the metastyle, which is well below the level of the postmetacrista. The centrocrista is V-shaped, but it is open labially so that the postparacrista and the premetacrista do not connect to each other. The postparacrista terminates on the floor of the styler shelf at a point which is below the apex of the C cusp. The premetacrista terminates at the base of the crista connecting the C and D styler cusps, so that the premetacrista is at a higher level than the postparacrista. The postmetacrista is strong, and slopes to the metastylar corner of the tooth, but is well above the level of the styler shelf. The styler shelf is very narrow and rather than being

typically flat from the major cusps (i.e. paracone and metacone) to the stylar cusps, there is a steeply incised valley between the major cusps and the stylar cusps. The protocone is low and very broadly based. It is positioned very close to the paracone and metacone, making the talon basin much reduced transversely. The protocone is also anteriorly shifted to a point just anterior to stylar cusp C, rather than being aligned with the paracone and stylar cusp B. The preprotocrista extends to the paraconule, whereas the postprotocrista reaches the metaconule. The angle between the two protocristae is very obtuse, in fact, it is very close to being linear anteroposteriorly. The paraconule is very distinct, not winged, and positioned near the base of the paracone. The metaconule is enlarged; it too is not winged and is positioned nearer the base of the metacone, so that its size and placement is "hypocone"-like. The metaconule is much larger than the paraconule.

*Discussion.* The holotype of *Ectocentrocristus foxi*, AMNH 77372, was first noted and figured by Sahni (1972, p. 383 and figure 14 O,P) and like *Hatcheritherium*, n. gen., described below, was referred to *Alphadon* cf. *rhiaster* (Clemens, 1966, p. 13, figure 12, table 4). However, the assignment of this specimen to *Alphadon* is incorrect, because *Ectocentrocristus* is not a peradectid, due to the centrocrista being highly invasive of the stylar shelf, rather than linear. In addition, stylar cusp B is not the largest stylar cusp (D is the largest and C is also larger than B), and all of the stylar cusps are aligned along the labial margin of the tooth. Thus, there is no ectoflexus, nor is stylar cusp C set lingually from the labial margin. The reduction of the transverse width of the stylar shelf also separates *Ectocentrocristus* from all peradectoids (Marshall *et al.*, 1990) with the exception of *Glasbius*. *Ectocentrocristus* differs from *Glasbius* in the nearly anteroposterior alignment of the conules with the protocone and in the invasiveness of the centrocrista into the stylar shelf. Rigby and Wolberg (1987) referred *Ectocentrocristus* to the Didelphidae which they equated to what is now recognized as the Peradectidae (Crochet, 1979). *Ectocentrocristus* has an invasive centrocrista, but, as mentioned, it is not "V"-shaped but open (i.e., the labial end of the postparacrasta does not connect to the labial end of the premetacrasta), which is a trait exhibited by polydolopimorphians. Rigby and Wolberg also erected a new subfamily for *Ectocentrocristus foxi*, which is no longer applicable due to this species being assigned as Polydolopiformes (see Table II).

*Ectocentrocristus* shares with all the basal (i.e. less highly derived) polydolopimorphians, the very invasive and open centrocrista, where the postparacrasta meets the stylar shelf at a point lower on the shelf than does the premetacrasta. Similar to all polydolopimorphians, *E. foxi* exhibits a narrowing of the stylar shelf, so that the distance between the stylar cusps and the paracone and metacone is reduced. In addition, the metaconule is enlarged. *Roberthoffstetteria* (early Paleocene, South America) also shares these features, plus the anteroposterior alignment of the conules with the protocone. However, *Ectocentrocristus* retains a more plesiomorphic set of morphological characters in being only incipiently bunoid and retains all cristae, which have been lost or highly reduced in the very bunoid *Roberthoffstetteria*. Finally, *E. foxi* differs from *Hatcheritherium*, n. gen., which has the most plesiomorphic molar morphology among the polydolopimorphians, by its alignment of the conules with the protocone, the open centrocrista and the reduction of the stylar shelf. The conclusion here is similar to that reached by Fox (1979, p. 96) that the type specimen of *Ectocentrocristus foxi* is different from the upper molar of any marsupicarnivore known then (or now)



**Fig. 5.** A–B, *Hatcheritherium alpha* n. gen. et. sp., Holotype—YPM 14912, an isolated right upper molar, probably a M1. A—occlusal view and B—lingual view. Scale bar = 1.0 mm.

Suborder HATCHERIFORMES nov.  
HATCHERIFORMES *incertae sedis*

*Hatcheritherium* n. gen.

*Alphadon* cf. *A. rhiaster* (Clemens, 1966, p. 13)

*Etymology.* Named for John Bell Hatcher who collected the specimens of this taxon.

*Holotype and Only Known Species.* *Hatcheritherium alpha*, n. sp.

*Diagnosis.* As for the holotype and the only included species.

*Hatcheritherium alpha* n. sp.

(Fig. 5A and B)

*Etymology.* *alpha*, in reference to being first or at the stem of the polydolopimorphian clade.

*Holotype.* YPM 14912, an isolated right upper molar, probably an RM1.

*Referred Specimen.* YPM 14911, RM3

*Age and Locality.* Lancian (late Maastrichtian). Locality is from Quarry 9, Lance Creek for both the type and referred specimens (see Clemens 1966, p. 13), Lance Formation, Niobrara County, Wyoming, USA.

*Measurements.* Holotype—YPM 14912, length: 3.1 mm, width: 3.5 mm; referred specimen—YPM 14911, length: 3.6 mm, width: 3.9 mm (Clemens, 1966, p. 15, table 4).

*Diagnosis.* The centrocrista is V-shaped, but the postparacrista and the premetacrista do not connect to each other. The premetacrista connects to the apex of a cusplule lingual to stylar cusp C, whereas the postparacrista connects just lingual to the base of the cusplule. Stylar cusps B, C, and D are separate, incipiently bladed, and imbricated relative to each other. Stylar cusp C is large to very large. Pre- and postprotoconular cingula are present; the metaconule is only slightly larger than the paraconule; cusps are less bunoid than in other polydolopimorphians.

*Description.* YPM 14912 in occlusal view is an equilateral triangle. The stylar shelf is narrow so that the bases of stylar cusp B and the paracone touch, whereas there is only a narrow space between stylar cusp D and the metacone. Stylar cusp A is large, conical, and sits at the labial end of an anterior cingulum. The anterior cingulum extends from the paraconule toward the base of the crown along the anterior flank of the paracone, from which it rises as more of a crest than a cingulum to near the apex of stylar cusp A. Stylar cusp B is large and only slightly smaller than the paracone. The preparacrista is deeply V-shaped, but very low in height. From the apex of the paracone the preparacrista swings slightly anteriorly as it descends into the valley between the paracone and stylar cusp B, where it swings posteriorly as it climbs to the apex of stylar cusp B. Almost as a continuation of the preparacrista, a labial crest descends the anterolabial face of stylar cusp B. Stylar cusp C is conical and separated from stylar cusp B by a small valley, which opens to a reduced ectoflexus. Stylar cusp C has an anterolingually directed crest which ends at the base of a small internal cusplule. The anterior base of stylar cusp D merges with the posterior base of C. Stylar cusp D is conical and also has a set of slightly obliquely oriented crests, one anterolingual and one posterolabial. Thus, stylar cusps B, C, and D all exhibit the characteristic of oblique crestring. Stylar cusp B > D > A > C. The metacone is subequal to, but larger than the paracone. The lingual faces of both the paracone and metacone are convex, whereas the labial faces are nearly flat, creating a very asymmetrical aspect in occlusal view (= pyramidal in outline). The centrocrista is V-shaped, but the postparacrista and the premetacrista do not connect to each other. The premetacrista connects to the apex of a cusplule lingual to stylar cusp C, whereas the postparacrista connects just lingual to the base of the cusplule. The postmetacrista is moderately developed, curved, and wrinkled along its distal third. The trigon basin is anteroposteriorly wide, although somewhat transversely reduced. The bottom of the basin is well below the level of the stylar shelf. Conules are well developed, winged and are slightly closer to the paracone and the metacone, respectively, than to the protocone. The preparaconular crest meets the anterior cingulum labially. The postmetaconular crest extends labially as a narrow cingulum below the metacone. The protocone is strong and comparatively large. At its base is a pair of cingula, one preprotoconular and one postprotoconular.

The referred specimen, an RM3 (YPM14911), is very similar to the type, apart from its larger size. Differences between the two specimens include a more wrinkled postmetacrista, a much larger stylar cusp C (stylar cusp B is comparatively smaller), the anterior wing of the preparacrista is more pronounced, compared to overall size of the tooth the paracone and the metacone are smaller in size, and the preprotoconular and postprotoconular cingula are less developed.

*Discussion.* The specimens were originally noted by Clemens (1966, p. 13, figure 12) and referenced as *Alphadon* sp., cf. *A. rhiaster*. The two upper molars can not be ascribed to *Alphadon* or to any other peradectid, because they are more bunoid (=rounded cusps and crests) and brachyodont (=low crowned) and because of the uniquely invasive centrocrista. The invasive and disjunct centrocrista of *Hatcheritherium* is different from the V-shaped centrocristae in didelphimorphs, dasyuromorphs, and peramelians as the premetacrista connects to the stylar shelf at a higher point than does the postparacrista, whereas in those taxa with a V-shaped centrocrista, the two cristae meet at a common point. This invasive and disjunct centrocrista is the hallmark (key synapomorphy) of the Order Polydolopimorphia. Among the basal taxa of the Order, this same invasive, yet disjunct centrocrista is

present, but usually is more open (i.e., more anteroposteriorly separated points of contact of the cristae with the stylar shelf). Thus, this characteristic feature can be seen in *Ectocentrocristus*, *Palangania* (Goin *et al.*, 1998a,b), and *Rosendolops* (Goin and Candela, 1996).

Cohort AMERIDELPHIA Szalay, 1982a

Order DIDELPHIMORPHIA Gill, 1872

Superfamily DIDELPHOIDEA Gray, 1821

Family HERPETOTHERIIDAE (Trouessart, 1879) Kirsch *et al.*, 1997 NEW RANK

*Nortedelphys* n. gen.

*Alphadon marshi* (part) Lillegraven (1969, p. 33)

*Etymology.* *Norte*, Castilian for north in reference to the earliest and northern occurrence for didelphoids, *-delphys*, in reference to an opossum marsupial.

*Holotype.* *Nortedelphys magnus* n. sp.

*Age and Distribution.* Lancian age (late Maastrichtian) from South Dakota, Wyoming and Montana, United States and Alberta, Canada (Figs. 1 and 2).

*Generic Definition.* Upper molars transversely wide, due to a wide stylar shelf and long trigon basin, moderate ectoflexus, large stylar cusp B, paracone and metacone subequal. On M1 and M2 stylar cusp C is not centrally located, the centrocrista is highly invasive and approaches the stylar shelf, the protocone is spire-like, and large winged conules are present. In the lower molars, the cristid obliqua intersects the trigonid below the carnassial notch. Anterior and posterior cingulids are well developed, the paraconid and the metaconid are approximate, and entoconids are spire-like and not bladed.

*Nortedelphys magnus* n. sp.

*Alphadon marshi* (part) Lillegraven (1969, p. 33, figure 15)

(Fig. 6, Table I)

*Etymology.* *magnus*, in reference to the larger size of the molars of this species.

*Holotype.* UA 2846, left maxillary fragment with LM1–M4, and left mandibular ramus with Lp3–m4.

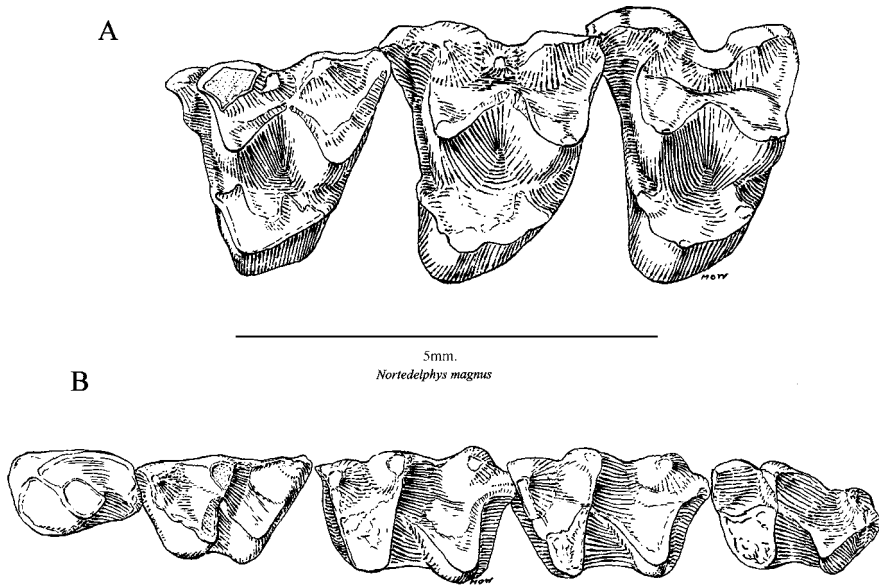
*Referred Specimen.* UCMP 45601, LM1.

*Age and Locality.* Lancian (late Maastrichtian). Holotype locality is KUA-1 (see Lillegraven, 1969, p. 12), Scollard Member of the Paskapoo Formation, 6 miles southwest of Scollard, Alberta, Canada (Figs. 1 and 2).

*Distribution.* UCMP 45601 from Nern-Baker (V-5619) from the Lance Formation, Niobrara County, Wyoming, USA.

*Measurements.* Table I.

*Diagnosis.* Largest species in the genus, conules are conical with prominent internal cristae, which flare anteriorly and posteriorly, respectively, from the tooth margin. In comparison with other species of *Nortedelphys*, the protocone is broader and less spire-like, with a more obtuse angle between the pre- and postprotocristae. The entoconid is larger and more spire-like and the posthypocristid forms a bladed crest on the anterolabial surface of the hypoconulid.



**Fig. 6.** *Nortedelphys magnus* n. gen. et. sp., Holotype—U.A. 2846, left maxillary fragment with M1–M4 (M1–3 figured), and left mandibular ramus with p3–m4. Originally illustrated in a line drawing by Lillegraven (1969: 34, fig. 15), but referred to there as *Alphadon marshi*.

*Description of Holotype.* UA 2846 is a left maxillary fragment with M1–4 and a left mandibular ramus with p3–m4 which were found in occlusion (Lillegraven, 1969). Upper molars increase slightly in transverse width from M1 to 4.

*M1.* This tooth is slightly shorter anteroposteriorly than M2, which is longer than M3 and all three molars are longer than M4. M1 has the most reduced styler shelf of the M1–3 molars. Even though broken, styler cusp B is the largest styler cusp. Styler cusp C is small and located close to styler cusp B and is aligned with B and D. The ectoflexus is shallow and restricted to the labial face of styler cusp C. Styler cusp A is the smallest of the styler cusps and is labiolingually compressed. The anterior cingulum is narrow and continuous lingually until it reaches the paraconular crest. Styler cusp D is well developed and has two main crests, one anterolingual which meets with styler cusp C at a notch, and a second which extends posterolabially to the metastyler corner. Styler cusp D is as tall as the paracone. A minute cuspsule at the metastyler corner could represent a styler cusp E, which is overlapped by the parastyler corner of M2.

The preparacrista contacts styler cusp B at its anterior face and is two-thirds of the length of the postmetacrista. The paracone is lower and narrower than the metacone. Both the metacone and the paracone are well separated from each other and are pyramidal in occlusal view. The centrocrista is very deep and almost contacts the lingual face of styler cusp C. The postmetacrista is almost straight and blade-like. The trigon basin is very deep. The paraconule and metaconule are close to the bases of their respective cones, with the paraconule closer to the paracone than the metaconule is to the metacone. Both conules are winged and flare anteriorly and posteriorly, respectively, from the pre- and postprotocristae.

The protocone is moderately developed, eccentric (i.e., anteriorly displaced with respect to other marsupials), with a flat anterior surface, that bears a small, peculiar, inclined

cingulum at its base. The postmetaconular crest forms a narrow cingulum just opposite of the apex of the metacone.

*M2*. Differs from *M1* as the tooth is much wider than long; the stylar shelf is wider; stylar cusp C is intermediate in position between stylar cusp B and stylar cusp D; the ectoflexus is deeper; the preparacrista is three-fourths of the length of the postmetacrista; stylar cusp A is lingually compressed; the cingulum at the base of the protocone is vestigial; stylar cusp B is better preserved in the *M2*, so that it can be seen that stylar cusp B and stylar cusp C are connected to each other by two curvilinear cristae, the labial crest bows labially and the lingual crest bows lingually thus enclosing a small valley between the two cristae.

*M3*. Differs from *M1* and *M2* as the tooth is transversely wider than anteroposteriorly long; there is a much wider anterior cingulum; the ectoflexus is deeper; stylar cusp B has a concavity on its anterior face; stylar cusp D is smaller; stylar cusp C is more lingually positioned due to the depth of the ectoflexus and it is located closer to stylar cusp D than to stylar cusp B; the preparacrista and the postmetacrista are parallel and subequal in length; and the centrocrista is less invasive than in *M1* or *M2*.

*M4*. The tooth is in early stage of eruption and, due to its location in the tooth row, is anteroposteriorly short. Most of the stylar shelf is missing, except for the parastylar corner on which the stylar cusps A and B are present. The preparacrista is the longest crest of the tooth; the paracone is the largest cusp of the tooth. The postmetacrista is very short due to the small size of the metacone and the reduction of the metastyle. The protocone is very narrow versus that in *M1*–*3*. Conules are compressed anteroposteriorly into blade-like crests.

*p3*. This tooth is anteroposteriorly shorter, but taller than *m1*. The large cusp (nominal protoconid) is surrounded by a cingulid which expands posteriorly to form a talonid-like structure. The talonid-like heel is divided in half by a central crest which extends from the apex of the main cusp.

The lower molars increase slightly in size from *m1* to *m3*, whereas the *m4* is as long as, but narrower than *m3*.

*m1*. The tooth is broken so that the posteriolabial half of the talonid including the hypoconid and hypoconulid are not present. The anterior cingulid is narrow and extends from the preprotoconular notch to the anterolabial corner. The metaconid is slightly posteriorly placed relative to the protoconid so that the rear wall of the trigonid is at a slightly oblique angle in occlusal view. The protoconid is proportionally smaller than on *m2*–*4*. The labiolingually compressed paraconid is more medially placed than in *m2*–*4*. The entoconid is well developed, conical, and bears a blade-like preentocristid.

*m2 and m3*. The paraconid is much closer to the metaconid, which is not posteriorly displaced, but rather in the same plane as the protoconid. This results in the pre- and postprotocristids being parallel to each other. The trigonid is much wider than long. The anterior cingulid is better developed than in the *m1*. The posterior cingulid is also well developed. The hypoconid on the *m2* is larger than on either *m1* or *m3*. The hypoconulid is large and more posteriorly oriented than in *m3* and *4*, where the hypoconulids are more vertical and more anteroposteriorly compressed. The entoconids are more even in size from *m2* to *m4* and more posteriorly placed successively from *m1* to *m4*. The cristid obliquas of *m2* and *m3* terminate anteriorly just labial to the carnassial notch. The main differences between *m2* and *m3* are (1) a vestigial cingulid is present at the anterior labial base of *m3*,

and (2) the talonid of m2 is wider than the trigonid, whereas in m3 the trigonid is wider than or equal to the talonid.

*m4*. This tooth differs from m2 and m3 in being narrower; the paraconid and metaconid are anteroposteriorly compressed so they are very close to each other. The talonid is much narrower due to the reduction of the hypoconid and the more lingual termination of the cristid obliqua so that it lies below the carnassial notch.

***Nortedelphys intermedius* n. sp.**

(Figs. 7 and 8)

*Etymology.* *intermedius*, in reference to the intermediate size of its molars compared to the other two species in the genus.

*Holotype.* UCMP 134776, LM3.

*Referred Specimens.* UCMP 47464, LM1; UCMP 132625, RM1; UCMP 53097, RM2; UCR 20885, LM3; UCMP 54479, RM3; UCMP 51385, RM1-2; UCMP 51427, LM1-2; UCMP 137350, Rm3; UCMP 46319, Lm3; and UCMP 47588, Lm1.

*Age and Locality.* Lancian (late Maastrichtian). Holotype locality V-87072, Hell Creek Formation, McCone County, Montana, USA (Figs. 1 and 2).

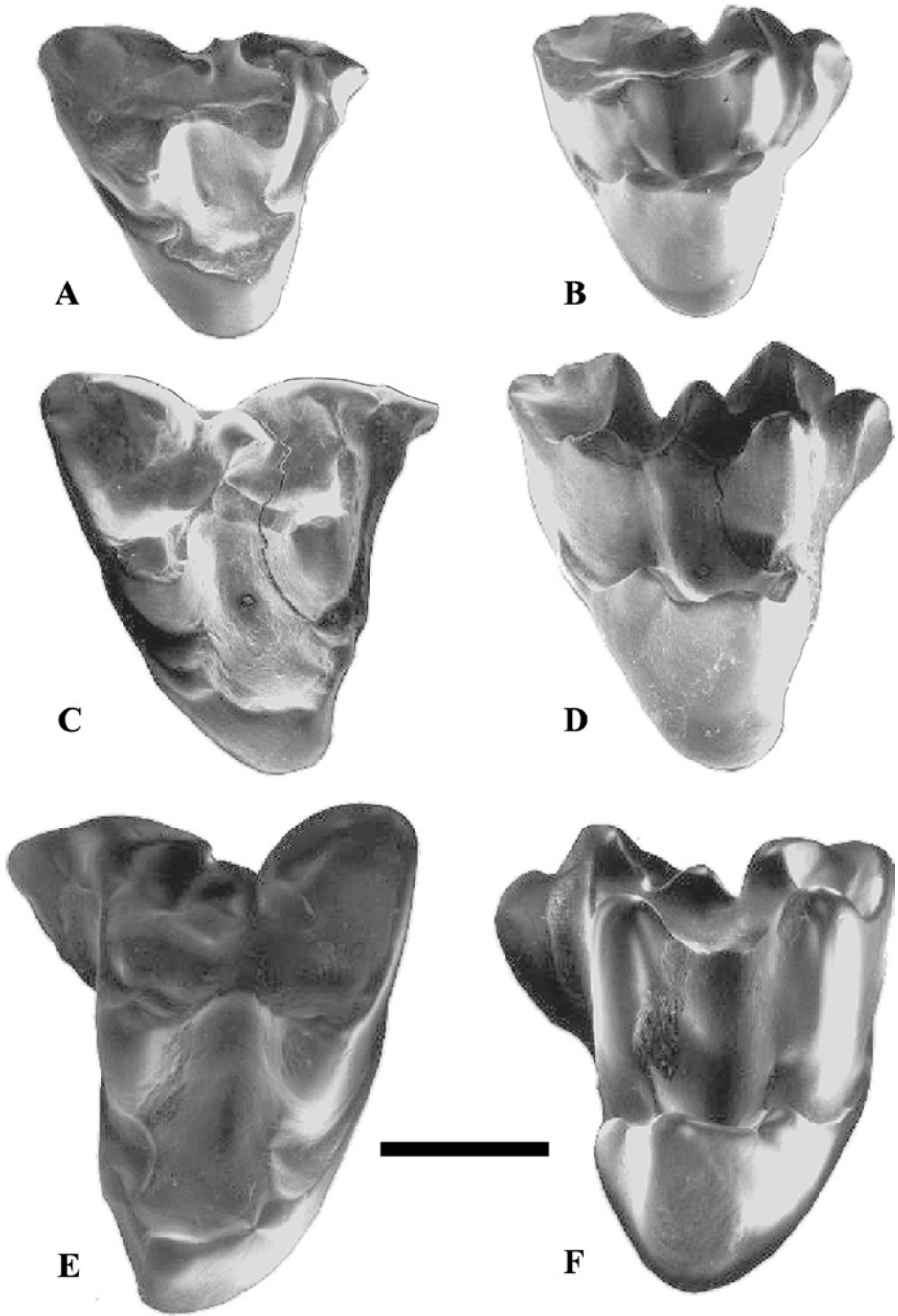
*Distribution.* UCMP 132625 from type locality; UCMP 46994, UCMP 51385, UCMP 46319, and UCMP 47588 from Lull 2 (V-5620), UCMP 54479 from Bushy Tailed Blowout (V-5711), UCMP 51427 and UCMP 53097 from Hatcher 2 (V5815), UW 497 from Lance Creek, Lance Formation, Niobrara County, Wyoming, USA; UCR 20885 and UCMP 137350 from the Bug Creek Anthills (V65127), Hell Creek Formation, McCone County, Montana, USA; Painter Ranch (V651), Lower Hell Creek Fm., Harding County, South Dakota, USA (based on unnumbered specimen in the collections of the Museum of Geology, South Dakota School of Mines & Technology, JAC, pers. observ.).

*Measurements.* Table I.

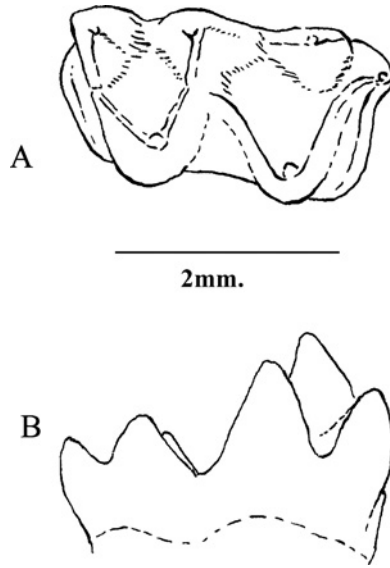
*Diagnosis.* *Nortedelphys intermedius* is intermediate in size between *N. magnus* and *N. minimus*; the conules are laterally compressed to form equally robust, vertically oriented, cristae. Styler cusp D is conical and bladed, with the cusp and cristae oriented oblique to the labial margin. The protocone is spire-like with an acute angle between the pre- and postprotocristae. The entoconid is smaller and more laterally compressed, and has a more robust preentocristid. The hypoconulid is more conical with the posthypoconid terminating at its base.

*Description of Holotype and Referred Specimens.* The holotype, UCMP 134776, is an LM3, which is much wider than anteroposteriorly long. The ectoflexus is moderate and deepest between styler cusp C and styler cusp D. Styler cusp A is pyramidal in shape due to cristae that extend from styler cusp B to the tip of the parastyle and from styler cusp A to the anterior cingulum. The anterior cingulum descends steeply from the crest between styler cusp B and styler cusp A, continues lingually below the paracone, and rises slightly to the base of the paraconule. Styler cusp B is the largest styler cusp, but is half of the size of the paracone, and is connected to the paracone by a preparacrista which is more robust from the paracone to base of the notch and then is much more gracile to the apex of styler cusp B. The preparacrista is curved posteriorly along its labial portion in that styler cusp B is directly opposite the paracone. Styler cusp C is at the tooth margin along the ectoflexus; is conical in shape, is equally distant and isolated from both styler cusp B and





**Fig. 7.** A–F, *Nortedelphys intermedius* n. sp.; Referred specimen, UCMP 132625, RM1, A—occlusal view and B—lingual view; Referred specimen, UCMP 53097, RM2, C—occlusal view and D—lingual view; Holotype, UCMP 134776, LM3, E—occlusal view and F—lingual view. Scale bar = 1.0 mm.



**Fig. 8.** A–B, *Nortedelphys intermedius* n. sp.; Referred specimen UCMP 46319, Lm3, A—occlusal view and B—lingual view.

stylar cusp D. A small crista extends from stylar cusp C posterolingually to the centrocrista, so that it appears as an extension of the premetacrista. Stylar cusp D is rounded anteriorly but flattened posteriorly. A crest extends from stylar cusp D along the margin towards but does not reach the metastylar corner. This crest incorporates a cusplule which may be considered as stylar cusp E. Stylar cusp  $B > D \gg C > A \gg E$ . The stylar shelf is wide, but basined. The preparacrista is shorter than the postmetacrista as the metastylar corner is extended somewhat labially. The paracone and metacone are equal in height, with the metacone being slightly more massive, and both are pyramidal in shape. The centrocrista is highly invasive, almost reaching the base of stylar cusp C. The conules are subequal in size with the metaconule being slightly larger. The conules are winged with the medial crests connecting to the interior surfaces of their respective cones. The conules are slightly closer to the paracone and metacone than they are to the protocone, and bulge out from the anterior and posterior margins of the tooth. A narrow posterior cingulum extends from the metaconule to below the metacone and disappears. The protocone is low and somewhat anteroposteriorly stretched. The angle between the pre- and postprotocristae is acute, but not greatly so.

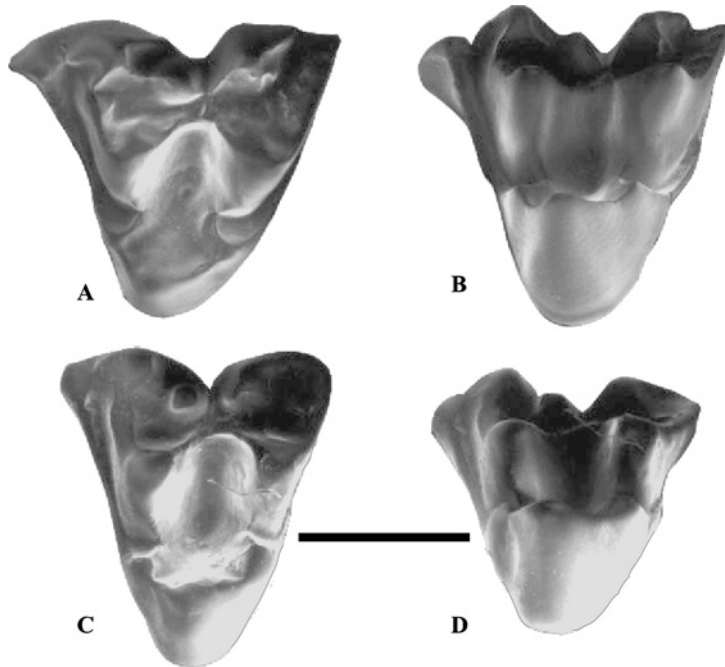
UCMP 46994, an LM1, is anteroposteriorly longer than transversely wide, primarily due to the reduction in width of the stylar shelf compared to the holotype (M3), because of the former's more anterior position in the tooth row. Thus, the preparacrista and the postmetacrista are both shorter in the M1 versus the holotype. In the M1, stylar cusp B has a strong posterior crest, not present in the M2, but there is still no connection to stylar cusp C. Stylar cusp C remains isolated from stylar cusp B and stylar cusp D. Stylar cusp D is more laterally compressed than in M2 and has a more prominent crest directed posterolingually. Stylar cusp  $B \gg$  stylar cusp  $C =$  stylar cusp  $D \gg$  stylar cusp A. There may be a minute

stylar cusp E on the posterior crest from stylar cusp D. The conules are less worn than in the holotype, are conical, and have the same pattern of cresting and position as in the holotype. The protocone is spired and shifted more anteriorly, as is typical of its more anterior position in the tooth row.

UCMP 53097, an RM2, is barely wider than long, typical of this tooth position. In comparison to the holotype, the ectoflexus in UCMP 53097 is much shallower, and stylar cusps B and D are more symmetrical about the ectoflexus. Consequently, the preparacrista and the postmetacrista are equal in length. Stylar cusp C is more isolated from stylar cusp B as the preparacrista is more linear, because stylar cusp B is slightly anterior to the paracone. Stylar cusp D is compressed and bladed with an oblique orientation with respect to the anteroposterior axis of the tooth, as it sits along the rear margin of the ectoflexus. Again, an apparent stylar cusp E is incorporated into the crest extending posterolabially from stylar cusp D. The stylar shelf is wide and the V-shaped centrocrista is highly invasive. The paracone and metacone are equal both in height and mass. The conules are laterally compressed and similarly winged as in the holotype. They are positioned midway between the protocone and the paracone and metacone, respectively. The protocone is spire-like with an acute angle between the pre- and postprotocristae. The protocone has a slightly more anterior position, so that it is nearly aligned with the paracone and stylar cusp B, more than in M1 and M3.

UCMP 47588, an Lm1, shows the trigonid and talonid equal in length, but the talonid is slightly wider than the trigonid. The anterior cingulid is narrow and originates just labial to the paraconid and descends to the crown base along the anterior face of the protoconid. The paraconid is lingually placed, compressed anteroposteriorly, and equal in height to the metaconid. A short, but robust preparacristid is directed anteriorly along the lingual margin, so that it projects beyond the anterior cingulid. The metaconid is conical and located posterior to the protoconid. There is a short and robust postmetacristid along the lingual margin which, along with the preentocristid, closes off the trigonid basin lingually. The protoconid is broken; however, it is clearly twice as massive as either the paraconid or metaconid. The angle between the pre- and postprotocristids is acute, but not extreme. The talonid cuspids are equal in height to the metaconid and paraconid. The hypoconid is spire-like. The cristid obliqua intersects the rear wall of the trigonid at the carnassial notch. The angle between the cristid obliqua and the posthypocristid is acute with the posthypocristid extending to the base of the hypoconulid. The hypoconulid is conical, twinned with the entoconid, and is very near, but not at, the posterolingual corner of the tooth. The hypoconulid is prominent and projects posteriorly beyond the posterior cingulid. The posterior cingulid begins just below the apex of the hypoconulid on the labial side of the cusp and descends labially to the crown base terminating at the posterolabial corner. The entoconid is laterally compressed, spire-like, and located anterior to the posterolingual corner of tooth. A short, but robust preentocristid meets the postmetacristid to block off the talonid basin on the lingual side. The entoconid is the tallest of the talonid cusps. The talonid basin is very narrow and deep.

UCMP 46319, Lm3, differs from the m1 by having a more anteroposteriorly compressed trigonid, in that the angle between the pre- and postprotocristae is more acute. The paraconid is more anteroposteriorly compressed, and the preparacristid is shorter, less robust, and anterolingually oriented. The talonid is longer than the trigonid and nearly equal (although wider) in width to the trigonid. The hypoconulid is at the posterolingual corner;



**Fig. 9.** A–D, *Nortedelphys minimus* n. sp.; Referred Specimen UW 27031, LM1, A—occlusal view and B—lingual view; Holotype, UCMP 72211, LM3, C—occlusal view and D—lingual view. Scale bar = 1.0 mm.

consequently, the posthypocristid is longer. The entoconid is more spire-like and anteriorly positioned, so only the preentocristid closes off the talonid basin lingually.

*Nortedelphys minimus* n. sp.

(Fig. 9, Table I)

*Etymology.* *minimus*, in reference to the smaller size of its molars compared to the other two larger species.

*Holotype.* UCMP 72211, LM3.

*Referred Specimens.* UCMP 137351, RM1; UW 27031, LM1; UCMP 52715, RM2.

*Age and Locality.* Lancian (late Maastrichtian). Holotype locality, Bug Creek Anthills (V-65127), Hell Creek Formation, McCone County, Montana, USA.

*Distribution.* UCMP 137351 from type locality; UCMP 52715 from Lull 2 (V-5620), Lance Formation, Niobrara County, Wyoming, USA; UW 27031 from Lance Creek, Lance Formation, Niobrara County, Wyoming, USA (Figs. 1 and 2).

*Measurements.* For the holotype, UCMP 72211 (Table I).

*Diagnosis.* Smallest species of the genus; less of a labial extension of the metastyle; conules are vertically oriented and pyramidal, with equally robust cristae; stylar cusp C is spire-like and set more lingually than stylar cusps B and D; stylar cusp D is more ovate than conical; the protocone is spire-like, with an acute angle between the pre- and postprotocristae.

*Description of Holotype and Referred Specimens.* The holotype, UCMP 72211, is an LM3, which is much wider than anteroposteriorly long, consistent with this tooth position. The parastyle and metastyle are equally developed; the ectoflexus is deep and reaches its most lingual point posterior to stylar cusp C. Stylar cusp A is prominent, conical, and connected to stylar cusp B by a low, narrow crest. A lingually directed crest from stylar cusp A, parallels the anterior cingulum to a point near the crown base. The cingulum continues beneath the paracone and rises up to the paraconule.

Stylar cusp B is the largest stylar cusp and located just anterior to the paracone. The preparacrista extends to the apex of the paracone and stylar cusp B. A posteriorly directed crest from the posterior face of stylar cusp B terminates in a small cuspule, which lies labial to the anterior half of stylar cusp C. A short posterolingual crest from stylar cusp B is directed toward stylar cusp C, which is located at the lingual end of the ectoflexus. Stylar cusp C is a prominent, robust, widely based cone with a distinct crest that nearly meets the posterolingual crest from stylar cusp B. This same crest extends anteroposteriorly from the anterior cusp base to the posterior cusp base, where it connects to an anterolingual crest from stylar cusp D. Stylar cusp D is a labiolingually compressed, bladed cusp, which is obliquely oriented, as it lies along the posterior margin of the ectoflexus. A posterolabial crest from stylar cusp D terminates prior to the metastylar corner. The stylar shelf is wide, with the preparacrista and the postmetacrista being subequal in length (the latter is the longer) and nearly parallel. Stylar cusp  $B > D > C > A$ . The paracone and metacone are equal in height, with the metacone being slightly more massive. They are both pyramidal in shape. The centrocrista is V-shaped, very invasive and directed to the posterior side of stylar cusp C. The conules are small, conical, and winged. The paraconule lies just labial to its posterior wing and is smaller than the metaconule. The metaconular wings are more robust and symmetrical with the anterior wing connecting to the metacone on its anterior face. The paraconule is closer to the paracone than to the protocone, whereas the metaconule lies midway between the metacone and the protocone. The protocone is spire-like and somewhat anteriorly positioned so that it is anterior of the notch in the ectoflexus, with the angle between the pre- and postprotocristae being approximately a right angle.

UW 27031, an LM1, differs from the holotype in being as equally long as wide, with the preparacrista bowed anteriorly and much shorter than the postmetacrista. Stylar cusp B has a stronger crest to stylar cusp A. Stylar cusp B is connected by a crest to stylar cusp C. The ectoflexus is deep. The stylar shelf is reduced anteriorly, thus the V-shaped centrocrista nearly reaches stylar cusp C. The metacone is equal in height, but more massive than the paracone. Both the paraconule and metaconule are closer to the the paracone and metacone, respectively, than in the holotype. The protocone is more anteriorly positioned and the angle between the pre- and postprotocristae is somewhat acute.

UCMP 52715, RM2, differs from the holotype in that it is more elongate anteroposteriorly, the metastyle is more labially extended than the parastyle, such features being a consequence of its tooth position. Stylar cusp C is both larger and more spire-like, and it is more isolated from stylar cusp B and stylar cusp D than in the holotype or the M1. Stylar cusp D is reduced, so that stylar cusp  $C > D$ . The preparacrista is bowed anteriorly and shorter than the postmetacrista as in the M1, but unlike the linear and long preparacrista of the holotype. The V-shaped centrocrista is no more invasive than that of the holotype, but because of the depth of the ectoflexus and the size of stylar cusp C, the labial apex of the centrocrista is very near the lingual base of stylar cusp C. The conules are

strongly winged and set near the paracone and metacone, respectively. The protocone is only slightly shifted anteriorly relative to the notch in the ectoflexus, but the angle between the pre- and postprotocristae is obviously obtuse, which differs from both the holotype and the M1.

## DISCUSSION

Several key features distinguish didelphimorphians from peradectians. In the upper molars, the centrocrista is V-shaped in the former, i.e., is labially invasive into the stylar shelf (the V-shape is in a horizontal plane, not in a vertical plane); in turn, peradectians have a linear and anteroposteriorly oriented centrocrista. The V-shape of the centrocrista results in the paracone and metacone having a pyramidal shape in occlusal view for didelphimorphians, whereas the cusps are more conical in peradectians.

Species of *Nortedelphys* represent Lancian didelphimorphians that have an anteroposteriorly compressed trigonid, so there is a more acute angle between the pre- and postprotocristids. Regardless of the angle varying along the tooth row, it is still more acute than in peradectians, such as in *Alphadon* or *Peradectes*.

Also, among the lower molars, the talonids feature greater distinctions between didelphimorphians and peradectians. Even though both clades show the metatherian condition of “twinned” entoconid and hypoconulid, this condition is differently expressed in each group. In *Nortedelphys*, the posthypoconid is long, so that it extends almost to the posterolingual corner of the talonid. The hypoconulid is located at the corner of the talonid, and the entoconid is more anteriorly placed along the lingual margin. The entoconid is much greater in size than, and is more closely “twinned” with, the hypoconulid. In *Alphadon* (or *Peradectes*), the posthypoconid is short, only extending to the anteroposterior midline, as the hypoconulid is located on the posterior margin just labial to the corner of the tooth and diagonal to the entoconid. Consequently the entoconid is in a more posterior position along the lingual margin, and the preentocristid is longer. The entoconid is equal to the hypoconulid in size and shape. Thus, although similar in size and in some occlusal features, *Nortedelphys* clearly differs from *Alphadon*, for which it is often mistaken in collections of Late Cretaceous marsupials (JAC, pers. observ.).

The species of *Nortedelphys* are more generalized than any Tertiary herpetotheriid because of their greater transverse width, the more equal size of the paracone and metacone, their narrower anteroposterior length (especially for M1 and M2), and deeper ectoflexus than that of *Swaindelphys* (Johanson, 1996; early Paleocene, North America) or later Tertiary herpetotheriids (see Krishtalka and Stucky, 1983). *Nortedelphys* also differs from *Swaindelphys* in having a less developed metaconule, less labiolingually compressed stylar cusps C and D, paraconid and metaconid are more approximate, the talonid is more elongate, the cristid obliqua meets the rear wall of the trigonid near the carnassial notch, and the trigonid and talonid widths are more equal. In having the paracone and metacone even more equal in size and height, *Nortedelphys*, however, seems to be more generalized than *Swaindelphys*.

*Nortedelphys* differs from pucadelphid didelphimorphians (Table II), such as those from the early Paleocene Tiupampa fauna of Bolivia (Marshall and de Muizon, 1988; de Muizon, 1991) and the medial Paleocene didelphids from the Itaborai fauna of Brazil (Marshall, 1987), in that the V-shaped centrocrista of the upper molars is much more

invasive of the wide stylar shelf, so that it approaches stylar cusp C (this defines the herpetotheriid didelphids). Additionally, *Nortedelphys* has a deeper ectoflexus than in the Paleocene or later didelphids. Finally, the more posterolingual position and the reduction of size of the hypoconulid is the result of the more lingual extension of the posthypocristid. This more elongate posthypocristid on the lower molar will then occlude with the more invasive centrocrista of the upper molars (specifically occluding with the premetacrista), which distinguishes *Nortedelphys* from the pucadelphids.

*Nortedelphys* thus represents the geologically oldest member and retains the most plesiomorphic dental traits of the didelphimorphian family Herpetotheriidae (contra Johanson, 1996, p. 1028). There is a continuum of acquisition of apomorphic molar character states from *Nortedelphys* to the traditional Eocene herpetotheriids with the morphology of *Swaindelphys* providing the connection between the more plesiomorphic morphology of *Nortedelphys* and the more derived molar morphology, such as seen in *Peratherium*. The features of the stylar shelf (i.e., short anteroposterior length along the labial margin, the presence of a moderate to deep ectoflexus, and a labial extension of the metastyle) and those associated with the protocone (acute angle of cristae about the protocone) are more plesiomorphic in *Nortedelphys* than in other herpetotheriids. *Swaindelphys* is derived in some of these traits: the ectoflexus is very shallow, the length of M1-2 is greater, and the angle between the pre- and postprotocristae is larger. The early Eocene (Wasatchian) herpetotheriids are much more derived, with a flattened ectoflexus, teeth that are longer than wide because of a posterior extension of the metastyle, and an obtuse angle formed by the crests about the protocone caused by the more anterolabial placement of the protocone. The lower molars show a continuous increase in the angle of cristids about the protoconid in response to the lengthening of the metastyle in the upper molars.

As an early representative of the Polydolopimorphia, *Hatcheritherium* is morphologically plesiomorphic to, but not yet the temporal precursor of, *Ectocentrocristus*, the Judithian representative of the Polydolopiformes and other taxa within the Polydolopimorphia as shown in Fig. 11. The polydolopimorphian clade is defined on the basis of an invasive centrocrista (i.e., projecting labially into the stylar shelf) of the upper molars in which the postparacrista terminates in the stylar shelf region lower in elevation than the distal end of the premetacrista. The premetacrista is longer as it extends further labially and bypasses the postparacrista in terminating in the stylar shelf at a higher elevation and at a more anterior position. Additional features include a reduction of the stylar shelf labiolingually, a metaconule that is larger than the paraconule and an enlargement of the protocone. These features support the affinities of *Hatcheritherium* and *Ectocentrocristus* with previously known polydolopimorphians such as *Prepidolops*, *Rosendolops*, *Bonapatherium*, *Epidolops*, *Chulpasia*, and *Gashternia* (bonapatheriiforms); *Polydolops* and *Roberthoffstetteria* (polydolopiforms); *Palangania* and *Glasbius* (hatcheriforms) and they would represent synapomorphies for the Polydolopimorphia (see also Goin and Candela, 1996, in press; Goin, 2003; Goin *et al.*, 2003). The morphology of *Hatcheritherium* is not only plesiomorphic relative to both polydolopiforms and epidolopiforms, but it is also basal to its own clade, the Hatcheriformes.

*Ectocentrocristus* is the earliest member of the Polydolopiformes (as well as the Polydolopimorphia) and possesses several key synapomorphies of this clade, such as the nearly anteroposterior alignment of the paraconule, protocone, and metaconule. Further derived features shared by *Roberthoffstetteria* and polydolopines include well-expanded

anterior and posterior cingula, which are at the same level as the trigon basin, a variable tendency to the development of neomorphic, accessory cusps at the labial face of the upper molars, and a paraconid placed labially with respect to the metaconid. Goin *et al.* (2003) argued in favor of the affinities of *Roberthoffstetteria* and polydolopines (*Polydolops* and allies), and proposed on this basis an interpretation of the molar cusp homologies of the latter.

The phyletic relationships summarized above imply that the basal Polydolopimorphia (*Hatcheritherium* or its precursor) were present in North America in Judithian time and that at or about that time, elements of at least two of the clades (hatcheriforms and polydolopiforms) of this tripartite ordinal radiation dispersed to South America.

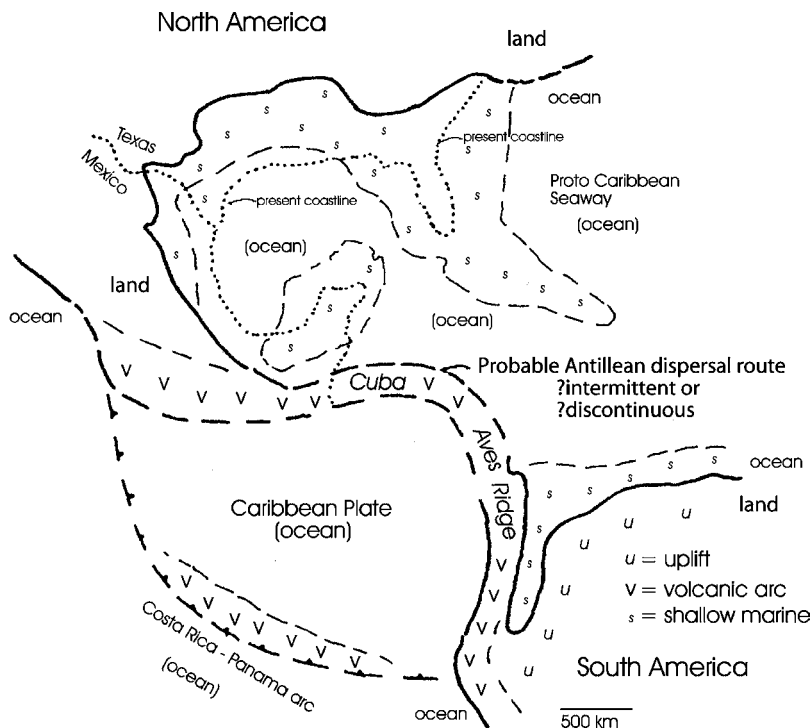
### TECTONIC RECONSTRUCTIONS OF THE CARIBBEAN REGION

Whereas the general geologic and tectonic setting of North America in the Late Cretaceous is generally well known, and Sempere *et al.* (1997) reviewed that for northwestern South America, an understanding of these aspects of the Caribbean Region is crucial to evaluating the potential of dispersal of land vertebrates between North and South America during this interval. The following summary is based on Pindell (1994), which is an abridged version of a more detailed treatment by Villamil and Pindell (1998). According to Pindell (1994) the Caribbean region underwent major reorganization during the Mesozoic Era.

In the late Triassic into the Jurassic, North and South America and western Africa (present day coordinates) were in virtual contact so that overland dispersal of terrestrial vertebrates was highly probable unless impeded by climatic or ecologic factors. The mid-Atlantic Ridge began to be expressed as North America and Africa drifted farther apart in the medial Jurassic, but this provided no major barriers to terrestrial vertebrate dispersal. That situation changed dramatically by the latest Jurassic (Oxfordian, ca. 160 Ma). From the Oxfordian to the Turonian (ca. 90 Ma), the Caribbean region became flooded by a marine seaway that was separated from the Pacific Ocean by only a relatively narrow volcanic arc that is reconstructed as having extended from southern Mexico to the northwest shoulder of Colombia. In that much of the physical evidence for the existence of this arc has been destroyed by the development of the Caribbean Plate from about the Campanian, little can be determined as to the actual physical characteristics of this Cordilleran arc and the role it may have played in dispersal of land vertebrates between North and South America.

An apparently better candidate as a pathway for such dispersal is provided by the Aves Ridge and adjacent Cuba in the Campanian and especially the Maastrichtian, when not only were this ridge and adjacent areas geologically active, but also the Sierra Madre of Mexico and the Central Cordillera of Colombia, to which the ridge complex was attached, or at least in close proximity, were undergoing uplift. The Aves Ridge route (Fig. 10) apparently gave the best chance of land vertebrate dispersal between North and South America since the medial Jurassic. This ridge complex began to break up in the Paleocene and was greatly breached by marine conditions by the medial Eocene. By then, however, a new Cordilleran volcanic arc apparently was established between southern Mexico and northwestern Colombia, so overland dispersals might have been supported, again, by such a route. That Cordilleran arc apparently was breached by the latest Eocene (ca. 35 Ma) and remained so until the establishment of the Panamanian isthmus at about 2.7 Ma, waif





**Fig. 10.** Plate tectonic reconstruction of the Caribbean region for the late Campanian through Maastrichtian, showing potential dispersal route for land vertebrates between North and South America, modified after Pindell (1994) and Villamil and Pindell (1998).

dispersals of edentates to North America at about 9 Ma, and edentates to North America and procyonid carnivores to South America at about 7 Ma notwithstanding (e.g., Woodburne and Swisher, 1995; Woodburne, 2004).

Regarding the marsupial and other groups pertinent to this report, the window of dispersal seems to begin in the Campanian, to be most likely in the Maastrichtian, and to wane in the Paleocene. The Aves Ridge and adjacent features are reconstructed by Pindell (1994) and Villamil and Pindell (1998) as being relatively narrow, so it seems likely that the arc system was ecologically limited and perhaps episodically discontinuous, as well. Thus, the dispersal probability is best proposed as having been a sweepstakes to a relatively strong filter (e.g., Simpson, 1953).

Rage (1978) summarized the distribution of elements of the snake groups Booidea and Aniloidea. Booidea comprise three families, Dinilysiidae, Xenopeltidae, and Boidae. The booid family Dinilysiidae is represented by a single specimen from the Late Cretaceous (Senonian) of Patagonia. Xenopeltidae are only known from Recent of Central America and Southeast Asia, and have no pertinent fossil record. According to Carroll (1988), boids are represented in Gondwanan regions of South (and Central) America, Africa, and Madagascar, and Australia (with fossils from the early Eocene and Miocene of SA and Africa), as well as North America, Europe, and southern continental Asia (relatively abundant fossils of Paleogene and early Neogene age in North America and Europe).

Among these, the subfamily Madtsoiinae (*Madtsoia*) is known in the late Paleocene and early Eocene of South America, and in the Late Cretaceous of Africa and Madagascar, according to Rage (1978), but Carroll (1988) indicated only an early Eocene record of the genus from South America. Rage (1978) posited a Gondwanan origin of the subfamily and also the presumptively more ancient family, which might be reflected in the Late Cretaceous presence of the booid *Palaeophis* in the Late Cretaceous of North Africa (Carroll, 1988). Rage (1978) favored a Gondwanan origin for the Booidea with the North American presence of the group resulting from a likely Late Cretaceous dispersal. If the Late Cretaceous African taxon is key, then the presence of two genera in the early Eocene of South America (Carroll, 1988) may be consistent with a northward dispersal in the Late Cretaceous, prior to the presence of *Helagras* in the Paleocene of North America. The North American record expands to eight genera in the Eocene, whereas there are six European Eocene genera, which would be considered as having dispersed from North America. Subsequently three Oligocene and eight Miocene genera occur in North America and four Oligocene genera and one Miocene genus in Europe (Carroll, 1988).

The Aniloidea comprises two families. The Uropeltidae (Recent, SE Asia) has no fossil record. Among the Aniliidae, *Coniophis* is known from the Lancian and Bridgerian of North America, the Campanian of Canada, and from the late Eocene of France, as well (along with another genus, *Eoanilus*; see also Carroll, 1988). Regarding Gondwana, Rage (1978) considered *Coniophis* as also known from the late Paleocene of South America (not reported in Carroll, 1988), and the continent also hosts a derived Miocene, taxon, *Colombophis*. Whether having originated in Laurasia or Gondwana, the Aniloidea, apparently reflect a dispersal event to or from South America prior to the late Paleocene, if the South American record is accurate.

Unless capable of oceanic swimming, the distribution of one, if not two groups of snakes summarized above suggests at least a minimally established overland connection between North and South America in the Late Cretaceous to possibly early Paleocene. Combined with the didelphimorphians considered in this report, the associated hadrosaurine dinosaurs as well as the purported presence of members of the Pantodonta (de Muizon and Marshall, 1992), and possibly Condylarthra, provides a growing list of taxa that together seem most compatible with an established overland dispersal pathway between North and South America that is better established than a "sweepstakes" model, but not as fully developed as a "corridor."

All of the above is consistent with the paleontological data discussed herein, and would allow the prediction that at least Mexico or some place in Central America was a source of marsupial diversification on the one hand and, on the other, that only a relatively limited number of marsupial lineages dispersed from anyplace in North America to South America in the Late Cretaceous, as discussed below.

## PHYLETIC AND BIOGEOGRAPHIC IMPLICATIONS

The presence of *Hatcheritherium* and *Nortedelphys* in deposits of Lancian age, and of *Ectocentrocristus* in Judithian deposits has implications for the dispersal history of a number of Paleogene and younger South American marsupial clades. Among these implications are the likely presence of the Didelphimorphia and Polydolopimorphia in South America

or at least some place south of the continental United States in the Late Cretaceous. The following discussion is directed to these implications.

The Herpetotheriidae (represented by *Nortedelphys*) are now known from deposits of Lancian age that range from Wyoming and western South Dakota northward into Montana and Alberta, Canada (Fig. 1). Early members of the polydolopimorphian clade are known from Judithian (*Ectocentrocristus*) and Lancian (*Hatcheritherium*) sediments. Both the didelphimorphian and polydolopimorphian radicles could be independently derived from a virtual peradectian. However, recognizing that caenolestoids and didelphimorphs are linked by sperm pairing in the living members (Temple-Smith, 1987), that caenolestoids have been linked with borhyaenoids on the basis of tarsal structure (Szalay, 1994), and that both didelphimorphs and polydolopimorphs are derived in basic molar structure relative to peradectians, it is plausible that if all ameridelphians share a common ancestor, this basal ameridelphian would have developed sperm pairing, a medial process of the squamosal and lacked a tympanic process of the alisphenoid (de Muizon *et al.*, 1997), but retained a peradectian molar morphology, which includes a linear centrocrista.

Once derived, the polydolopimorphian radicle, with its invasive and open, but not V-shaped centrocrista, appears to have separated into two major lineages, one leading from *Hatcheritherium*, via *Ectocentrocristus*, to *Roberthoffstetteria*, and also to polydolopines; and a second leading from *Hatcheritherium*, to *Rosendolops* (Goin and Candela, 1996), bonapartheriids, and epidolopines (Fig. 11). In that *Ectocentrocristus* is of Judithian age, the separation of these two lines is at least that old (Fig. 11).

In this paper, we revise the classification presented by Marshall *et al.* (1990) (Table II here). In this classification, Stagodontidae are transferred from Borhyaenoidea to the Peradectia; *Nortedelphys* is added to the Herpetotheriidae and this new familial ranking recognized (see Kirsch *et al.*, 1997). Additionally, the Derorhynchidae is raised to family status within the Didelphimorphia (Goin *et al.*, 1999). The Protodidelphidae is transferred to the Didelphimorphia (Goin *et al.*, 1998a,b). *Andinodelphys* is placed as Ameridelphia *incertae sedis*. *Ectocentrocristus* and *Roberthoffstetteria* are added to the Polydolopiformes as *incertae sedis*. *Glasbius* and *Palangania* are allocated as Hatcheriformes *incertae sedis*. The Polydolopimorphia is considered as Marsupialia *incertae sedis* in that present evidence for this order does not include any decisive characteristics which can document its affinity to any of the three marsupial cohorts. However, it was recently suggested that polydolopimorphians and microbiotherians could be allied to each other (Goin, 2003). Three features that support this inference are as follows: in the upper molars, reduced styler shelf and enlarged protocones; in the lower molars, the reduction of the paraconid. If further research proves this inference correct, then polydolopimorphians would belong to the australidelphian rather than to the ameridelphian clade.

These actions have the consequences that (1) the Alphadelphia remains paraphyletic; (2) at least two South American clades (Didelphoidea and Polydolopimorphia) are considered as likely to have originated in, or to have been derived from, taxa known from the Late Cretaceous of North America. This is consistent with the ca. 70–75 m.y. age of the progenitors in North America and a plausible dispersal to South America about that time.

Up to now the South American Late Cretaceous mammal record reflects the presence there of only nontherian mammals, known collectively as the Alamitian faunal facies. Originally described from Patagonia (Bonaparte, 1990, 1996), Alamitian elements also are

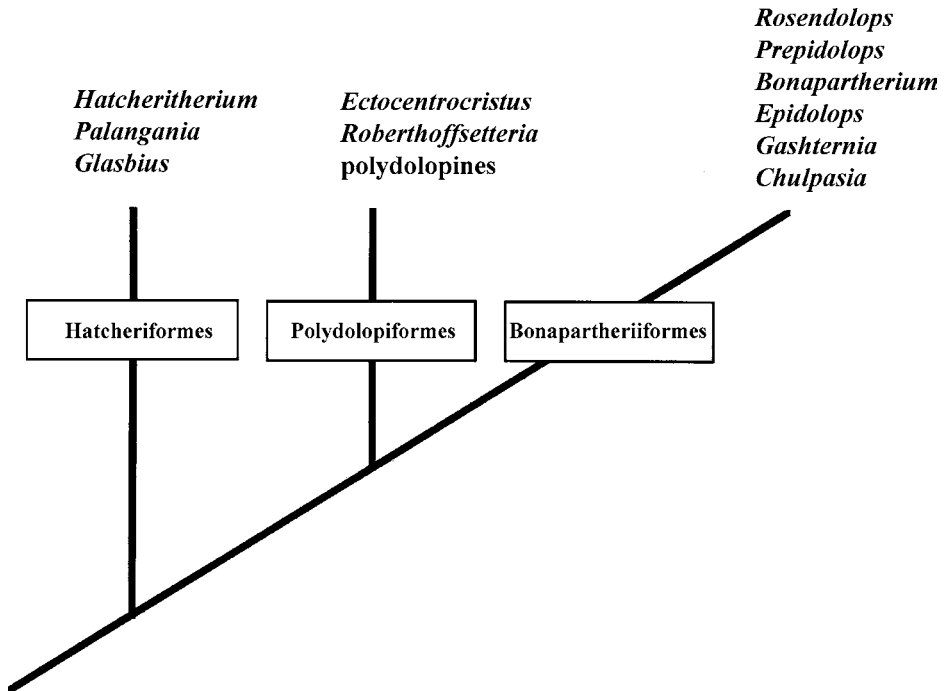


Fig. 11. Proposed relationships within the marsupial Order Polydolopimorphia illustrating phylogenetic grouping of the three suborders discussed herein.

now known from the late Maastrichtian of Madagascar (Krause *et al.*, 1999) and Australia, in that monotremes (Archer *et al.*, 1992, 1993; Flannery *et al.*, 1995; Woodburne, 2003) are considered as a constituent. The Alamitian faunal facies also extends into the Maastrichtian (Rougier *et al.*, 2001) in part coeval with the marsupial dispersal time proposed herein. Figure 2 also indicates a gap in the South American faunal record persists from the latest Cretaceous (72 Ma) into the early Paleocene (63 Ma), by which time placental and marsupial mammals are well represented along with some persistent Alamitian taxa (*Monotrematum sudamericanum*; Pascual *et al.*, 1992).

The diversity of marsupial (and placental) mammals in the Paleocene faunas of South America (e.g., de Muizon and Brito, 1993) has led to predictions of their Late Cretaceous presence in that continent, which still are unfulfilled.

Whereas Alamitian faunas show only nontherian mammals, the presence of therian taxa during the Late Cretaceous still is permitted by the available evidence. The material reported herein reinforces the thesis favoring a Late Cretaceous presence of therian mammals in South America (e.g., de Muizon and Marshall, 1992; Woodburne and Case, 1996). The data summarized above are consistent with the marsupial lineages stemming from North America and having entered South America in the interval of 72 to 63 Ma.

The basal radiation of the Didelphimorphia includes members of the Didelphoidea, following the classification above (Table II). Prior to the recognition of *Nortedelphys*,

members of this superfamily have their oldest record in South America: (1) pucadelphids, *Incadelphys* and *Mizquedelphys*, are known from the Tiupampa Fauna (early Paleocene) and (2) didelphids *Itaboraidelphys*, *Mirandatherium*, and *Carolopaulacoutoia* are known from the Itaborai Fauna (late Paleocene). Whereas, all of the genera included in these families were placed in the subfamily Didelphinae (Marshall *et al.*, 1990), and are now considered as pertaining to the Didelphoidea, *Nortedelphys* is attributed to the Herpetotheriidae, which was otherwise unknown prior to the early Paleocene (Torrejonian; Marshall *et al.*, 1990; Johanson, 1996).

On the basis of the information presented above, herpetotheriids are not found in pre-Lancian aged deposits in North America, and among collections appraised by us, we have seen no potential close relatives in these or older deposits there. On the other hand, members of the phylogenetically more basal group, the Pucadelphidae, are known from early Paleocene deposits in South America (Marshall *et al.*, 1990). In this context, we suggest that the Pucadelphidae arose from a Late Cretaceous group in either southern North America or northern South America, for which the most likely candidate appears to be the ameridelphian *Andinodelphys* from the Tiupampian of Bolivia (Marshall and de Muizon, 1988; de Muizon *et al.*, 1997). Although still possessing a linear centrocrista typical of the peradectian group, *Andinodelphys* shows ameridelphian derived cranial character states in which the medial process of the squamosal reaches the foramen ovale and the frontonasal contact inhibits a nasolacrimal contact (de Muizon *et al.*, 1997), as well as having an elongate sulcus for the entocarotid artery and a mastoid process well separated by the facial sulcus from the epitympanic recess (JAC, pers. observ.). Dentally, *Andinodelphys* and *Mizquedelphys* (which has the most plesiomorphic molar morphology of the pucadelphids), each retain many plesiomorphic features, including twinned C cuspules. Whereas *Andinodelphys* has a more robust and posterolabially oriented postmetacrista, *Mizquedelphys* has a weak to moderately invasive V-shaped centrocrista.

If the *Andinodelphys*—pucadelphid relationship is borne out by future work (e.g., Ladevéze, 2004, p. 211), we favor a hypothesis that the Didelphoidea underwent most of its early evolution in a place outside of (and most likely south of) the continental United States, with the didelphoid clade having South America as its major center of radiation, whereas the herpetotheriids evolved in a North American theater. Under this scenario, the Lancian occurrence of *Nortedelphys* would represent a dispersal from a more southerly location (although not necessarily as far south as South America). The early Paleocene *Swaindelphys* (Johanson, 1996) represents an intermediate-aged glimpse of the group, which is otherwise better (and more widely) represented in the early Eocene of North America (Marshall *et al.*, 1990).

Previous references to these Lancian-aged herpetotheriids described here as the three species of *Nortedelphys* (Marshall *et al.*, 1990, p. 77; Case, 1992) were concerned with aspects of marsupial biogeography. The marsupial record in North America from the Maastriichtian (Lancian) through the Paleocene to the early Eocene is very irregular. This family of didelphoids may be tracking thermoclines or resources, which are tracking temperature. So as temperatures increased during the latest Cretaceous (Lancian mammal age; Huber, 1998; Keller, 2001), these marsupials, represented by *Nortedelphys*, migrated from somewhere in the southern portion of North America into the more northern latitudes from Wyoming to southern Canada. This migration may even have been more extensive northward and then eastward as a didelphoid marsupial has been reported from the Maastriichtian of northern

Europe (Martin *et al.*, 2003). When temperatures decreased, as in the early Paleocene, herpetotheriids disappeared in the better studied sections in North America, to make a brief appearance in the Torrejonian (To 3; i.e., *Swaindelphys*) in Wyoming (Johanson, 1996). Herpetotheriids quickly disappeared again from the North American record (presumably restricting their range again to somewhere else in North America) and did not return until the early Wasatchian (e.g. *Peratherium*) of Wyoming (Krishtalka and Stucky, 1983).

The above evidence and implications support the hypothesis that at least two orders typical of the South American radiation of marsupials were present in the Late Cretaceous faunas of North America and that these taxa or their relatives dispersed to South America about that time (late Campanian to early Maastrichtian, ca 70–75 m.y.). Crochet and Sige (1993) suggested that *Chulpasia mattaueri* from the Late Cretaceous or Paleocene Umayo Formation of southern Peru shares many features with *Glasbius* (Lancian, North America). Whereas we (above) place these genera in separate groups, the similarities still are striking, and better material may suggest a closer affinity between them. If so, that could represent another trans-Caribbean link of marsupials in the Late Cretaceous. Finally, it has been suggested that at least some lineages of the Sparassodonta (borhyaenids and allies) may have had North American origins (Rougier *et al.*, 2001; Goin, 2003).

Cifelli *et al.* (1997) indicated that both marsupials and hadrosaurid dinosaurs first appear in the North American record about 98 Ma. Bonaparte and Rougier (1987) record the presence of hadrosaurs in Patagonian deposits of late Campanian age, and Case *et al.* (1998, 2000) demonstrate a late Maastrichtian occurrence of this dinosaur family in the Antarctic Peninsula. Neoceratopsians also have their oldest North American record in the Cedar Mountain assemblage of Utah (Cifelli *et al.*, 1997), and subsequently appear in Patagonia in the Maastrichtian (Coria, 1998).

De Muizon and Brito (1993), de Muizon (1991), and de Muizon and Marshall (1992) show that the Tiupampa Fauna of Bolivia contains a diversity of marsupial and placental mammals, considered to be early Paleocene in age (Flynn and Swisher, 1995). In addition to relict mammalian taxa (a gondwanathere and a monotreme), Peligran/Tiupampian-aged faunas from Patagonia are composed of a diversity of derived marsupials on one hand, and the pantodont (*Alcidedorbignya*), two mioclaenine condylarths, and a “palaeoryctoid” on the other (de Muizon and Marshall, 1992). Whereas the condylarths likely can be accounted for by a dispersal from North America in the early Paleocene, the diversity of marsupials, which includes a peradectid, a microbiotheriid, a diversity of pucadelphids (*Pucadelphys*, *Incadelphys*, *Mizquedelphys*, *Jaskhadelphys*, and *Tiulordia*), a possible derorhynchid (aff. *Derorhynchus*), two borhyaenoids (*Allqokirus*, *Mayulestes*), and a relatively derived polydolopimorphian (*Epidolops*), indicate that marsupials underwent considerable diversification prior to the early Paleocene. A pre-Tertiary radiation of ameridelphian marsupials is consistent with the presence of herpetotheriids (species of *Nortedelphys*) and early polydolopimorphians (*Ectocentrocristus* and *Hatcheritherium*) being represented in Judithian to Lancian-aged deposits in North America. The primitive aspect of the pantodont also leaves open the possibility of a Maastrichtian dispersal of the group to (or from) South America (de Muizon and Marshall, 1992).

At the moment, geophysical data (see above) also are consistent with the proposal that elements of the North American marsupial fauna dispersed across the Caribbean region during the latest Cretaceous. Perhaps the marsupials of this fauna dispersed between the Americas following the route used by angiosperm forests as they extended their range

southward, or that of other terrestrial vertebrates such as hadrosaurs and neoceratopsians. The growing diversity of taxa involved (possibly including booid and aniloid snakes, pantodonts and perhaps some condylarths) increases the likelihood that the trans-Caribbean dispersal pathway resembled a filter route, in contrast to a series of waif dispersals on the one hand or a genuine corridor on the other.

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