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Symmetrodonts from the Late Cretaceous of Southern Utah and Distribution of Archaic Mammals in the Cretaceous of North America

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ABSTRACT

New materials of Spalacotheriidae (Symmetrodonta, Mammalia) from the Late Cretaceous (Turonian through early Campanian) of the Kaiparowits region, Utah, add to knowledge of three species, *Symmetrodontoides oligodontos*, *S. foxi*, and *Spalacotheridium mckennai*. Details of molar structure (e.g., reduction of m7, proportions of lower molar paraconid and metaconid) clarify relationships of these taxa, indicating that 1) *S. mckennai* is derived with respect to geologically older *S. noblei*; 2) *Symmetrodontoides* spp. form a monophyletic, terminal clade; and 3) all can be included in a monophyletic subfamily, Spalacolestinae. North American spalacotheriids represent an endemic group that enjoyed a modest radiation in the medial Cretaceous and maintained a broad geographic distribution through the early Campanian. Symmetrodonts are but one of a number of archaic mammalian groups known from faunas of the North American Cretaceous, which are otherwise dominated by multituberculates and marsupials. The history of these groups is poorly understood but evidently complex. Some, such as triconodontids (and picopsids), also represent North American endemics that radiated in the medial Cretaceous and may have been restricted to northerly faunas in the Campanian; others, such as spalacotheriids and a possible clade of marsupial-like tribosphenic mammals, may have been restricted to the south during at least part of the Campanian. Deltatheroidans, known in North America as early as the Turonian, may have arrived on the continent via immigration from Asia on two separate occasions.

INTRODUCTION AND BACKGROUND

The Kaiparowits region of southern Utah includes a well-exposed, thick, relatively continuous series of largely terrigenous sedimentary rocks spanning much of the Upper Cretaceous. Vertebrate faunas including mammals have been recovered from a number of horizons (Eaton and Cifelli, 1988; Eaton and others, in press). Though some units remain poorly sampled and significant gaps exist between some of the fossil-bearing horizons, these assemblages collectively merit attention for several reasons. First, they include representation of an otherwise poorly known interval in mammalian history, the early Late Cretaceous (see, e.g., Clemens and others, 1979). Second, the faunas span nearly 20 Ma and thereby provide unique evidence bearing on in situ changes in the terrestrial ecosystem through the Late Cretaceous; the nearby fauna from the uppermost Cedar Mountain Formation, central Utah, extends this record to the Albian-Cenomanian boundary

(Cifelli and others, 1997; Eaton and Nelson, 1991). Finally, the uppermost, late Campanian part of the sequence is correlative with vertebrate-yielding units ranging from southern Canada to southern Texas, and suggests some degree of biogeographic zonation or provinciality in the Late Cretaceous of North America (e.g., Cifelli, 1994; Lehman, 1997; Rowe and others, 1992).

Among the rarest of the mammals from the Cretaceous of the Kaiparowits region are the symmetrodonts. These are of particular interest to students of mammalian evolution because their “reversed triangle” pattern formed by principal molar cusps is thought to be antecedent to the more complex molar crowns seen in eupantotheres and, ultimately, tribosphenic mammals—marsupials, placentals, and fossil relatives (e.g., Butler, 1939; Patterson, 1956). The Order Symmetrodonta was founded on taxa from the Late Jurassic (Simpson, 1925). More ancient, extremely primitive forms (see Cassiliano and Clemens, 1979; Prothero, 1981; Sigogneau-Russell, 1983; Sigogneau-Russell and

Hahn, 1995) were later added, as well as Cretaceous taxa, some of which are highly specialized (e.g., Bonaparte, 1990; Fox, 1985; Sigogneau-Russell, 1989, 1991; Sigogneau-Russell and Ensom, 1997). Thus recognized, the Symmetrodonta is a heterogeneous, long-ranging assemblage of debatable taxonomic standing (e.g., Prothero, 1981; Rougier and others, 1996). Indeed, many included species are known only by isolated teeth, and as a result symmetrodonts are commonly ignored in general treatments of mammalian relationships, despite their widely acknowledged importance (e.g., Rowe, 1988).

The Cretaceous of southern Utah has yielded three symmetrodonts (Cifelli, 1990a; Cifelli and Madsen, 1986), all referable to the Spalacotheriidae. This family, known from the Cretaceous both of the New and Old World, appears to be monophyletic, with North American taxa placed in the endemic subfamily Spalacolestinae (see Cifelli and Madsen, in press). Each of the spalacotheriids from southern Utah was based on one or two teeth only. Herein we describe newly-collected fossils that add to knowledge of these species and their relationship with other members of the Spalacotheriidae. We also describe enigmatic specimens, from the same Upper Cretaceous

units of southern Utah, that evidently belong to symmetrodonts or other primitive mammals. Finally, we comment on the geographic and temporal distribution of symmetrodonts and other groups of archaic mammals that persisted, in a limited fashion at least, through much of the Late Cretaceous in the Western Interior of North America.

METHODS

All specimens reported herein consist of isolated teeth or dentigerous jaw fragments, collected by underwater screenwashing and associated fossil concentration and recovery techniques (Cifelli and others, 1996). Rock samples from the Wahweap Formation, indurated with calcium carbonate, were disaggregated in dilute (10%) acetic acid. Dental terminology (see discussion in Cifelli and Madsen, in press) is shown in Fig. 1A, B. Measurements, in mm, were taken with a Reflex microscope (see MacLarnon, 1989). These data are automatically recorded to 0.001 mm, and the figures are given here verbatim, although this does not account for measurement error. Teeth of spalacotheriids are extremely small and fragile, and as a result

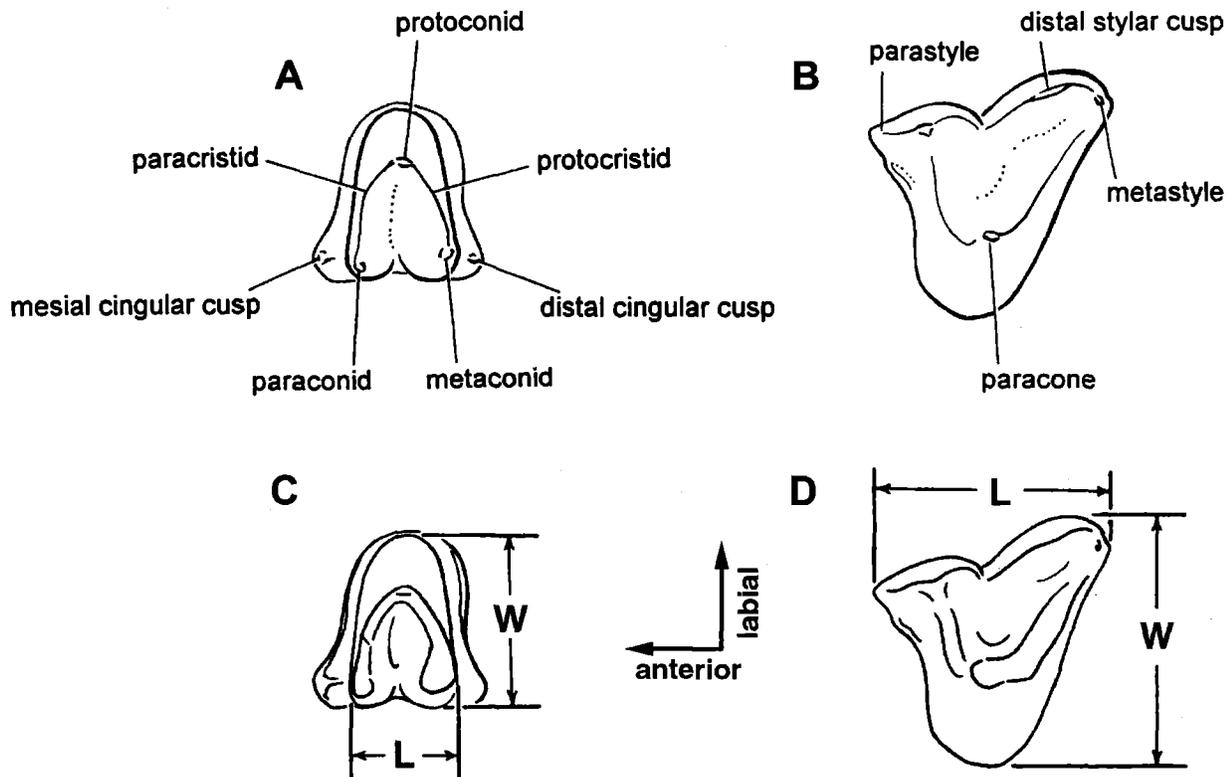


Figure 1. Measurements and dental terminology. A, C, right lower molar in occlusal view. B, D left upper molar in occlusal view. Abbreviations: L, greatest mesiodistal length; W, greatest labiolingual width (after Cifelli and Madsen, in press).

lower molars commonly lack parts of the cingulum; hence, measurements (Fig. 1C, D) were taken minus the cingulum. The identification of tooth locus, important in assessing intraspecific and interspecific differences, is problematic for spalacotheriids, in which specimens consist of isolated teeth and the dental formula includes a high number of molars that differ from each other in subtle ways. Our identification of tooth position is based on comparison with taxa known by partial or complete tooth series: *Spalacotherium*, *Zhangheotherium*, *Symmetrodontoides canadensis*, and *Spalacolestes cretulablatta* (Cifelli and Madsen, in press; Fox, 1976; Hu and others, 1997; Simpson, 1928). Recent study of a large sample, representing three species (including *S. cretulablatta*) from the medial Cretaceous Mussentuchit local fauna (Cifelli and Madsen, in press), provided additional criteria for refinement of these identifications. Based on analogy with closely related taxa and on evidence presented herein, we tentatively regard the dentition of spalacotheriids from the Cretaceous of southern Utah to include seven lower and six upper molars on each side of the jaw. The anterior- and posteriormost molars are the most distinctive and easily recognized; with these exceptions, the identifications should be regarded as tentative. All species under consideration were originally based on lower molars; upper molars are referred to the respective species based on morphological appropriateness, size, and occurrence (see Cifelli and Madsen, in press; Fox, 1985). We follow the standard practice of using lower and upper case letters for lower and upper teeth, respectively.

The following abbreviations are used for institutions cited in the text: MNA, Museum of Northern Arizona, Flagstaff; OMNH, Oklahoma Museum of Natural History, Norman; UALVP, Laboratory for Vertebrate Paleontology, University of Alberta, Edmonton.

GEOLOGICAL SETTING AND AGE

The Cretaceous System of the Kaiparowits region, Utah, consists of (in ascending order) the Dakota, Tropic, Straight Cliffs, Wahweap, Kaiparowits, and Canaan Peak formations (Bowers, 1972; Gregory and Moore, 1931). The middle, carbonaceous member of the Dakota Formation is of Cenomanian age (Eaton, 1991) and has yielded a diverse assemblage of terrestrial vertebrates (Eaton and Cifelli, 1988; Eaton and others, in press), including mammals (Cifelli and Eaton, 1987; Eaton, 1993a, 1995). Symmetrodonts are reportedly present in the unit, but they are under study elsewhere and are not included in this report. The Tropic and large parts of the Straight Cliffs formations are of marine origin. The latter unit includes four members, in ascending order: Tippet Canyon, Smoky Hollow, John Henry, and Drip Tank (Peterson, 1969). The

Smoky Hollow Member consists of interbedded mudstones, carbonaceous mudstones, and coals (Eaton, 1991). This unit has yielded a diverse fauna of mammals and other terrestrial vertebrates (Cifelli, 1990a; Eaton, 1995; Eaton and Cifelli, 1988; Eaton and others, in press) from the middle zone of Peterson (1969). This horizon is believed to be of late middle to early late Turonian age (Eaton, 1995). Fossils reported herein come from three sites in the Smoky Hollow Member: MNA 995 (= OMNH V843), OMNH V4, and OMNH V60 (Fig. 2). The stratigraphic positions of these sites are given by Eaton (1987, 1991, 1995). The overlying John Henry Member has yielded a frustratingly small assemblage of mammals (Eaton and Cifelli, 1988; Eaton and others, in press), including a single specimen reported herein. The unit is partly marine. OMNH V856 is a site in the middle of the John Henry Member and its age is constrained by early Coniacian molluscs from the base of the unit and late Santonian bivalves near the top (Eaton, 1991). The Wahweap Formation

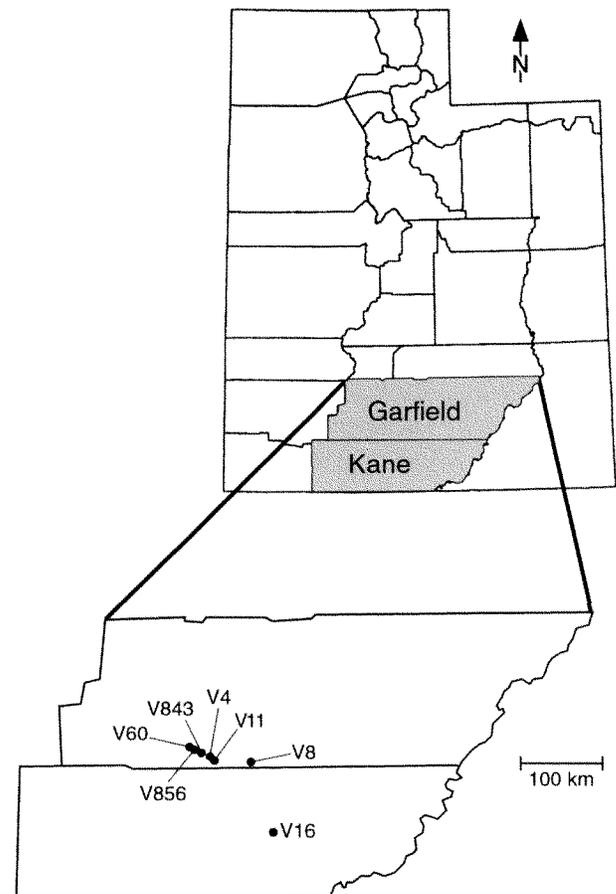


Figure 2. Locator map showing Garfield and Kane counties, Utah (above); enlargement below shows location of OMNH sites mentioned in the text.

consists of sandstones (for which it was originally named by Gregory and Moore, 1931) and mudstones. Because it is bounded by terrestrial units (the Drip Tank Member of the Straight Cliffs Formation below and the Kaiparowits Formation above), its age is poorly constrained; evaluation of the vertebrate fauna (Eaton and others, in press) suggests closest comparison with the early Campanian upper Milk River Formation, Alberta (Eaton, 1991). *Symmetrodonts* were recovered from three sites in the Wahweap Formation, OMNH V8, V11, and V16 (see Cifelli, 1990b; Eaton, 1987, 1991). A single specimen of a *Symmetrodont*, not considered by us, was reported from the Paunsaugunt Plateau, to the west of the Kaiparowits region, by Eaton (1993b). The relative stratigraphic position of the site from which it was collected is uncertain; it may be equivalent to the Wahweap Formation (Eaton, 1993c) or Kaiparowits Formation (Eaton and others, 1998). Another specimen not considered by us, referred to *Symmetrodontoides* sp., has been reported from a horizon unquestionably within the Kaiparowits Formation, on the Kaiparowits Plateau (Eaton and others, in press). Detailed information for localities referred to herein is on file at OMNH and is available to qualified investigators upon request.

SYSTEMATIC PALEONTOLOGY
Order Symmetrodonta Simpson, 1925
Family Spalacotheriidae Marsh, 1887
Symmetrodontoides Fox, 1976
S. foxi Cifelli and Madsen, 1986
Fig. 3

Newly-referred Specimens. OMNH 20135, left m4; 23358, left m7; MNA V4653, left M4. MNA V6461, a left lower molar from the Paunsaugunt Plateau, was referred to this species by Eaton (1993b). We have not studied this specimen; and cannot comment on it, except to note that it represents a posterior tooth locus. Based on evidence presented below, it is probably not m7[?], as originally suggested.

Localities and Horizon. OMNH localities V8 (MNA V4589, holotype; MNA V4522), V11 (OMNH 20135, MNA V4653), and V16 (OMNH 23358); Garfield and Kane counties, Utah (Fig. 2); Wahweap Formation ([?]lower Campanian). MNA V6461 is from MNA locality 1073, in rocks of uncertain correlation, on the Paunsaugunt Plateau (see Eaton, 1993b; Eaton and others, 1998).

Description. The holotype, MNA V4589, was originally considered to be m4; comparison with the similar species, *Spalacolestes cretulablatta*, suggests that it is m2 and that the original referred specimen, MNA V4522, is probably m6 (or m5), not m7 as previously thought (Cifelli and Madsen, 1986). Specimens in hand now include representation of four lower and one upper molar loci. The second

lower molar is similar to that of *S. oligodontos* but noticeably larger, with bases of paraconid and metaconid slightly more separated; in addition, the height differential between paraconid and metaconid is greater on m2 of *S. foxi*, and the protocristid is less deeply notched. The fourth lower molar (Fig. 3A, B) differs from the second in predictable ways: it is larger and more transverse, and the paraconid projects lingually, as it does in other species of *Symmetrodontoides* and *Spalacolestes* (Cifelli and Madsen, in press). The sixth lower molar is smaller and proportionately less transverse than m4, though the paraconid still projects lingually. The seventh lower molar (Fig. 3C, D) is of particular interest in that, among American spalacotheriids, it is otherwise known only for *Spalacolestes*. This tooth is considerably smaller and is relatively longer, less transverse, and lower crowned than preceding molars, from which it also differs in the complete lack of a metaconid. Indeed, identification of tooth locus and referral to this species would not be obvious were it not so closely similar to m7 of *Spalacolestes cretulablatta*. It differs from m7 of this species in having a less expanded mesial cingulum and a distal cingular cusp that projects more posteriorly, in being proportionately longer mesiodistally, in having broader based cusps, and in having lesser development of the crest descending distolingually from the apex of the protoconid.

The only upper molars previously described for *Symmetrodontoides* evidently pertain to anterior loci (Fox, 1985). M4 of *S. foxi* (Fig. 3E, F) is, by comparison, a more anteroposteriorly compressed, acute-angled tooth that is nearly symmetrical in occlusal outline. Small, slightly projecting parastyle and metastyle are present, with a faint swelling in the region of the distal styler cusp. Compared to M4 of *Spalacolestes*, this tooth in *Symmetrodontoides foxi* is slightly more obtusely-angled, with lesser projecting parastyle and paraconal crests more weakly developed. The M4 of *Spalacotheridium noblei* (Cifelli and Madsen, in press, fig. 16F, G) has a more projecting metastyle than in *Symmetrodontoides foxi*.

Comments. This species is generally similar in the structure of its lower molars to other species of *Symmetrodontoides*; it is larger than the geologically older *S. oligodontos* and smaller than the presumably contemporaneous *S. canadensis*. The lingually projecting paraconid on lower molars appears to be a synapomorphy uniting species of *Spalacolestes* and *Symmetrodontoides*, to the exclusion of other known Spalacotheriidae. *Spalacotheridium* has lower molars with paraconid and metaconid subequal in height, a presumably primitive condition (Sigogneau-Russell and Ensom, 1997). In both *Symmetrodontoides* and *Spalacolestes* the paraconid is lower than the metaconid; the discrepancy is greater among species of *Symmetrodontoides*, suggesting that this may be a fur-

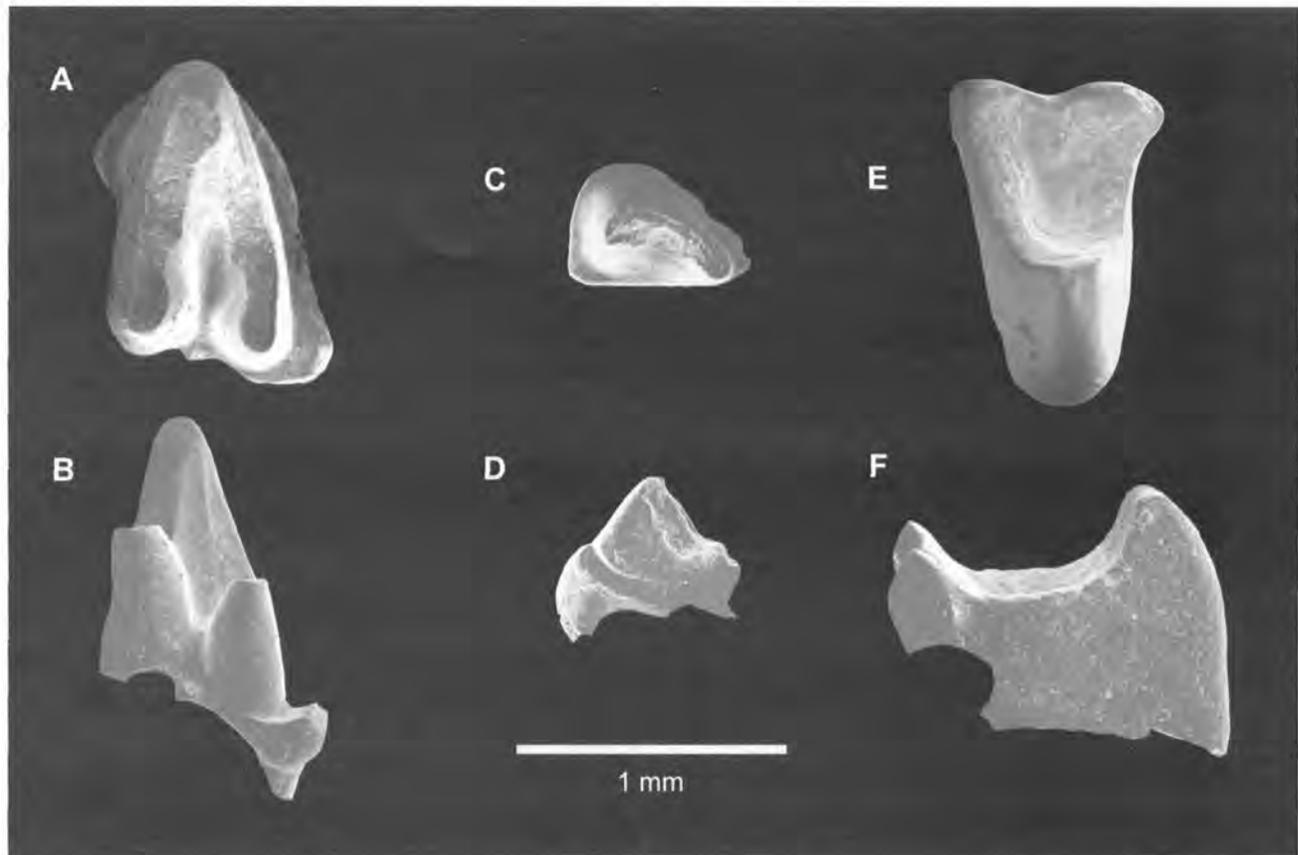


Figure 3. *Symmetrodontoides foxi*. A, B, OMNH 20135, left m4 in occlusal (A) and lingual (B) views. C, D, OMNH 23358, left m7 in occlusal (C) and lingual (D) views. E, F, MNA V4653, left M4 in occlusal (E) and mesial (F) views. Tooth roots and/or jaw fragments removed to improve clarity.

Table 1. Dental measurements (in mm), lower molars of *Spalacotheriidae*.

	m1		m2		m4		m6		m7	
	L	W	L	W	L	W	L	W	L	W
<i>Symmetrodontoides foxi</i>					0.711	1.205			0.550	0.384
<i>Symmetrodontoides oligodontos</i>			0.682	0.895	0.576	0.922				
			0.561	0.852						
<i>Spalacotheridium mckennai</i>	—	0.859			0.520	0.711	0.471	0.575		

ther derived condition uniting these taxa. Most significant among the newly-described materials of *S. foxi* is m7, which shows that this tooth was reduced (and lacked a metaconid), as is the case with *Spalacolestes*. Judged by comparison to *Spalacotherium*, reduction of m7 appears to be a derived character within Spalacolestinae, but in the absence of evidence from other taxa (*Spalacotheroides*,

Spalacotheridium), the phylogenetic significance of this feature is uncertain. The reduction of the m7 and loss of a postvallid shearing surface also implies a differential molar count, with one fewer in the upper series, as was apparently also the case in *Spalacolestes*. The structure of the upper molar contrasts with what is seen in more primitive spalacotheriids such as *Zhangheotherium*, *Spalacotherium*,

and *Spalacotheroides* (see Butler, 1939; Hu and others, 1997; Patterson, 1956; Simpson, 1928), and is consistent with the morphology of Late Cretaceous members of the family from North America (Cifelli and Madsen, in press).

S. oligodontos Cifelli, 1990

Figs. 4–5

Newly-referred Specimens. MNA V6047, left m2; OMNH 29523, left m2 in dentary fragment; MNA V6755, left m4; OMNH 29525, left M1; MNA V6048, OMNH 29040, left M2; OMNH 29039, right M6.

Localities and Horizon. OMNH localities V4 (OMNH 20381), V60 (OMNH 29039, 29040), V843 (= MNA 995; MNA V5789, V6048; V6755, OMNH 29523, 29525); Garfield County, Utah (Fig. 2); Smoky Hollow Member, Straight Cliffs Formation (Turonian).

Description. The holotype and original referred specimen, MNA V5789 and OMNH 20381, are now believed to be m6 and m4, respectively, not m7 and m4 or 5 as originally suggested (Cifelli, 1990a), based on comparison with *Spalacolestes* (Cifelli and Madsen, in press). Materials now in hand include representation of three lower and

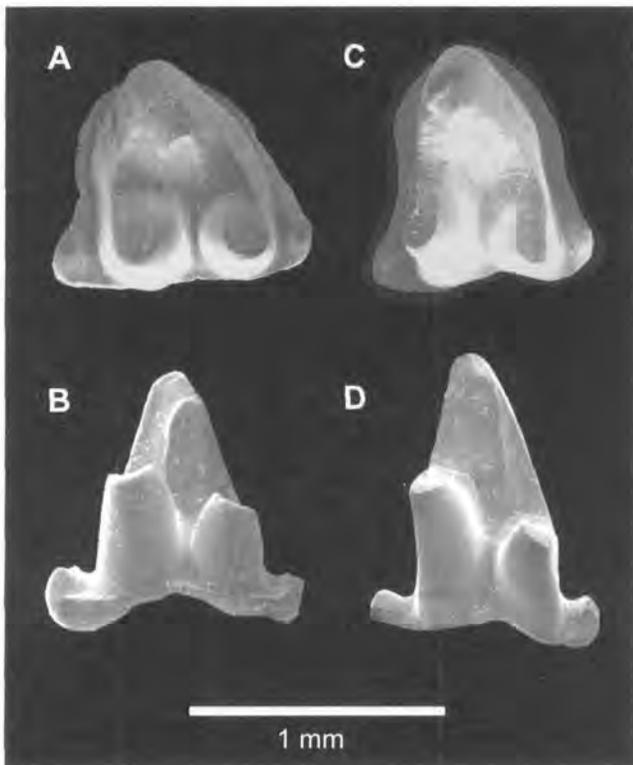


Figure 4. *Symmetrodontoides oligodontos*, lower molars. A, B, OMNH 29523, left m2 in occlusal (A) and lingual (B) views. C, D, MNA V6755, left m4 in occlusal (C) and lingual (D) views. Tooth roots and/or jaw fragments removed to improve clarity.

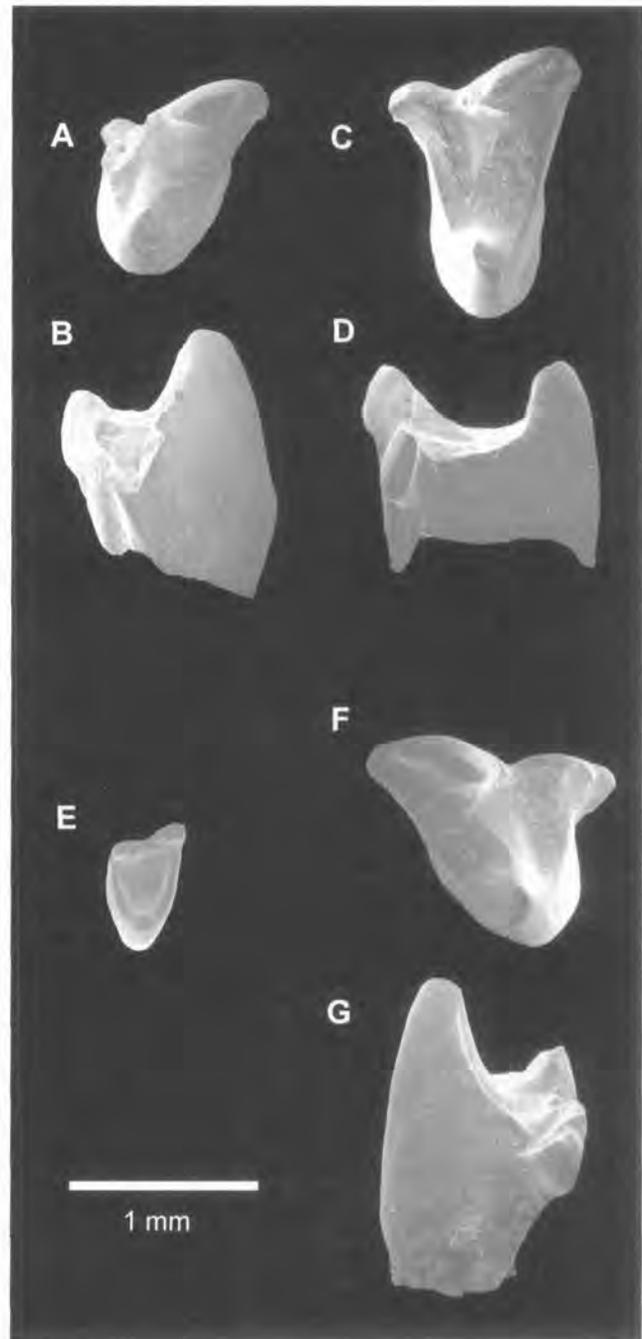


Figure 5. *Symmetrodontoides oligodontos* (A–E) and *Symmetrodontoides* sp. cf. *S. oligodontos* (F–G), upper molars. A, B, OMNH 29525, left M1 in occlusal (A) and mesial (B) views. C, D, OMNH 29040, left M2 in occlusal (C) and mesial (D) views. E, OMNH 29039, right M6 in occlusal view. F, G, OMNH 32874, right M6 in occlusal (F) and mesial (G) views. Tooth roots and/or jaw fragments removed to improve clarity.

three upper molar loci. As in other spalacotheriids, m4 is taller, broader, and more mesiodistally compressed than m2, with paraconid and metaconid that appear to have more gracile bases (Fig. 4). As well, the paraconid projects lingually on this tooth and on m6, which is not the case with m2; m6 is smaller and, especially, narrower than m4.

The paracone of M1 (Fig. 5A, B) has a bulbous base, but the lingual face is tightly curved toward the apex of that cusp, in this respect differing from M1 of *Spalacolestes*, in which the paracone retains a gently curved lingual face for almost its entire height. The mesiolabial corner of the tooth is missing, but it is clear that the preparacrista was weakly developed and placed very low on the crown. A small but distinct distal stylar cusp is present; the metastyle is weak. The postparacrista bears a flat, strap-like wear facet, as described for *S. canadensis* (Fox, 1976, 1985). The paracone of M2 (Fig. 5C, D) has a more tightly folded lingual face than in M1, and the tooth is slightly more acute. The distal stylar cusp and metastyle have about the same degree of development as they do on M1. The parastyle projects strongly; the preparacrista is markedly lower than the postparacrista but is well developed; it descends to the parastylar projection. M2 is quite similar to that of *S. canadensis*, UA 16272 (described by Fox, 1985), which we regard as probably representing the same locus. It differs from this tooth in having a smaller distal stylar cusp and in having a more pinched, less hook-like parastyle. M2 of *S. oligodontos* differs from that of *Spalacolestes cretulablatta* in being more acute and in having a paracone that has a less bulbous base and a tightly folded, rather than gently curving lingual face; the parastyle on M2 appears to be smaller in *Symmetrodontoides oligodontos*. M6 (Fig. 5E) is a slightly asymmetrical tooth, with the paracone placed somewhat distally. A faint parastyle is present; a small knob at the distolabial corner of the tooth could represent the distal stylar cusp, metastyle, or a combination of both. The preparacrista is

only slightly lower than the postparacrista; as for posterior molars in other species of *Symmetrodontoides* and *Spalacolestes*, the paraconal cristae and the raised labial face of the tooth enclose a shallow trigon basin. M6 of *Symmetrodontoides oligodontos* differs from that of *Spalacotheridium noblei* in having a parastyle that does not project so strongly; it is quite similar to that of *Spalacolestes cretulablatta*, differing in having what appears to be more salient paracristae (this appearance may be due to the fact that available specimens of the latter are all somewhat worn).

Comments. Known lower molars of *Symmetrodontoides oligodontos* do not deserve much comment; they are morphologically similar to other species of *Symmetrodontoides* and *Spalacolestes* (see Cifelli and Madsen, in press). Among the upper molars, however, the morphology of M1-2 differs from that of *Spalacolestes*, in which the paracone tends to have a more gently curved lingual face. Judged by comparison to *Spalacotheridium* and the hypothesized relationships among these taxa (Cifelli and Madsen, in press), the condition in *Spalacolestes* appears to be primitive. In turn, this suggests that *Symmetrodontoides* is advanced with respect to the morphology of M1-2—as might be expected in relation to its younger geological age. M6 has a more weakly projecting parastyle than seen in *Spalacotheridium* and, in this and other respects, it is similar to that of *Spalacolestes*. Judged by comparison to outgroup taxa such as *Spalacotherium* (see Simpson, 1928), the presence of a strong parastyle on M6 appears to be primitive, in turn suggesting that the loss of this condition may represent a synapomorphy of *Spalacolestes* and *Symmetrodontoides*.

Symmetrodontoides sp. cf. *S. oligodontos*
Fig. 5F–G

Referred Specimen. OMNH 32874, right M1.

Locality and Horizon. OMNH locality V856, Garfield

Table 2. Dental measurements (in mm), upper molars of Spalacotheriidae.

	M1		M2		M4		M5		M6	
	L	W	L	W	L	W	L	W	L	W
<i>Symmetrodontoides foxi</i>					0.795	1.240				
<i>Symmetrodontoides oligodontos</i>	—	1.017	1.014	1.254					0.480	0.785
				0.928						
<i>Symmetrodontoides</i> cf. <i>S. oligodontos</i>	1.308	1.073								
<i>Spalacotheridium mckennai</i>							0.490	0.741		

County, Utah (Fig. 2); John Henry Member, Straight Cliffs Formation (Coniacian-Santonian).

Description. This tooth (Fig. 5F, G) is extremely similar to M1 of *S. oligodontos*, with which it cannot, unfortunately, be compared in detail because the single M1 known for *S. oligodontos* is heavily worn and incomplete. OMNH 32874 is in pristine condition and preserves details that are obscure in *S. oligodontos*. The parastyle is well-developed and hooklike, though it is smaller and more slender than in *S. canadensis*. A small stylocone, weak or absent in other spalacotheriids known from the medial and Late Cretaceous of North America (Cifelli and Madsen, in press; Fox, 1985), is clearly present. The paracone has a less bulbous base and a more tightly curved lingual face than in *Spalacolestes cretulablatta*; the distal styler cusp is well developed.

Comments. Available evidence is insufficient to establish the specific identity of this tooth, which is, alas, the only well-preserved specimen of a spalacotheriid recovered to date from the John Henry Member of the Straight Cliffs Formation. However, its close similarity to M1 of *Symmetrodontoides oligodontos* and the consistency of differences from other species of *Symmetrodontoides* and *Spalacolestes* suggest that it may be referable to *Symmetrodontoides oligodontos*. If so, *S. oligodontos* would be extended from the late middle or early late Turonian to at least the middle Santonian, giving the species an estimated range of about 6 Ma (Gradstein and others, 1995).

Spalacotheridium Cifelli, 1990

S. mckennai Cifelli, 1990

Fig. 6

Newly-referred Specimens. OMNH 29524, mesial part of right m1; MNA V6046, left m3 or 4 lacking the tip of the paraconid; OMNH 29526, corroded ?left m6; MNA V6756, right M5.

Locality and Horizon. OMNH locality V843 (=MNA 995), Garfield County, Utah (Fig. 2); Smoky Hollow Member, Straight Cliffs Formation (Turonian).

Description. The holotype, MNA V5792, was originally thought to represent m4; comparison with a large sample of a similar species from the Cedar Mountain Formation now suggests that it is more probably m2 (Cifelli and Madsen, in press). Materials currently include representation of four lower and one upper molar loci. The first lower molar is represented by only a fragment and therefore is not figured. The paraconid is low and is anteriorly placed, as in *Spalacotheridium noblei* and species of *Spalacolestes*; it appears to differ from these taxa, however, in being relatively shorter and in having a base that is more completely conical. The second molar has been described previously (Cifelli, 1990a); it is strongly similar to that of

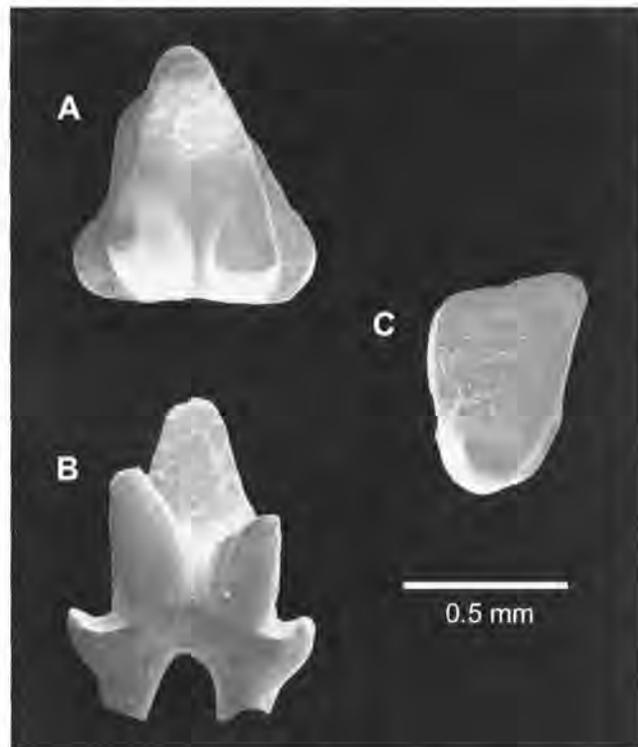


Figure 6. *Spalacotheridium mckennai*. A, B, MNA V6046, left m3 or 4 in occlusal (A) and lingual (B) views. C, MNA V6756, right M5 in occlusal view. Tooth roots and/or jaw fragments removed to improve clarity.

the geologically older *Spalacotheridium noblei*, being somewhat larger and falling slightly outside the range of variation for proportions in that species (Cifelli and Madsen, in press). As with other taxa, m3 or 4 (Fig. 6A, B) is larger and more mesiodistally compressed than m2; it differs from posterior lower molars of *Spalacolestes* and *Symmetrodontoides* in being more symmetrical, without a lingually projecting paraconid and with paraecristid and protocristid that are of approximately equal length. The sixth lower molar (not figured) is poorly preserved; it is slightly larger and less mesodistally compressed than comparable teeth of *Spalacotheridium noblei*.

The M5 (Fig. 6C) is very similar to that of *Spalacotheridium noblei*, differing from *Spalacolestes* in having a slightly more rounded paracone (in occlusal view) and a more gently rounded, less angular metastylar region. It differs from M5 of *Spalacotheridium noblei* in lacking a projecting parastyle and in having a less curved lingual slope on the paracone (in mesial view).

Comments. When initially described on the basis of a single tooth belonging to the type (and then only) species (Cifelli, 1990a), *Spalacotheridium* was recognized primarily on the basis of its subequal lower molar paraconid and

metaconid. This was a distinction, to be sure, from other North American spalacotheriids, but one that was not satisfying in view of the lack of knowledge on variability. New materials, including those described herein and an additional species from central Utah (Cifelli and Madsen, in press) uphold the distinctiveness of these dainty little symmetrodonts. The cited lower molar characteristic (subequal paraconid and metaconid) is distinctive among North American spalacotheriids (the condition is unknown for *Spalacotheroides*) and, in this and several other features, *Spalacotheridium* appears to be primitive with respect to *Spalacolestes* and *Symmetrodontoides*. The lack of a projecting parastyle on M5 of *Spalacotheridium mckennai*, representing a presumably derived condition, accords with its younger geologic age than its congener, *S. noblei*, in which the parastyle is present on M5.

?Symmetrodonta, fam., gen. and sp. indet.

Fig. 7A–J

Specimens. MNA V6305, fragment of left maxilla with one premolar; MNA V4622, V6364, OMNH 29041, 29043, isolated cheek teeth.

Localities and Horizons. OMNH localities V843 (=MNA 995; MNA V6305, V6364), V60 (OMNH 29041, 29043), and V8 (MNA V4622), Garfield County, Utah (Fig. 2). Localities V843 and V60 are in the Smoky Hollow Member of the Straight Cliffs Formation (Turonian); locality V8 is in the Wahweap Formation (?lower Campanian).

Description. Included here are several puzzling small teeth that are clearly mammalian. Except for the single specimen embedded in a fragment of maxilla, it cannot be determined with certainty whether individual specimens are upper or lower teeth. However, variation in the sample suggests that both may be present. Similarly, variation among the specimens suggests that several tooth positions may be represented.

MNA V6305 (Fig. 7A, B) includes a tiny, two-rooted premolar. The crown is simple, consisting almost entirely of the paracone, which is labiolingually compressed but does not possess well-defined mesial and distal carinae. Faint steps at the mesial and distal bases of the tooth, best developed lingually, suggest the presence of accessory cusps; there is no labial cingulum, but a vague swelling connects the basal cusps lingually. The simple morphology of the tooth suggests the possibility that it occupied a mesial position in the series. No other clearly defined alveoli are present on the maxilla, which preserves the alveolar margin both mesial and distal to the tooth in place, indicating the presence of diastemata adjacent to that tooth.

The remaining four cheek teeth are generally similar in having three principal cusps that are more or less mesio-

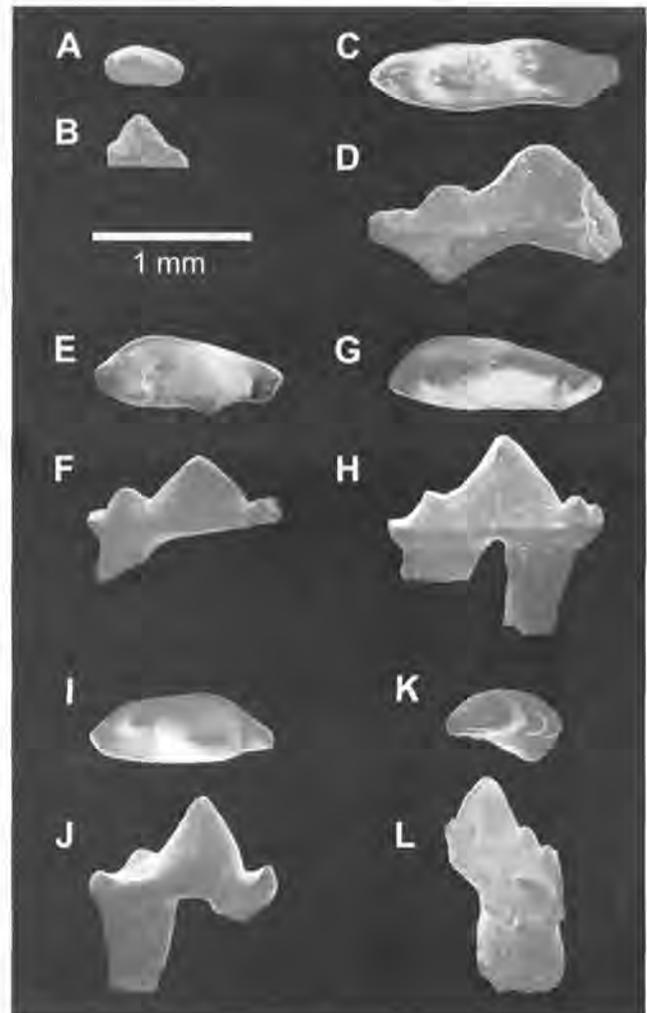


Figure 7. ?Symmetrodonta (A–J) and ?Mammalia, indet. (K–L). A, B, MNA V6305, fragment of left maxilla with one premolar in occlusal (A) and lingual (B) views. C, D (MNA V4622), E, F (MNA V6364), G, H (OMNH 29043), I, J, (OMNH 29041), isolated cheek teeth in occlusal (C, E, G, I) and lingual (D, E, H, J) views. K, L, MNA V7349, ?incisor in occlusal (K) and lingual (L) views.

odistally oriented with respect to the main tooth axis. The most divergent of these is MNA V4622 (Fig. 7C, D). The specimen is broken mesial to the principal cusp, but it clearly was extremely low crowned and mesodistally elongate. If a lower cheek tooth, it is apparently from the left side, because the distal cusp is placed somewhat lingually; a faint cuspule is present at the distal margin of the tooth, and again assuming that it is a left lower tooth, a basal cingulum is present lingually.

MNA V6364 (Fig. 7E, F), OMNH 29043 (Fig. 7G, H), and 29041 (Fig. 7I, J) are progressively higher crowned. The first two differ in only minor ways; a labial cingulum

is present distal to the main cusp, whereas the lingual cingulum is complete. The mesial cusp is placed near the base of the crown, along the mesodistal axis of the tooth, whereas the distal cusp is on the flank of the principal cusp and is somewhat lingually situated; a small, basal cuspule is present distally. OMNH 29041 has a more trenchant principal cusp, with the mesobasal cusp placed somewhat lingually. The distal cusp is much lower than on MNA V6364 or OMNH 29043, being about the same height as the mesial cusp; as well, it is placed somewhat labial to the main cusp. A weak cingulum is present labially but not lingually.

Comments. MNA V6305 differs from premolars of known Cretaceous tribosphenidans in being more conical, with a more symmetrical, less recumbent principal cusp, and in having small, subequally developed basal cuspules. The only non-multituberculate, non-tribosphenidan mammals known from the Wahweap and Straight Cliffs formations are spalacotheriid symmetrodonts. Unfortunately, the premolars of Spalacotheriidae are not well known: about the best that can be said is that the morphology of MNA V6305 is consistent with its referral to the family, based on *Spalacotherium* (see Simpson, 1928). If this is the case, then diastemata separated some of the anterior premolars in some member or members of Spalacolestinae.

General form and the distribution of cusps and cingula suggests that one of the remaining specimens (OMNH 29041) is an upper tooth and the rest are lowers. They are not, strictly speaking, premolariform, but neither do they really resemble molars of a known mammal; in particular, shearing surfaces are lacking, and wear instead seems to be confined to the occlusal surfaces of the major crests and the cusp apices. In addition, the mesial and distal cusps are more weakly developed than are, for example, paraconid and metaconid, and the crowns in general are rather low. MNA V6364, in particular, greatly resembles the single, semimolariform tooth in UALVP 12086, considered by Fox (1976) as possibly representing m1 of *Symmetrodontoides canadensis*. The dentary fragment supporting this tooth clearly is from the front of the jaw (it bears two mental foramina), hence the tooth (and, by implication, the teeth from the Cretaceous of the Kaiparowits region) occupied a relatively anterior position in the cheek-tooth series. Comparison to similar taxa from the Cedar Mountain Formation (Cifelli and Madsen, in press), however, suggests that the tooth of UALVP 12086 is not part of a spalacotheriid molar series. It is possible that these teeth are premolars or deciduous premolars of spalacotheriids known from their respective faunas. However, it is also possible that they represent another type of symmetrodont or other clade of archaic mammal; for example, an obtuse-angled symmetrodont, *Mictodon simpsoni*, is

Table 3. Dental measurements (in mm),
?Symmetrodonta and ?Mammalia indet.

Specimen	Tooth	L	W
MNA V 6305	?premolar	0.504	0.277
MNA V4622	?premolar	—	0.375
MNA V6364	?premolar	1.211	0.442
OMNH 29041	?premolar	1.169	0.379
OMNH 29043	?premolar	1.335	0.390
MNA V7349	?incisor	0.748	0.446

also known from the same local fauna in the upper Milk River Formation as *Symmetrodontoides canadensis* (see Fox, 1984a).

?Mammalia, incertae sedis
Fig. 7K–L

Specimen. MNA V7349, ?incisor.

Locality and Horizon. OMNH locality V843 (=MNA 995), Garfield County, Utah (Fig. 2); Smoky Hollow Member, Straight Cliffs Formation (Turonian).

Description. The crown of this tooth (Fig. 7K, L) is asymmetrical and lanceolate, with a trenchant, labiolingually compressed principal cusp aligned with one edge (rather than the center) of the single root. Sharp crests descend mesially and distally from this central cusp; on the mesial side, which overhangs the root, a small cuspule is present basolingually. On the distal side, two cuspules are present near the base of the crest descending from the principal cusp, and another is present lingually.

Comments. Mammalian affinities for MNA V7349 are suggested by the complexity of the tooth crown and by the presence of a strong root that appears to have been implanted in a socket in the jaw. It is possible that the specimen belongs to some kind of reptile with thecodont teeth, perhaps an ornithischian, but it does not compare closely with any of the groups typical of the North American Cretaceous. If mammalian, the presence of a single root and the general form of the crown suggests that it is an anterior tooth, probably an incisor. Vaguely analogous, complex crowned incisors are known for North American Cretaceous Triconodontidae (Cifelli and Madsen, 1998), but these are quite different and triconodonts are otherwise unknown from the Late Cretaceous of the Kaiparowits region (see discussion below). It is not inconceivable that MNA V7349 belongs to a spalacotheriid, though the only symmetrodont for which the incisors are known, *Zhangheotherium*, has simple, conical incisors (Hu and others, 1998).

DISCUSSION: DISTRIBUTION OF
ARCHAIC MAMMAL GROUPS IN THE
LATE CRETACEOUS OF NORTH AMERICA

It has long been recognized that North American communities of the Late Cretaceous included mammal assemblages dominated by multituberculates and marsupials, with eutherians playing a lesser role (e.g., Simpson, 1929). This general pattern became well established with publication of the now-classic mammalian faunas of Judithian and Lancian age (e.g., Clemens, 1963, 1966, 1973; Lillegraven, 1969; Lillegraven and McKenna, 1986; Sahni, 1972). It thus came as a surprise when symmetrodonts—long thought to be primitive mammals restricted to the Jurassic—were reported from the North American Early Cretaceous (Patterson, 1955) and, subsequently and more surprisingly, the Late Cretaceous (Fox, 1972b). These occurrences are part of a more general and poorly appreciated phenomenon: the survival of archaic, relictual clades of mammals into and, in some cases, through the Late Cretaceous in North America. The milestone fauna in this respect is that of the early Campanian upper Milk River Formation, which includes a triconodont (Fox, 1969) and a host of primitive tribosphenic mammals (e.g., Fox, 1972b, 1982) in addition to symmetrodonts. Additional records of these and other relict groups have been reported from a variety of geographic areas and ages, from the medial to latest Cretaceous, and from Canada to the Big Bend, Texas (e.g., Cifelli, 1994; Cifelli and others, 1997; Clemens and Lillegraven, 1986; Eaton, 1993a; Eaton and others, in press; Fox, 1974; Lillegraven and McKenna, 1986). As illustrated by the remarkable case of a therapsid in the Paleocene of Canada (Fox and others, 1992), these range extensions serve to underscore the inadequacies of the fossil record and, perhaps, sampling biases. More importantly, though, these occurrences reflect taxonomic distributions that, when better known, will be of interest in evaluating endemism, provinciality, biogeographic interchange, and the changing constituency of North America's terrestrial ecosystem through the Cretaceous. Unfortunately, available data do not yet provide the basis for such an evaluation, and we accordingly restrict the following discussion to what is known about the distribution of symmetrodonts and other archaic mammalian groups in the Cretaceous of North America, and what hints they suggest about the histories of these taxa.

SYMMETRODONTS

North American spalacotheriids appear to form a monophyletic group, Spalacolestinae, characterized by taxa that are increasingly specialized through time; their proximal sister taxon is *Spalacotherium*, from the Early Cretaceous of western Europe (Cifelli and Madsen, in press). Hence

they represent an endemic radiation derived from a probable Laurasian ancestor, and unlike many other groups of terrestrial vertebrates, were not part of one or more Late Cretaceous immigration events from Asia (Cifelli and others, 1997). Spalacotheriids are rare in Aptian-Albian faunas, being known by only a few specimens from the Trinity Group of Texas (Patterson, 1956) and one from the Cloverly Formation, Montana (RLC, unpubl. data). By contrast, four or more species are present in the Albian-Cenomanian of Utah, where they far outnumber in abundance any other group of mammals except multituberculates (Cifelli and Madsen, in press). One or more species, currently under study, are present in the Cenomanian Dakota Formation of southern Utah (J. G. Eaton, pers. commun.), and two are known from the Smoky Hollow Member of the Straight Cliffs Formation, southern Utah (Cifelli, 1990a, this study). Of these, *Spalacotheridium*, which is also known from the Albian-Cenomanian, makes its last appearance, while *Symmetrodontoides*, also known from the Campanian, first appears in the fossil record. As several specimens are known for each taxon from Turonian and Campanian units in which spalacotheriids occur, their abundance may be characterized as modest but not exceptionally rare. It is also noteworthy that *Symmetrodontoides* is known both from Alberta (Fox, 1976) and southern Utah (Cifelli and Madsen, 1986, this study), suggesting that it was a fairly widespread, if not extremely abundant taxon. *Symmetrodontoides foxi* also has been reported from the Paunsaugunt Plateau, to the west of the Kaiparowits region, in rocks that may be equivalent to either the Wahweap (early Campanian) or Kaiparowits (late Campanian) formations (Eaton, 1993b; Eaton and others, 1998). *Symmetrodontoides* sp. is recorded from low in the Kaiparowits Formation on the Kaiparowits Plateau (Eaton and others, in press, J. G. Eaton, pers. commun.). Spalacotheriids are not known in North America later than about the early late Campanian. Mammalian faunas of the late Campanian (Judithian land-mammal age) are sufficiently well known and geographically widespread, ranging from Canada to Mexico (Cifelli, 1990c, d, 1994; Fox, 1979a, b, c, 1980a; Lillegraven and McKenna, 1986; Montellano, 1992; Rigby and Wolberg, 1987; Sahni, 1972), to suggest that this disappearance probably represents extinction of Spalacotheriidae throughout western North America early in the late Campanian. Given that the last record is in the early late Campanian of southern Utah and that spalacotheriids are unknown from more northerly faunas after the early Campanian, it is possible that the group maintained a southerly distribution near the end of its temporal range. Obtuse-angled symmetrodonts of the North American Late Cretaceous deserve only passing mention because they are known by the single specimen of *Mictodon simpsoni*, from the early Campanian of Alberta (Fox, 1984a). If this tooth proves to

represent a valid taxon of Tinodontidae, it could reflect immigration from Asia or a relictual, northern distribution of a North American endemic. It could also simply be a relict of a group that was more widely distributed in North America, though this is somewhat less likely, as there is no evidence of such a group from older or contemporaneous faunas elsewhere in the Cretaceous on this continent.

TRICONODONTS

Triconodontidae represent another archaic group of mammals long thought to be restricted to the Jurassic in North America (Simpson, 1929), but now known from the Cretaceous. The taxa known from the Cretaceous of North America appear to form a monophyletic cluster within the family; ancestry of this clade is debatable, but it extends into the Early Cretaceous or, more likely, Jurassic (Cifelli and others, 1998). One rather abundant species, *Astroconodon denisoni*, is known from the Aptian-Albian Trinity Group of Texas and Oklahoma (Patterson, 1951; Slaughter, 1969, Turnbull and Cifelli, unpubl. data); and a single specimen of a triconodontid has recently been reported from the Arundel Clay (Albian) of Maryland (Cifelli and others, in press). Three or more species, modest in abundance, are known from the contemporaneous Cloverly Formation, Montana (Cifelli and others, 1998), and the somewhat younger Cedar Mountain Formation, Utah (Cifelli and Madsen, 1998). Morphologically, these taxa are quite similar; *Astroconodon* (or something similar to it) is known from all three units, and *Corviconodon* is known from the Cloverly and Cedar Mountain formations, indicating wide temporal and geographic distribution. The last record of the group is the highly specialized *Alticonodon*, from the early Campanian of Alberta (Fox, 1969, 1976). Curiously, triconodonts remain unknown from the Late Cretaceous of Utah. Given the extensive sampling, the numerous rock units that have yielded faunas, and the diagnostic nature of triconodontid remains (even a fragment of a tooth is readily identified), we cautiously suggest that Triconodontidae became locally extinct by the Cenomanian. Given the relationship of *Alticonodon* to an endemic North American clade, existing data also suggest that the group retained a northern distribution in North America, before becoming extinct on the continent during the Campanian.

EUPANTOTHERES

One of the most startling occurrences of archaic mammal groups in the North American Cretaceous is that of a dryolestid eupantothere, represented by a single, fragmentary tooth from the late Campanian "Mesaverde" Formation of Wyoming (Lillegraven and McKenna, 1986). This family, characteristic of Late Jurassic assemblages of

both North America and Europe (Simpson, 1928, 1929), is known from several taxa in the Campanian of Argentina (Bonaparte, 1990). Given the lack of other occurrences in the Judithian or elsewhere of North America, not much can be said of this record, other than the obvious observation that dryolestids were almost certainly neither abundant nor diverse in the Cretaceous of North America. Given the extensive sampling from numerous, geographically and temporally widespread sites through the medial and Late Cretaceous, the absence of dryolestids elsewhere in North America is disconcerting. The taxon from the "Mesaverde" Formation could be a relict of North American Jurassic Dryolestidae, or it may represent an immigrant (from an unidentified source) that achieved ephemeral and limited success on the continent in the Late Cretaceous.

TRIBOTHERES

In North America, marsupials are first known from the Cenomanian (Cifelli and Eaton, 1987; Eaton, 1993a) or, perhaps, Albian-Cenomanian (Cifelli and others, in press); eutherians do not appear until the early Campanian (Cifelli, 1990d; Fox, 1984b). Faunas from the Early through latest Cretaceous, however, record the presence of a diverse variety of tribosphenic mammals (Cifelli, 1990a, b, 1994; Cifelli and others, in press; Clemens and Lillegraven, 1986; Eaton, 1993a; Fox, 1972a, 1980b, 1982; Lillegraven and McKenna, 1986) that do not fit conveniently into either category and are usually termed Theria of meta-therian-eutherian grade (Kielan-Jaworowska and others, 1979; Patterson, 1956) or tribotheres (Butler, 1978). Most of these are inadequately known and are either primitive or uniquely specialized, so that their relationships are enigmatic and they cannot be unravelled here. The least ambiguous (but still arguable) taxa fall into three possible phylogenetic clusters. *Picopsis*, a taxon characterized by upper molars that have a reduced anterior styler shelf but that are otherwise remarkably primitive, was first reported from the early Campanian upper Milk River Formation, Alberta (Fox, 1980b). Similar, probably related taxa are present in the Turonian of southern Utah (Cifelli, 1990a, unpubl. data), the Albian-Cenomanian of central Utah (Cifelli and others, 1997), and, possibly, the Maastrichtian of Wyoming (Cifelli, 1990a); in each fauna, one or two taxa are generally represented by a few teeth each. The "group," if it is one, obviously is archaic, extending at least to the Albian. The "group" is not obviously related to mammals from elsewhere, although a vague resemblance to *Comanchea*, from the Aptian-Albian of Texas (Jacobs and others, 1989), has been noted (Cifelli, 1993a). The great stratigraphic range of the "group" on the continent indicates that later taxa probably are not immigrants, but beyond this their distribution is difficult to interpret. Their apparent

absence from southerly faunas after the Turonian and persistence in the early Campanian of Alberta and Maastrichtian of Wyoming suggests the possibility that, like triconodontids, they maintained a northerly distribution after becoming regionally extinct elsewhere. Nonetheless, they are rare, poorly speciose mammals, so that the possibility exists that this pattern reflects a sampling bias.

A second possible clade of tribotheres includes *Iugomortiferum*, from the early Campanian of southern Utah, and *Paleomolops*, from the late Campanian of Texas (Cifelli, 1990b, 1994). Both are marsupial-like, and in fact the former was included in the Marsupialia by McKenna and Bell (1997). Origin of the group is uncertain, but a guess is that it lies within an endemic, North American radiation of metatherians that appears to have taken place in the medial Cretaceous (e.g., Cifelli, 1993a, b; Cifelli and others, in press). Absence of similar taxa from well-sampled northerly faunas, particularly those of the Judithian, suggests that this putative clade maintained a southerly distribution during the Campanian, as may also be true of spalacotheriid symmetrodonts.

A third clade of tribotheres from the Cretaceous of North America is the Deltatheroidea. This group, widely accepted as monophyletic, is mainly Asiatic in distribution and may (or may not) ultimately be related to marsupials (e.g., Cifelli, 1993a; Kielan-Jaworowska and Nesson, 1990; Muizon, 1994; Rougier and others, 1998). The generally-accepted sister taxon of Deltatheroidea is *Kielantherium* from the Early Cretaceous of Mongolia (Butler, 1990; Cifelli, 1993a; Dashzeveg and Kielan-Jaworowska, 1984; Kielan-Jaworowska, 1992; Marshall and Kielan-Jaworowska, 1992), implying early divergence, at a very primitive stage, for the group (Kielan-Jaworowska, 1992). In North America, the earliest record of a deltatheroidan, or something closely related, is in the Turonian of southern Utah (Cifelli, 1990a). Some workers have further suggested a relationship of *Picopsis* (mentioned above) and *Potamotelses*, both from the early Campanian of Alberta, to (or within) Deltatheroidea (Butler, 1990; Marshall and Kielan-Jaworowska, 1992). This may be the case, but it is not supported by existing evidence, which consists of primitive characters only (Cifelli, 1993a). Specimens very similar to those referred to Asiatic *Deltatheroidea* have been reported from late Campanian and Maastrichtian horizons in Alberta and Wyoming (Fox, 1974). Taken at face value, the close similarity of the North American specimens to those belonging to Asian *D. cretacicus* argues for a recent common ancestor, implying interchange between the continents during the Campanian (Fox, 1974). Given the hypothesized relationships of and within the group, and its antiquity in the Old World, an Asian origin is suggested. Assuming these resemblances reflect close relationship,

the presence of a deltatheroidan (or close relative) in the Turonian of southern Utah must be explained otherwise, the most logical being an older interchange between the two continents, thought to have occurred in the medial Cretaceous (Cifelli and others, 1997).

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