

Chapter 5

Marsupial Mammals from the Albian–Cenomanian (Early–Late Cretaceous) Boundary, Utah

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ABSTRACT

The Mussentuchit local fauna, upper Cedar Mountain Formation (Cretaceous: Albian–Cenomanian), Utah, includes the geologically oldest marsupials: *Kokopellia juddi*, described previously, and three new taxa named herein. *Adelodelphys muizoni*, new genus and species, and *Sinbadelphys schmidtii*, new genus and species, both unassignable to family, are among the smallest of Cretaceous marsupials; *Pariadens mckennai*, new species, tentatively assigned to Stagodontidae, is among the largest. The three are morphologically similar: they bear certain dental specializations of Marsupialia (e.g., presence of labial postcingulid and “twinning” of hypoconulid and entoconid on lower molars), but are plesiomorphic with respect to most or all Late Cretaceous marsupials in other features (e.g., relatively lingual position of conules, lack of stylar cusps C or D on upper molars). Compared to Late Cretaceous (Cenomanian–Maastrichtian) assemblages of North America, the marsupials of the Mussentuchit local fauna are rare and low in morphologic and taxonomic diversity. Biogeographic origin of Marsupialia and their antiquity in North America remain unknown. However, patterns of diversification and differentiation suggest that the taxa from the Cedar Mountain Formation lie near the base of North America’s Cretaceous marsupial radiation.

INTRODUCTION

Though marsupials and placentals have dominated mammalian faunas throughout the Cenozoic, they were among the last major clades of mammals (both living and extinct) to appear in the fossil record, and among the last to be discovered in rocks of Mesozoic age: taxa now generally referred to each group were first reported near the end of the 19th century (e.g., Marsh, 1889a; Cope, 1892).¹ Most, but perhaps not all (see Szalay and Trofimov, 1996; Fox, 1997a, for contrasting views), of the Mesozoic record for marsupials comes from North America. Cretaceous marsupials are represented almost exclusively by teeth and jaw fragments, a fossil record aptly described as “an odontologist’s delight” (Clemens, 1979: 192). The earliest reported and best-known assemblage

of Cretaceous marsupials is from the last part (ca. 65.5–69 Ma, Maastrichtian) of the period, the Lancian North American land mammal age (NALMA, Lillegraven and McKenna, 1986; age estimates for NALMAs from Cifelli et al., in press; other geochronologic ages approximated from Gradstein et al., 1995). A few geologically older marsupials, from the preceding Judithian land mammal age (ca. 74–79 Ma, Campanian), were described early in the 20th century (Matthew, 1916; Woodward, 1916), but many years were to elapse before representation of pre-Lancian marsupials improved significantly. Judithian assemblages are now comparatively well known (Sahni, 1972; Fox, 1979a, 1979b, 1981; Lillegraven and McKenna, 1986; Cifelli, 1990a, 1994; Montellano, 1992). Aquilan (ca. 83–84 Ma, late Santonian or early Campanian) marsupials were first described in 1971 and are now known from several local faunas (e.g., Fox, 1971b, 1987a; Cifelli, 1990b; Eaton, 1990; Eaton et

¹ The third major clade of living mammals, Monotremata, remained unrepresented by Mesozoic fossils until nearly a century later (Archer et al., 1985).

al., 1998). Currently, the geologically oldest mammals generally accepted as marsupials are from the late Cenomanian (ca. 94–96 Ma) of Utah (Cifelli and Eaton, 1987; Eaton, 1993) and Texas (Jacobs and Winkler, 1998).

Herein I describe marsupials from the upper part, or Mussentuchit Member (see Kirkland et al., 1997, 1999) of the Cedar Mountain Formation, Emery County, Utah (fig. 5.1). Included taxa are not well known, being represented exclusively by isolated teeth (many incomplete), yet these marsupials are noteworthy despite their poor morphological representation. Their age is rather tightly constrained: multiple, highly concordant $^{40}\text{Ar}/^{39}\text{Ar}$ determinations from an ash directly associated with the fauna (Cifelli et al., 1997, 1999b) yield a mean age of 98.39 ± 0.07 Ma, which is indistinguishable from the Albian–Cenomanian (Early–Late Cretaceous) boundary (e.g., Obradovich, 1993; Gradstein et al., 1995). To date, the taxa described below are the oldest known marsupials. The Mussentuchit local fauna has been intensively sampled using microvertebrate concentration and recovery techniques (Cifelli et al., 1996a); some 80 vertebrate taxa are included. Fossil vertebrate localities are confined to a narrow stratigraphic zone, yet diverse paleoecological settings are represented. Taxonomic composition from site to site varies accordingly; some species, for example, appear to have had rather specific habitat requirements and are restricted to one or a few sites (e.g., Cifelli and Madsen, 1999). Mammals from the Mussentuchit local fauna described thus far include a marsupiallike taxon (Cifelli, 1993a; Cifelli and Muizon, 1997), three triconodontids (Cifelli and Madsen, 1998), four or more spalacotheriid “symmetrodonts” (Cifelli and Madsen, 1999), and nine or more multituberculates (Eaton and Cifelli, 2001). Statistical tests suggest that the available sample includes all or almost all mammals that are likely to be recovered from the Mussentuchit local fauna (Goldberg, 2000). For present purposes, the record from the Cedar Mountain Formation can be taken at face value insofar as marsupial diversity and abundance are concerned. This completeness of faunal representation, together with tight geographic and stratigraphic distribution of localities, makes the Mussen-

tuchit local fauna, and its contained marsupials, a useful point of reference for comparison to other assemblages of North America.

ANATOMICAL ABBREVIATIONS

Standard abbreviations are used for cheek teeth (upper and lower case letters refer to upper and lower teeth, respectively): dP/p, deciduous premolar; M/m, molar; P/p, premolar. In the interest of brevity, referred specimens are simply listed by tooth position, without detail on preservation or missing parts. Measurements (in mm), taken with a Reflex microscope (MacLarnon, 1989), follow those of Lillegraven (1969), with abbreviations after Lillegraven and McKenna (1986): AP, anteroposterior length; ANW, anterior width (trigonid of lower molars); POW, posterior width (taloid of lower molar). Dental terminology is shown in figure 5.2.

INSTITUTIONAL ABBREVIATIONS

MNA, Museum of Northern Arizona, Flagstaff
OMNH, Oklahoma Museum of Natural History,
Norman

METHODS

Both quarrying and underwater screen-washing procedures were employed in the course of sampling the Mussentuchit local fauna. As a result, some of the mammals (e.g., the marsupial *Kokopellia* and the spalacotheriid “symmetrodont” *Spalacolestes*) are represented by dentigerous jaws (see Cifelli and Muizon, 1997; Cifelli and Madsen, 1999). All of the specimens reported herein, however, are isolated teeth that were recovered via screen washing. Taxonomic associations and identification of tooth position were based on presumed homology with structurally similar taxa known by dentulous jaws (e.g., Cifelli, 1993a), relative size, and morphological appropriateness. Comparisons are mainly restricted to structurally comparable marsupials from the Late Cretaceous of North America; the “tribotheres” *Pappotherium* and *Holoclemensia* are included (where appropriate) as outgroups, to facilitate interpretation of character polarity (see Butler, 1978, 1990; Kielan-Jaworowska et al., 1979; Clemens and Lillegraven, 1986; Cifelli, 1993b).

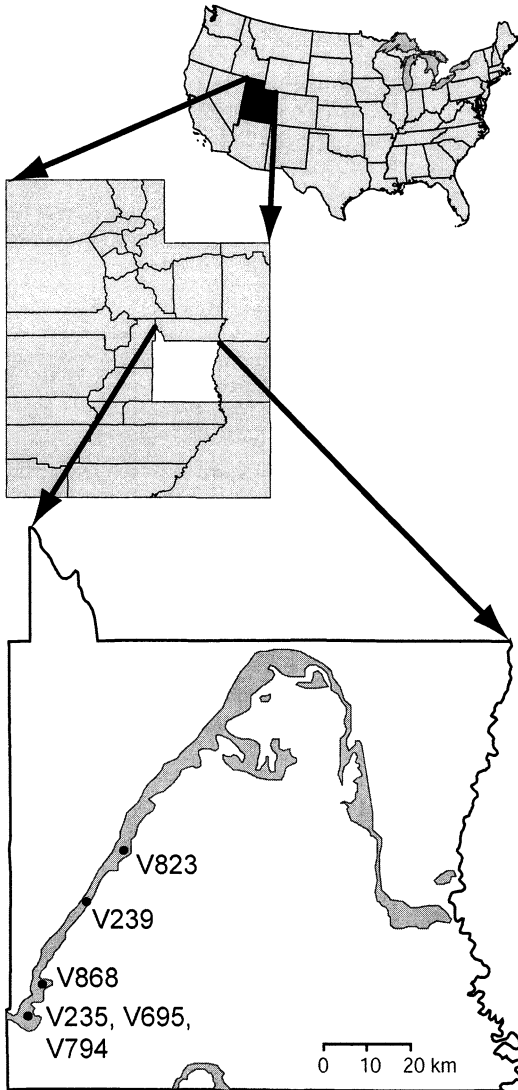


Fig. 5.1. Locator maps. Top, continental United States with Utah shaded in black. Center, county map of Utah, showing Emery County in white. Bottom, Emery County, showing distribution of OMNH sites (numbers preceded by "V") that yielded specimens described herein; outcrop of Cedar Mountain Formation shaded in gray. Modified after Eaton and Cifelli (2001: fig. 1).

Only six of the 12 best-sampled sites in the Cedar Mountain Formation yielded specimens belonging to one or more of the three species reported below. These six sites represent higher-energy depositional settings (channel or splay) than the remainder (flood-

plain, oxbow, see Goldberg, 2000). Stratigraphic documentation for sites is given in Cifelli et al. (1999b); detailed locality data are on file at the Oklahoma Museum of Natural History and are available to qualified investigators upon request.

SYSTEMATICS

COHORT MARSUPIALIA ILLIGER, 1811

SUPERORDER "AMERIDELPHIA" SZALAY, 1982,
NEW RANK

Order and family incertae sedis

COMMENT: The names *Marsupialia* Illiger, 1811, and *Metatheria* Huxley, 1880, have long been used interchangeably (see Simpson, 1945; McKenna and Bell, 1997). The hypothesis that *Deltatheroida* may represent a sister taxon to marsupials (Kielan-Jaworowska and Nessov, 1990; Marshall and Kielan-Jaworowska, 1992) has prompted usage of *Metatheria* as a more inclusive taxon (*Deltatheroida* + *Marsupialia*), with *Marsupialia* being defined as a crown group (Rougier et al., 1998) within *Metatheria*. The affinities of *Deltatheroida* remain debatable (Cifelli, 1993b; Luo et al., 2002); regardless, a crown-based definition of *Marsupialia* poses a taxonomic conundrum for many fossil taxa. Late Cretaceous, North American "marsupials" (as traditionally recognized) are clearly more closely related to crown *Marsupialia* than are *Deltatheroida*, and some, at least, appear to have had developmental attributes otherwise peculiar to the living forms (e.g., Cifelli et al., 1996b). It is probable that the North American Cretaceous radiation includes a number of successive sister taxa to crown *Marsupialia*, and it is possible that some belong within the crown (e.g., Aplin and Archer, 1987). At present, it appears to be more practical to define *Marsupialia* as a stem-based clade, thereby preserving the well-established, long-standing convention (e.g., Simpson, 1927, 1929, 1945; Clemens, 1966; Lillegraven, 1969; McKenna and Bell, 1997) of including relevant Cretaceous taxa within it.

Suprafamilial and, in many cases, suprageneric allocations of Cretaceous taxa within *Marsupialia* are problematic and will likely remain unsatisfactory until the known fossil

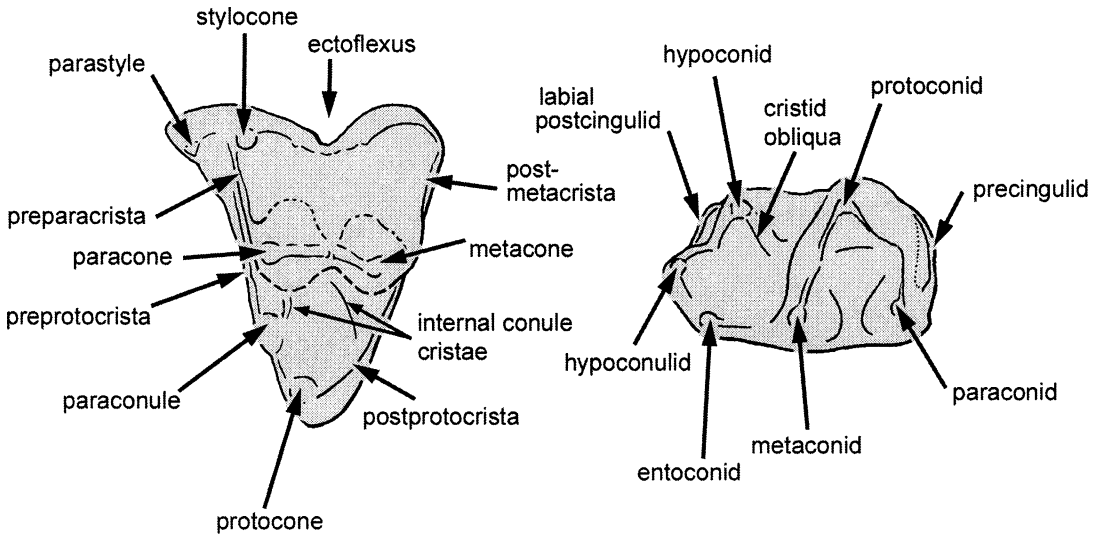


Fig. 5.2. Dental terminology. Left upper (left) and lower (right) molars of *Kokopellia juddi*.

record improves dramatically. Recent marsupial classifications (e.g., Archer, 1984; Aplin and Archer, 1987; Reig et al., 1987; McKenna and Bell, 1997) generally follow Szalay (1982) in recognizing a fundamental dichotomy between Australidelphia and Ameridelphia. The latter is implicitly paraphyletic, as it includes ancestry of Australidelphia; herein, I simply expand the concept of “Ameridelphia” to include stem taxa from the Cretaceous of North America (see Szalay, 1994, for an alternative arrangement). Early marsupials characterized by a generally plesiomorphic molar pattern (e.g., *Alphadon*) have long been referred to the Didelphidae, an extant group with a similar molar pattern (e.g., Simpson, 1929, 1945; Clemens, 1966). Recent studies of dental, cranial, and postcranial anatomy (e.g., Szalay, 1994; Muizon et al., 1997; Muizon and Cifelli, 2001) have identified apomorphies that nest Didelphidae among marsupial groups endemic to South America, to the exclusion of Cretaceous taxa. An alternative taxonomic scheme, placement of *Alphadon* and dentally similar Cretaceous taxa with Peradectidae (e.g., Crochet, 1979, 1980; Marshall et al., 1990; Cifelli, 1990a), is plagued by similar problems: comparative studies support monophyly of Tertiary Peradectidae, to the exclusion of dentally similar taxa from the Cretaceous (Krishtalka and Stucky, 1983; Montellano, 1992; Eaton,

1993; Johanson, 1996a). *Alphadon* and one or more dentally similar Cretaceous mammals are sometimes placed in their own suprageneric taxon, Alphadontinae or Alphadontidae (Marshall et al., 1990; Eaton, 1993), though the utility of such a grouping has been questioned (note Johanson, 1996b). This is of little concern in the present context: the genera treated herein are plesiomorphic with respect to Alphadontidae, and (with one tentative exception) they are treated as “Ameridelphia” incertae sedis.

Adelodelphys, new genus

Figure 5.3, table 5.1

TYPE AND ONLY SPECIES: *Adelodelphys muizoni*, new species.

ETYMOLOGY: *Adelos*, Greek, “unseen” or “obscure”, in allusion to its small size and scarcity; *delphys*, Greek, “womb”, a commonly used suffix for opossums or opossum-like marsupials. The species is named for Christian de Muizon, in recognition of his contributions to knowledge of early marsupials.

HOLOTYPE: OMNH 25615, right M1 lacking posterolabial corner.

HYPODIGM: The type, and OMNH 27596, 33083, 33085, 33090 (M2); 33087, 33091, 33092 (M3); 27638 (M4); 25807, 27268,

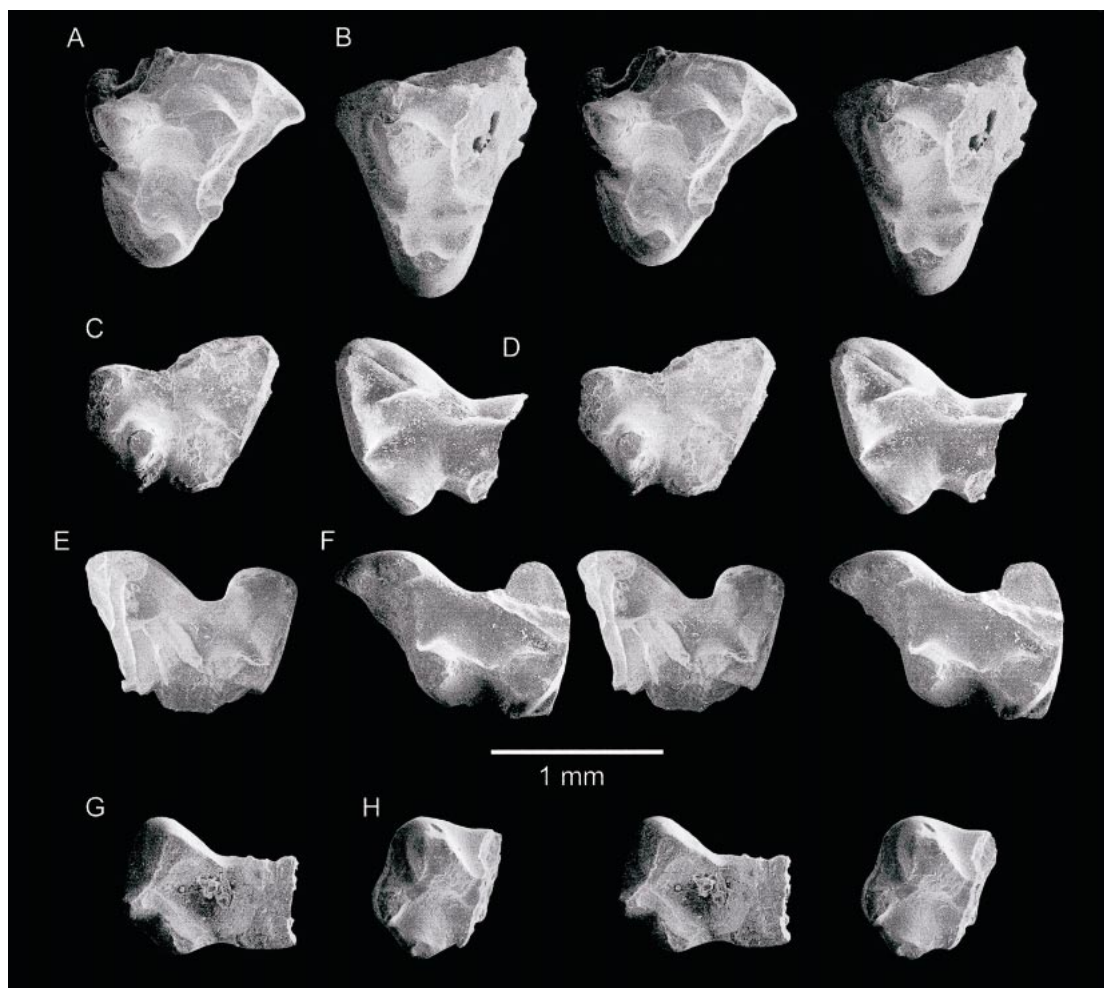


Fig. 5.3. *Adelodelphys muizoni*. **A**, right M1 (OMNH 25615, holotype); **B**, left M2 (OMNH 33083); **C**, left M2 (OMNH 33085); **D**, right M2 (OMNH 33090); **E**, left M3 (OMNH 33092); **F**, left M3 (OMNH 33087); **G**, talonid of left mx (OMNH 27469); **H**, talonid of left mx (OMNH 27555). All stereopairs of occlusal view.

27469, 27555, 30595 (mx); and 33999 (m4?).

LOCALITIES: OMNH localities V235, V239, V695, V794, and V868 (fig. 5.1); Mussentuchit Member, Cedar Mountain Formation (Albian–Cenomanian); Emery County, Utah.

DIAGNOSIS: Small marsupial characterized mainly by its lack of derived characteristics with respect to other members of the cohort; molars structurally similar to those of *Kokopellia*. Differs from *Pappotherium* and *Holoclemensia* in: upper molars with proto-

cone more expanded anteroposteriorly and transversely; postprotocrista extending past base of metacone; conules much more developed and with strong internal cristae; lesser height differential between paracone and metacone; lower molars with labial postcingulid present, entoconid more lingually situated, broader talonid, and lesser height differential between trigonid and talonid (presumed apomorphies). Differs from *Kokopellia* in: upper molars with bases of paracone–metacone more distinctly joined; styler shelf with weaker, less cuspidate rim; M3 with

TABLE 5.1

Dental Measurements of *Adelodelphys muizoni*

| ID | Tooth | AP | ANW | POW |
|------------|-------|-------------------|------|------|
| OMNH 25615 | M1 | — | 1.29 | — |
| OMNH 33083 | M2 | — | 1.55 | — |
| OMNH 33087 | M3 | 1.36 | — | — |
| OMNH 33092 | M3 | 1.34 ^a | — | — |
| OMNH 27268 | mx | — | — | 0.64 |
| OMNH 27469 | mx | — | — | 0.62 |
| OMNH 27555 | mx | — | — | 0.64 |
| OMNH 30595 | mx | — | — | 0.52 |
| OMNH 33999 | m4? | — | — | 0.63 |

^aEstimated measurement.

postmetacrista directed labially (not posterolabially), ectoflexus much deeper, and anterior part of stylar shelf wider, with parastyle projecting in a more labial direction; lower molars with weaker labial postcingulid and with entoconid more lingually placed. Differs from *Anchistodelphys* and most other Late Cretaceous marsupials in the foregoing features and: upper molars with protocone more anteroposteriorly compressed (except *Aenigmadelphys*, *Albertatherium*) and conules placed closer to protocone; lower molars with weaker entoconid, less well-joined to hypoconulid. Further differs from *Aenigmadelphys*, *Varalphadon*, and most other Cretaceous marsupials in lacking a stylar cusp in the D position.

DESCRIPTION: *Adelodelphys* ranks among the smallest of all Cretaceous marsupials, being comparable in size to *Alphadon perexiguus* (see Cifelli, 1994). The stylar shelf of upper molars is bordered by a thin, sharp rim and is devoid of cusps other than the parastyle and stylocone [a faint swelling is present between positions C and D on OMNH 33085 (fig. 5.3C), at position D on OMNH 33092 (fig. 5.3E), and between D and E on OMNH 33090 (fig. 5.3D)]. The ectoflexus increases in depth through the series, forming a strong embayment on M3 (fig. 5.3E, F). The anterior part of the stylar shelf is broad labiolingually and the postmetacrista is almost transversely aligned on this tooth. These features, together with the deep ectoflexus, give the M3 of *Adelodelphys* a striking appearance. No specimen preserves both paracone and metacone in unworn condition, but it appears

that the former was only slightly taller than the latter. Both conules are well developed and bear strong internal cristae, an apomorphy relative to *Pappotherium* and *Holoclemensia*. As in *Kokopellia*, however, the conules are placed about halfway between protocone and paracone–metacone, respectively (a plesiomorphy relative to most Late Cretaceous marsupials). The postprotocrista extends past the base of the metacone on the single specimen in which the condition can be judged (OMNH 33085).

Lower molars are represented mainly by talonids (fig. 5.3G, H); what remains of the trigonid on OMNH 30595 suggests that the paraconid may have been slightly lower than the metaconid. As in early marsupials and in contrast to *Pappotherium* and *Holoclemensia*, the trigonid appears to have been relatively low and the talonid broad. A labial postcingulid is present, and the hypoconulid is lingually situated and closely approximated to the entoconid. However, *Adelodelphys* differs from most Late Cretaceous marsupials in that the labial postcingulid is weaker, the hypoconulid and entoconid not as well joined, and the entoconid is lower (all presumed plesiomorphies).

Sinbadelphys, new genus

Figures 5.4–5.5, table 5.2

TYPE AND ONLY SPECIES: *Sinbadelphys schmidt*, new species.

ETYMOLOGY: Sinbad, in reference to the Head of Sinbad, a prominent landmark of the San Rafael Swell, Utah; joined in contraction with *delphys*, Greek, “womb”, a commonly used suffix for opossums or opossumlike marsupials. The species is named for David F. Schmidt, in recognition of his long-term dedication to mammal collections in general, and this field project in specific.

HOLOTYPE: OMNH 26451, left M2 lacking protocone.

HYPODIGM: The type, and OMNH 30582 (M1); 30587 (M1?); 33088 (M2?); 26448, 27642 (M2 or 3); 27597, 33081 (M3); 27523, 27643, 33093 (Mx); 30580, 33084 (M4); 33069 (dp3); 30591, 30598 (m1); 25800, 26439, 29618, 33074, 33970 (m2 or 3); 26724, 27646, 30594 (mx); 25797, 25801, 26725, 33071, and MNA 5666 (m4).

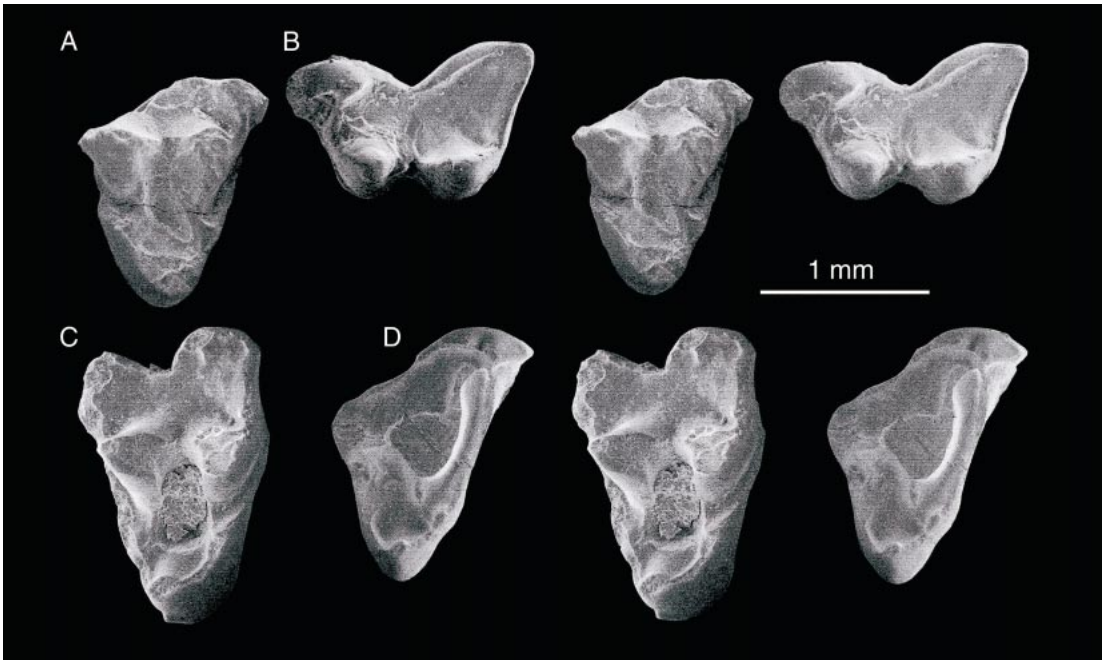


Fig. 5.4. *Sinbadelphys schmidti*, upper molars. **A**, right M1 (OMNH 30582); **B**, left M2 (OMNH 26451, holotype); **C**, left M3 (OMNH 33081); **D**, right M4 (OMNH 33084). All stereopairs of occlusal view.

LOCALITIES: OMNH localities V235, 239, 695, 794, 823 (=MNA 1072), and 868 (fig. 5.1); Mussentuchit Member, Cedar Mountain Formation (Albian–Cenomanian); Emery County, Utah.

DIAGNOSIS: Small marsupial characterized mainly by plesiomorphies with respect to other members of the cohort; molars structurally similar to those of *Kokopellia*. Differs from *Pappotherium* and *Holoclemensia* in: upper molars with protocone better developed, both anteroposteriorly and labiolingually; conules better developed, with strong internal cristae; lesser height differential between paracone and metacone; and variable extension of postprotocrista past base of metacone; lower molars with lesser height differential between trigonid and talonid, broader talonid, labial postcingulid present, entoconid lingually placed (presumed apomorphies). Differs from *Kokopellia* in smaller size and in having: upper molars with weaker, less cusate rim on stylar shelf; deeper ectoflexus; paracone and metacone of more nearly equal height; protocone less transversely developed; lower molars with

entoconid lingually placed and relatively taller. Differs from *Adelodelphys* in larger size and in having: upper molars with bases of paracone and metacone not as tightly joined, protocone better developed transversely, stylar shelf more robust; M3 with relatively broader distal stylar shelf and postmetacrista that is longer and directed more obliquely (i.e., less transversely oriented); lower molars with subequal paraconid and metaconid; stronger labial postcingulid; and entoconid that is much better developed, trenchant and bladelike (not cusate), and more distinctly joined to hypoconulid. Differs from *Anchistodelphys* in having upper molars with more anteroposteriorly compressed protocone, deeper ectoflexus, and parastyle projecting more labially (based on M3 only). Differs from most or all Late Cretaceous Marsupialia in relatively lingual position of conules (about halfway between protocone and paracone–metacone, not adjacent to bases of respective latter two cusps) and hyperextension of internal conule cristae, which commonly extend up from the bases

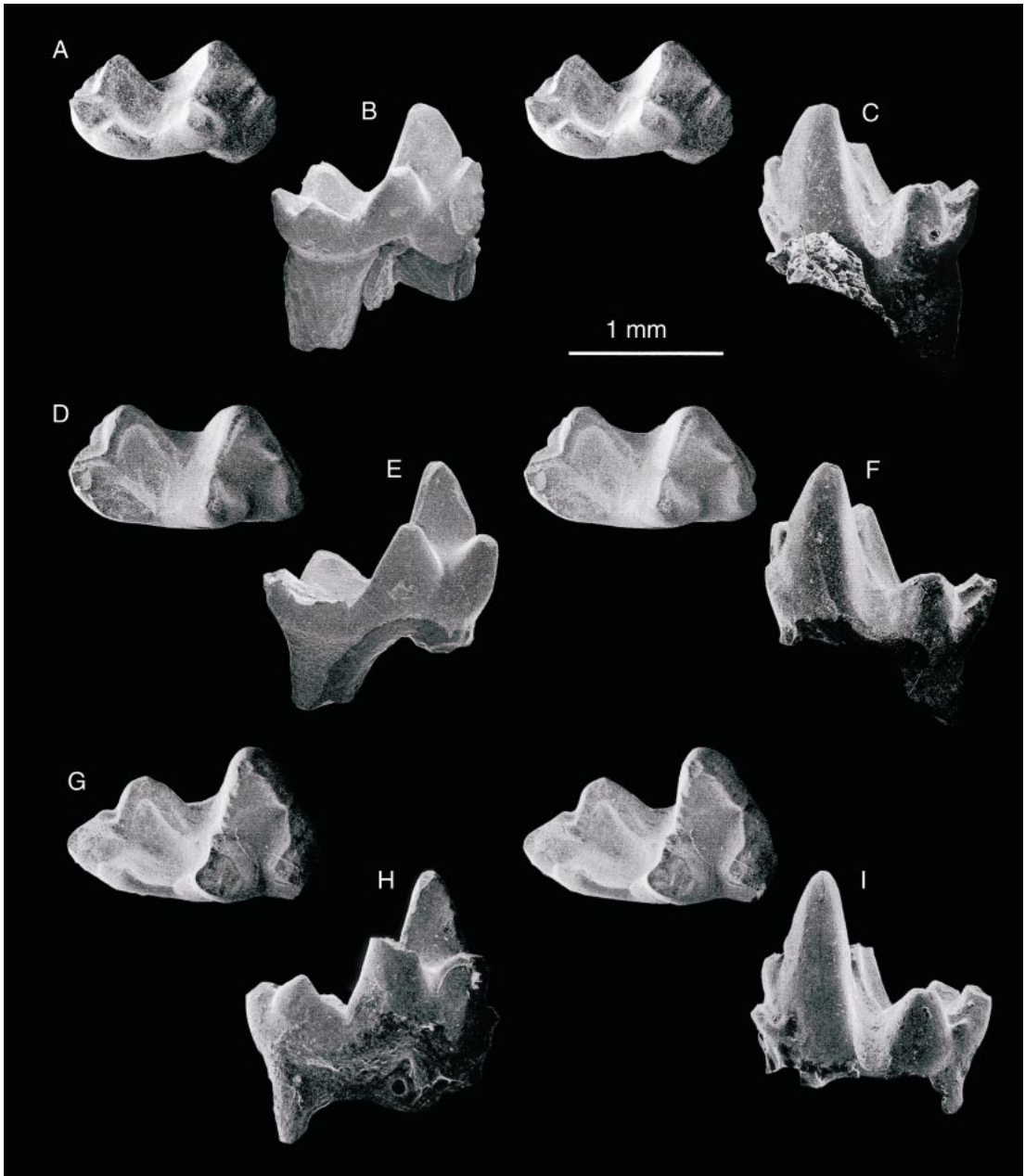


Fig. 5.5. *Sinbadelphys schmidti*, lower molars. **A–C**, left m1 (OMNH 30598); **D–F**, left m2 or 3 (OMNH 33074); **G–I**, left m4 (OMNH 25797). **A, D, G**, occlusal view (stereopairs); **B, E, H**, lingual view; **C, F, I**, labial view.

of paracone and metacone to form lingual keels on those cusps.

DESCRIPTION: Like *Adelodelphys*, *Sinbadelphys* is among the smallest of Cretaceous marsupials, though it is slightly larger than

Adelodelphys: the dental measurement for which samples are most nearly satisfactory, POW of lower molars (tables 5.1–5.2), shows nonoverlapping ranges of variation (*Adelodelphys muizoni*, range = 0.52–0.66, \bar{x}

TABLE 5.2
Dental Measurements of *Sinbadelphys schmidtii*

| ID | Tooth | AP | ANW | POW |
|------------|---------|------|------|------|
| OMNH 30582 | M1 | — | 1.37 | — |
| OMNH 30587 | M1? | — | — | — |
| OMNH 26451 | M2 | 1.50 | — | — |
| OMNH 33088 | M2? | 1.89 | — | — |
| OMNH 27642 | M2 or 3 | — | — | 1.79 |
| OMNH 33084 | M4 | 1.31 | 1.82 | 1.15 |
| OMNH 33069 | dp3 | 1.39 | 0.66 | 0.70 |
| OMNH 30591 | m1 | — | 0.62 | — |
| OMNH 30598 | m1 | 1.40 | 0.71 | 0.75 |
| OMNH 25800 | m2 or 3 | — | 0.97 | — |
| OMNH 26439 | m2 or 3 | 1.57 | 1.00 | 0.82 |
| OMNH 29618 | m2 or 3 | 1.55 | 0.87 | 0.87 |
| OMNH 33074 | m2 or 3 | 1.51 | 0.81 | 0.80 |
| OMNH 33970 | m2 or 3 | 1.57 | — | — |
| OMNH 26724 | mx | — | — | 0.98 |
| OMNH 27646 | mx | — | — | 0.83 |
| OMNH 30594 | mx | — | — | 0.89 |
| MNA 5666 | m4 | 1.72 | 0.96 | 0.78 |
| OMNH 25797 | m4 | 1.57 | 1.02 | 0.75 |
| OMNH 25801 | m4 | — | 1.01 | 0.90 |
| OMNH 26725 | m4 | — | — | 0.83 |
| OMNH 33071 | m4 | 1.66 | 0.92 | 0.76 |

= 0.61, CV= 0.10, N = 4; *Sinbadelphys schmidtii*, range = 0.75–0.98, \bar{x} = 0.83, CV = 0.08, N= 12; CV of pooled samples = 15.2). Except for the stylocone, styelar cusps are lacking, with only a narrow rim present at the labial margin of the styelar shelf (minor styelar cuspules, as described for *Adelodelphys*, are not present on any of the teeth in the available sample). The ectoflexus deepens from M1 to M3, where it appears to be deeper than in most Late Cretaceous marsupials. Paracone and metacone are about equal in height (e.g., fig. 5.4B), a point of contrast with the condition in *Pappotherium* and *Holoclemensia*, and a similarity to most Cretaceous marsupials (note Clemens and Lillegraven, 1986). Similarly, the protocone is more expanded (both transversely and anteroposteriorly) than in the Trinity therians, and the postprotocrista extends labially past the base of the metacone (fig. 5.4C). The conules differ from those of *Pappotherium* and *Holoclemensia* in being much more strongly developed and in having strong internal cristae. As with *Kokopellia* and *Adelodelphys*, however, the conules are more lin-

gually placed than in Late Cretaceous marsupials, wherein they are typically near the bases of paracone and metacone, respectively.

Lower molars of *Sinbadelphys* (fig. 5.5) are similar to those of Late Cretaceous marsupials in a number of respects: compared to *Pappotherium* and *Holoclemensia*, the talonid is relatively broad (though it does not exceed the trigonid in width, as is often the case among Campanian–Maastrichtian taxa), and the trigonid-talonid height differential reduced. A labial postcingulid is present, the hypoconulid is lingually placed, the paraconid is in (or near) alignment with metaconid and entoconid, and the entoconid is strongly developed and well joined to the hypoconulid. The position of the hypoconulid contrasts with the plesiomorphic condition in *Kokopellia*; expansion of the entoconid and its tight connection to the hypoconulid are apomorphies lacking in *Adelodelphys*. The anterolingual face of the paraconid bears a faint keel, as is common among early marsupials; this presumed apomorphy may be related to “twinning” of entoconid with hypoconulid and their apposition to the anterior face of the succeeding molar (Muizon and Cifelli, 2001).² The lower molars of *Sinbadelphys* are otherwise unremarkable in structure: the paraconid and metaconid are subequal in height, and the cristid obliqua attaches to the trigonid below the notch of the protocristid.

FAMILY? STAGODONTIDAE MARSH, 1889b

Pariadens Cifelli and Eaton, 1987

Pariadens mckennai, new species

Figure 5.6, table 5.3

HOLOTYPE: OMNH 33072, left m4.

ETYMOLOGY: For Malcolm C. McKenna, in recognition of his contributions to knowledge of mammalian history.

HYPODIGM: The type, and OMNH 33076 (m1) and 33971 (m2 or 3).

LOCALITY: OMNH V868 (fig. 5.1); Mus-sentuchit Member, Cedar Mountain Forma-

² This character was brought to my attention by Dave Archibald, who further pointed out (personal communication) that a similar paraconid keel is encountered among some early eutherians such as *Paranictoides* (see Archibald and Averianov, 2001: fig. 1A).

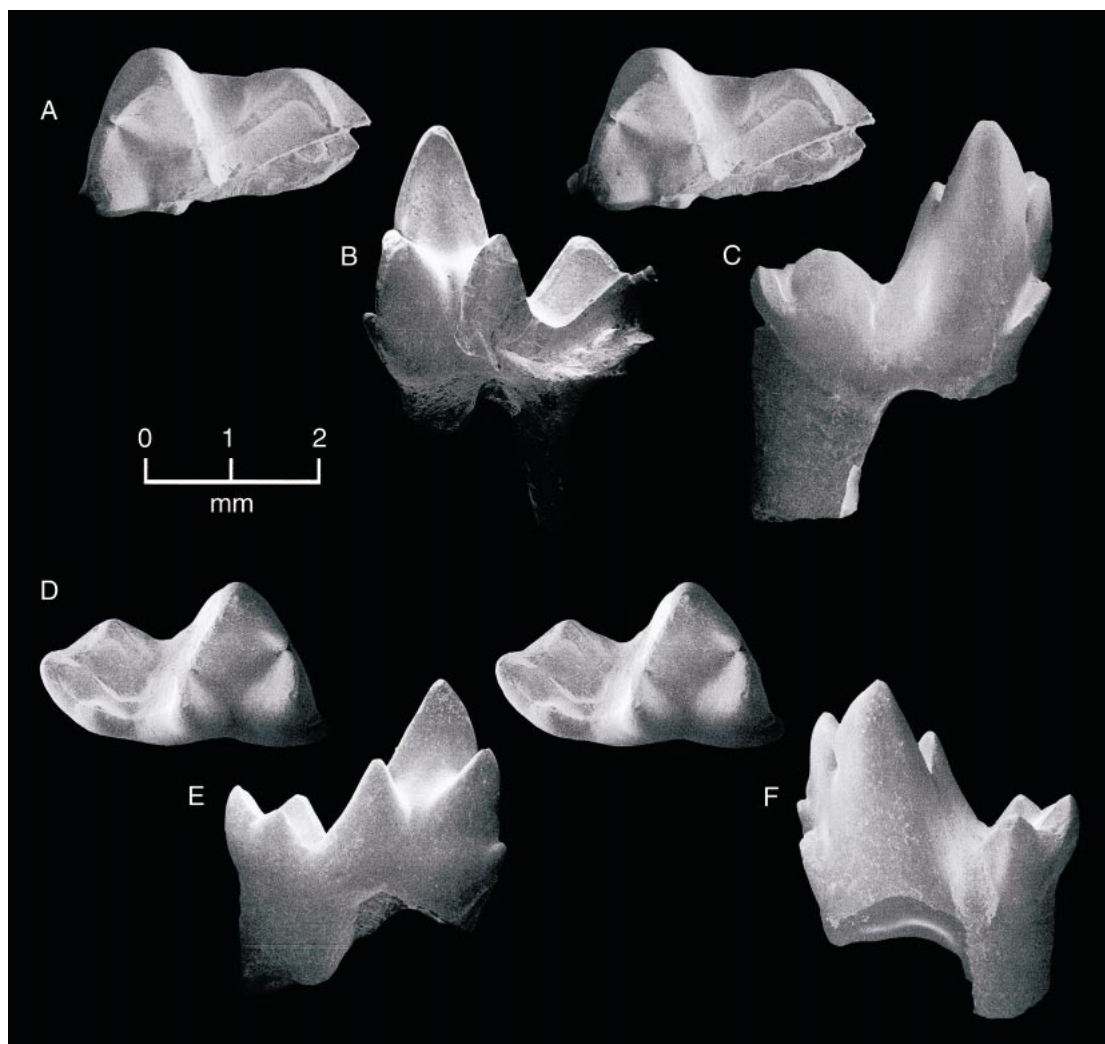


Fig. 5.6. *Pariadens mckennai*. A–C, right m2 or 3 (OMNH 33971); D–F, left m4 (OMNH 33072, holotype). A, D, occlusal view (stereopairs); B, E, lingual view; C, F, labial view.

tion (Albian–Cenomanian); Emery County, Utah.

DIAGNOSIS: Differs from *Pariadens kirklandi* in having lower molars with relatively narrower talonids (particularly m4) and greater height differential between trigonid and talonid; stronger precingulid; stronger paraconid keel, variably including a basal cuspule; entoconid not as strongly developed and less strongly joined to hypoconulid; m4 not elongate relative to preceding molars.

DESCRIPTION: *Pariadens mckennai* is considerably larger than other marsupials of the

Mussentuchit local fauna, being comparable in size to Judithian *Turgidodon praesagus* (see Fox, 1979a). Except for the differences noted in the diagnosis, lower molars of *P. mckennai* compare favorably with those of *P. kirklandi* (the only other species of the genus), from the somewhat younger (late Cenomanian) Dakota Formation, Utah (Cifelli and Eaton, 1987; Eaton, 1993). The paraconid and metaconid are subequal in height on m1, at least, and probably on m2 or 3, whereas the paraconid is somewhat the taller of the two on m4 (fig. 5.6E). This is comparable to

TABLE 5.3
Dental Measurements of *Pariadens mckennai*

| ID | Tooth | AP | ANW | POW |
|------------|---------|-------------------|-------------------|------|
| OMNH 33076 | m1 | 2.65 ^a | 1.58 ^a | 1.64 |
| OMNH 33971 | m2 or 3 | 3.31 ^a | 1.65 | 1.34 |
| OMNH 33072 | m4 | 3.19 | 1.82 | 1.42 |

^aEstimated measurement.

the variation seen in *P. kirklandi*, and consistent with the pattern seen in other mammals having paraconid–metaconid proportions that vary through the molar series (e.g., *Eodelphis*, see Matthew, 1916; *Didelphodon*, see Clemens, 1966; *Kielantherium*, see Dashzeveg and Kielan-Jaworowska, 1984: fig. 1B, D). The anterolingual face of the paraconid is strongly keeled, as is typical of the Late Cretaceous stagodontids *Eodelphis* and *Didelphodon* (Clemens, 1966; Fox, 1981). On one specimen, OMNH 33072, a basal cusplule is present on the paraconid keel. This cusplule is separate from the precingulid, so that the two structures resemble cusps e and f, respectively, as seen in various early mammals, including basal Boreosphenida (Kielan-Jaworowska and Cifelli, 2001; Luo et al., 2002). On other specimens (e.g., OMNH 33971), the anterolingual cusplule is absent and the precingulid is more labiolingually developed. On all specimens, the cristid obliqua meets the trigonid below the notch in the protocristid, not behind the protoconid, as in *Eodelphis* and *Didelphodon*. The labial postcingulid is well developed, though obscure on one specimen owing to wear (OMNH 33072).

DISCUSSION

By comparison to “tribotheres” (such as *Holoclemensia*, *Pappotherium*), early eutherians (e.g., *Prokennalestes*, see Kielan-Jaworowska and Dashzeveg, 1989; *Murtoilestes*, see Averianov and Skutschas, 2000, and Averianov and Skutschas, 2001; *Otlestes*, see Nesson, 1985, and Nesson et al., 1994; *Montanalestes*, see Cifelli, 1999b), and deltatheroidans (Kielan-Jaworowska and Nesson, 1990; Marshall and Kielan-Jaworowska, 1992; Rougier et al., 1998; Kielan-Jaworowska and Cifelli, 2001), *Adelodelphys*, *Sin-*

badelphys, and *Pariadens* share a number of dental apomorphies with Marsupialia: upper molars with more anteroposteriorly developed protocone, stronger conules and internal conule cristae, reduced height differential between paracone and metacone; lower molars with lingually placed paraconid and hypoconulid, labial postcingulid, reduced height differential between trigonid and talonid, relatively broader talonid (Clemens, 1979; Clemens and Lillegraven, 1986; Cifelli, 1993b; Eaton, 1993). Within Marsupialia, however, the taxa from the Cedar Mountain Formation are generally plesiomorphic. States for several of the foregoing characters (particularly relative development and proportions of cusps) must be regarded as incipient, by comparison to well known Late Cretaceous genera such as *Alphadon*. Similarly, other apomorphies shared by most or all Late Cretaceous marsupials are lacking; e.g., consistent presence of styler cusps in the C or D positions (Clemens, 1979; Fox, 1987b; Marshall et al., 1990; Cifelli, 1990b; Cifelli and Muizon, 1997), and labial placement of conules, near the respective bases of paracone and metacone (Cifelli, 1993b; Rougier et al., 1998). The three genera from the Cedar Mountain Formation are generally similar in molar morphology; only in *Pariadens* is there a hint of specializations seen among Late Cretaceous marsupials of North America. When first described from the Dakota Formation, *Pariadens* was tentatively referred to Stagodontidae, on the basis of several features of the lower dentition (Cifelli and Eaton, 1987; see discussion by Eaton, 1993). Fossils from the Cedar Mountain Formation show only the suggestion of stagodontid affinities for *Pariadens*: large size, incipient tendency toward enlargement of the paraconid, and (perhaps) incipient tendency toward hypertrophy of the paraconid keel and precingulid on lower molars.

Marsupials appear to have been established in North America by the beginning of the Late Cretaceous. Where did they come from, and can antecedents be recognized in older faunas? Mammals of Aptian–Albian age (about 10–15 Ma older than those of the upper Cedar Mountain Formation) are known from several units in North America (Jenkins and Crompton, 1979; Jenkins and

Schaff, 1988; Winkler et al., 1990; Cifelli et al., 1998, 1999a; Cifelli, 1999b). To date, only the Trinity Group, Texas and Oklahoma, has yielded an appreciable diversity of taxa with tribosphenic molars (Patterson, 1956; Slaughter, 1971; Butler, 1978; Jacobs et al., 1989; Cifelli, 1997; Kielan-Jaworowska and Cifelli, 2001). Of these, *Holoclemensia* was originally posited as a marsupial on the basis of molar characteristics (Slaughter, 1968, 1971; see also Fox, 1971b, 1975). Subsequent comparisons have failed to confirm some purported similarities (e.g., “twinning” of hypoconulid with entoconid, paracone–metacone proportions) of *Holoclemensia* to marsupials, and suggest that others (e.g., presence of stylar cusp C) are probably homoplasies (Jacobs et al., 1989; Cifelli, 1990a; see also Turnbull, 1971; Butler, 1978; Eaton, 1993; Cifelli, 1999b). Hershkovitz (1995: 163) described *Adinodon pattersoni* as a marsupial (“family Marmosidae”) from the Trinity Group, based on an edentulous dentary fragment with 13 alveoli, interpreted as representing four incisors, the canine, three premolars, and one molar (the specimen was first reported by Patterson, 1956, who identified the last eight alveoli as representing four premolars). The basis for referral to Marsupialia, a “staggering” of the incisor series (a condition that is, in any case, lacking in early marsupials), cannot be confirmed, and *Adinodon* is best regarded as a nomen dubium (Cifelli and Muizon, 1997).

Summing up, none of the tribosphenic mammals now known from the Trinity Group has unambiguous marsupial apomorphies. Beyond the Albian–Cenomanian boundary, the antiquity of marsupials in North America remains speculative. Given the poor fossil record for North America and the fact that only the Trinity Group has yielded a reasonably diverse mammal fauna of Early Cretaceous age, it is entirely possible that marsupials were present on the continent during the Aptian–Albian, and await discovery. Bearing in mind that most fossils of this age consist of isolated teeth, it is also possible that dental criteria alone are insufficient to adequately judge the affinities of known taxa. The origin of North America’s Late Cretaceous marsupial radiation via a late Early Cretaceous immigration event is also con-

ceivable, but currently within the realm of conjecture. At least two³ possible marsupials have been described from the Late Cretaceous of Asia: *Asiatherium*, from the Maastichtian of Mongolia (Trofimov and Szalay, 1994; Szalay and Trofimov, 1996); and *Marsasia*, from the Coniacian of Uzbekistan (Nessov, 1997; Averianov and Kielan-Jaworowska, 1999). Affinities of these taxa remain uncertain (note Fox, 1997b; McKenna and Bell, 1997); hence their biogeographic implications are equally uncertain. The balance of existing evidence is equivocal, though origin of the Asiatic taxa from within the North American radiation is a viable hypothesis (Cifelli, 2000).

It is noteworthy that marsupials are neither diverse nor abundant elements of the Mussentuchit local fauna. If *Kokopellia juddi* is included (Cifelli and Muizon, 1997; McKenna and Bell, 1997; see phylogeny of Rougier et al., 1998), Marsupialia are represented by only four species, collectively known from 57 specimens—about 4% of the total number of cataloged mammal specimens from the Mussentuchit Member of the Cedar Mountain Formation. Collecting bias is unlikely, given the extent and diversity of sampling. It is therefore reasonable to conclude that marsupials were rare, at least locally, both in terms of number of species and numbers of individuals belonging to those species.

The marsupial component of the Mussentuchit local fauna is depauperate by comparison to assemblages from the Late Cretaceous of North America (Clemens, 1979; Archibald, 1982; Fox, 1997b; see table 5.4). In the Mussentuchit local fauna, marsupials constitute only 17% (four of 24 species) of the mammalian fauna, with a diversity less than half (44%) that of Multituberculata. By contrast, all reasonably well-sampled Late Cretaceous mammalian faunas (for present purposes, those having 15 or more species) of North America include at least six marsupials, comprising more than 30% of the fauna; and marsupial diversity equals or exceeds that of multituberculates. The Mussen-

³ A third, represented by the unnamed “Gurlin Tsav skull” (Kielan-Jaworowska and Nessov, 1990; Szalay and Trofimov, 1996), is implicitly placed within Marsupialia by the phylogeny of Rougier et al. (1998).

TABLE 5.4
Marsupial Component of Mammalian Diversity in the Late Cretaceous of North America^a

| % marsupial diversity: | Mussentuchit (Albian-Cenomanian) | Dakota (late Cenomanian) | Aquilan (Santonian-Campanian) | Judithian (Campanian) | Lancian (late Maastrichtian) |
|------------------------------|-------------------------------------|-----------------------------|----------------------------------|--------------------------|---------------------------------|
| All mammals | 17 | 38 | 36 | 44 | 41 |
| Tribosphenic mammals | 50 | 67 | 63 | 70 | 55 |
| Non-multituberculata mammals | 27 | 60 | 55 | 70 | 55 |
| Multituberculata | 44 | 100 | 100 | 117 | 120 |
| Number of mammal taxa | 24 | 16 | 28 | 16 | 29 |

^aTaxa treated at the species level; those not positively identified to species were included only if they are thought to be distinct from named elements of the same fauna. One local fauna (single locality or tightly grouped set of localities) for each age was chosen for comparison, based on extensiveness of sampling and availability of published data. Faunas and sources: Mussentuchit local fauna: Cifelli (1999a), Cifelli and Madsen (1998, 1999), Cifelli and Muizon (1997), Cifelli et al. (1999b). Dakota: Eaton (1993, 1995), Eaton et al. (1999). Aquilan, Verdigris Coulee local fauna: Fox (1971a, 1971b, 1976, 1980, 1982, 1984, 1985, 1987a). Judithian, Hill County local fauna: Montellano (1992). Lancian, type Lance Formation: Clemens (1963, 1966, 1973), Fox (1974), Krause (1992), Johanson (1996b).

tuchit local fauna clearly is transitional in some respects: it differs from those of Aptian–Albian (and older) age in the presence of many taxa otherwise known from the Late Cretaceous onward, yet also includes archaic elements rare or absent in younger assemblages (Cifelli et al., 1997). Among mammals, for example, the Mussentuchit local fauna includes at least four species of spalacotheriid “symmetrodonts” (Cifelli and Madsen, 1999) and three of triconodontids (Cifelli and Madsen, 1998). Both of these groups persisted until the Aquilan (Fox, 1969, 1972, 1976; Cifelli and Gordon, 1999), though as minor elements of the mammalian fauna. It is probable that these taxa, as well as early marsupials, were mainly faunivorous, with large species incorporating vertebrate as well as invertebrate prey into their diets (e.g., Simpson, 1933; Lillegraven et al., 1979). Ecological replacement (either passive or competitive) of spalacotheriids and triconodontids by marsupials may account, at least in part, for differences in mammalian composition between the Mussentuchit local fauna and Late Cretaceous assemblages.

Issues surrounding the initial radiation of marsupials in North America—its origin (biogeographic and phylogenetic), timing, and dynamics—cannot be adequately addressed on the basis of the existing fossil record. With the limitations of the fossil record

in mind, however, several observations bear further rumination. (1) The Mussentuchit local fauna, dated at about 98.5 Ma, includes the oldest known marsupials. (2) The marsupials of this fauna are morphologically similar and are characterized mainly by plesiomorphies with respect to geologically younger taxa. (3) Four marsupial species are recognized in the Mussentuchit local fauna; each of the species is rare. Density and diversity of sampling, together with representation of other elements of the fauna, suggest that the record for this assemblage reflects original abundance and diversity of marsupials relative to other mammals. (4) Abundance, morphologic diversity, and taxonomic diversity of marsupials in the Mussentuchit local fauna contrasts sharply with what is seen in Late Cretaceous assemblages of North America, where marsupials are conspicuous and dominant elements. (5) The mammalian fauna of the Dakota Formation, Utah, is of late Cenomanian age, 3–5 Ma younger than that of the upper Cedar Mountain Formation. Marsupials of the Dakota Formation (see Eaton, 1993) are relatively more abundant and are morphologically and taxonomically more diverse than those of the upper Cedar Mountain Formation: composition of the Dakota fauna, at least in terms of marsupials, resembles that of other Late Cretaceous assemblages from North America.

These observations suggest the working hypothesis that the Mussentuchit local fauna includes the basal radiations of marsupials in North America, whatever the timing and place of origin for the cohort Marsupialia.

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REFERENCES

- Aplin, K.P., and M. Archer. 1987. Recent advances in marsupial systematics with a syncretic classification. In M. Archer (editor), *Possums and possums: studies in evolution*: xv–lxxii. Sydney: Surrey Beatty and the Royal Zoological Society of New South Wales.
- Archer, M. 1984. The Australian marsupial radiation. In M. Archer and G. Clayton (editors), *Vertebrate zoogeography and evolution in Australasia*: 633–808. Carlisle: Hesperian Press.
- Archer, M., T.F. Flannery, A. Ritchie, and R. Molnar. 1985. First Mesozoic mammal from Australia—an Early Cretaceous monotreme. *Nature* 318: 363–366.
- Archibald, J.D. 1982. A study of Mammalia and geology across the Cretaceous–Tertiary boundary in Garfield County, Montana. University of California Publications in Geological Sciences 122: 1–286.
- Archibald, J.D., and A.O. Averianov. 2001. *Paranyctoides* and allies from the Late Cretaceous of North America and Asia. *Acta Palaeontologica Polonica* 46: 533–551.
- Averianov, A.O., and Z. Kielan-Jaworowska. 1999. Marsupials from the Late Cretaceous of Uzbekistan. *Acta Palaeontologica Polonica* 44: 71–81.
- Averianov, A.O., and P.P. Skutschas. 2000. Eutherian mammal from the Early Cretaceous of Russia and biostratigraphy of the Asian Early Cretaceous vertebrate assemblages. *Lethaia* 33: 330–340.
- Averianov, A.O., and P.P. Skutschas. 2001. A new genus of eutherian mammal from the Early Cretaceous of Transbaikalia, Russia. *Acta Palaeontologica Polonica* 46: 431–436.
- Butler, P.M. 1978. A new interpretation of the mammalian teeth of tribosphenic pattern from the Albian of Texas. *Breviora* 446: 1–27.
- Butler, P.M. 1990. Early trends in the evolution of tribosphenic molars. *Biological Reviews* 65: 529–552.
- Cifelli, R.L. 1990a. Cretaceous mammals of southern Utah. I. Marsupial mammals from the Kaiparowits Formation (Judithian). *Journal of Vertebrate Paleontology* 10: 295–319.
- Cifelli, R.L. 1990b. Cretaceous mammals of southern Utah. II. Marsupials and marsupial-like mammals from the Wahweap Formation (early Campanian). *Journal of Vertebrate Paleontology* 10: 320–331.
- Cifelli, R.L. 1993a. Early Cretaceous mammal from North America and the evolution of marsupial dental characters. *Proceedings of the National Academy of Sciences USA* 90: 9413–9416.
- Cifelli, R.L. 1993b. Theria of metatherian-eutherian grade and the origin of marsupials. In E.S. Szalay, M.J. Novacek, and M.C. McKenna (editors), *Mammal phylogeny: Mesozoic differentiation, multituberculates, monotremes, early therians, and marsupials*: 205–215. New York: Springer-Verlag.
- Cifelli, R.L. 1994. Therian mammals of the Terlingua local fauna (Judithian), Aguja Formation, Big Bend of the Río Grande, Texas. *Contributions to Geology, University of Wyoming* 30: 117–136.
- Cifelli, R.L. 1997. First notice on Mesozoic mammals from Oklahoma. *Oklahoma Geology Notes, Oklahoma Geological Survey* 57: 4–17.
- Cifelli, R.L. 1999a. Therian teeth of unusual design from the medial Cretaceous (Albian–Cenomanian) Cedar Mountain Formation, Utah. *Journal of Mammalian Evolution* 6: 247–270.
- Cifelli, R.L. 1999b. Tribosphenic mammal from the North American Early Cretaceous. *Nature* 401: 363–366.
- Cifelli, R.L. 2000. Cretaceous mammals of Asia and North America. *Journal of the Paleontological Society of Korea, Special Publication* 4: 49–85.

- Cifelli, R.L., and J.G. Eaton. 1987. Marsupial from the earliest Late Cretaceous of western US. *Nature* 325: 520–522.
- Cifelli, R.L., J.J. Eberle, D.L. Lofgren, J.A. Lillegraven, and W.A. Clemens. In press. Mammalian biochronology of the latest Cretaceous. In M.O. Woodburne (editor), *Late Cretaceous and Cenozoic mammals of North America: biostratigraphy and geochronology*. New York: Columbia University Press.
- Cifelli, R.L., and C.L. Gordon. 1999. Symmetrodonts from the Late Cretaceous of southern Utah and distribution of archaic mammals in the Cretaceous of North America. *Geology Studies*, Brigham Young University 44: 1–16.
- Cifelli, R.L., J.I. Kirkland, A. Weil, A.L. Deino, and B.J. Kowallis. 1997. High-precision $^{40}\text{Ar}/^{39}\text{Ar}$ geochronology and the advent of North America's Late Cretaceous terrestrial fauna. *Proceedings of the National Academy of Sciences USA* 94: 11163–11167.
- Cifelli, R.L., T.R. Lipka, C.R. Schaff, and T.B. Rowe. 1999a. First Early Cretaceous mammal from the eastern seaboard of the United States. *Journal of Vertebrate Paleontology* 19: 199–203.
- Cifelli, R.L., and S.K. Madsen. 1998. Triconodont mammals from the medial Cretaceous of Utah. *Journal of Vertebrate Paleontology* 18: 403–411.
- Cifelli, R.L., and S.K. Madsen. 1999. Spalacotheriid symmetrodonts (Mammalia) from the medial Cretaceous (upper Albian or lower Cenomanian) Mussentuchit local fauna, Cedar Mountain Formation, Utah, USA. *Geodiversitas* 21: 167–214.
- Cifelli, R.L., S.K. Madsen, and E.M. Larson. 1996a. Screenwashing and associated techniques for the recovery of microvertebrate fossils. *Oklahoma Geological Survey Special Publication* 96–4: 1–24.
- Cifelli, R.L., and C. de Muizon. 1997. Dentition and jaw of *Kokopellia juddi*, a primitive marsupial or near marsupial from the medial Cretaceous of Utah. *Journal of Mammalian Evolution* 4: 241–258.
- Cifelli, R.L., R.L. Nydam, A. Weil, J.D. Gardner, J.I. Kirkland, J.G. Eaton, and S.K. Madsen. 1999b. Vertebrate fauna of the upper Cedar Mountain Formation (Cretaceous; Albian–Cenomanian), Emery County: the Mussentuchit local fauna. In D.D. Gillette (editor), *Vertebrate paleontology in Utah*: 219–242. Salt Lake City: Utah Geological Survey, Miscellaneous Publication 99–1.
- Cifelli, R.L., T.B. Rowe, W.P. Luckett, J. Banta, R. Reyes, and R.I. Howes. 1996b. Origin of marsupial pattern of tooth replacement: fossil evidence revealed by high resolution X-ray CT. *Nature* 379: 715–718.
- Cifelli, R.L., J.R. Wible, and F.A. Jenkins, Jr. 1998. Triconodont mammals from the Cloverly Formation (Lower Cretaceous), Montana and Wyoming. *Journal of Vertebrate Paleontology* 18: 237–241.
- Clemens, W.A. 1963. Fossil mammals of the type Lance Formation, Wyoming. Part I. Introduction and Multituberculata. *University of California Publications in Geological Sciences* 48: 1–105.
- Clemens, W.A. 1966. Fossil mammals from the type Lance Formation, Wyoming. Part II. *Marsupialia*. *University of California Publications in Geological Sciences* 62: 1–122.
- Clemens, W.A. 1973. Fossil mammals of the type Lance Formation, Wyoming. Part III. Eutheria and summary. *University of California Publications in Geological Sciences* 94: 1–102.
- Clemens, W.A. 1979. *Marsupialia*. In J.A. Lillegraven, Z. Kielan-Jaworowska, and W.A. Clemens (editors), *Mesozoic mammals: the first two-thirds of mammalian history*: 192–220. Berkeley: University of California Press.
- Clemens, W.A., and J.A. Lillegraven. 1986. New Late Cretaceous, North American advanced therian mammals that fit neither the marsupial nor eutherian molds. *Contributions to Geology*, University of Wyoming, Special Paper 3: 55–85.
- Cope, E.D. 1892. On a new genus of Mammalia from the Laramie Formation. *American Naturalist* 26: 758–762.
- Crochet, J.-Y. 1979. Diversité systématique des Didelphidae (Marsupialia) européens tertiaires. *Géobios* 11: 365–378.
- Crochet, J.-Y. 1980. Les Marsupiaux du Tertiaire d'Europe. Paris: Éditions de la Fondation Singer-Polignac.
- Dashzeveg, D., and Z. Kielan-Jaworowska. 1984. The lower jaw of an aegialodontid mammal from the Early Cretaceous of Mongolia. *Zoological Journal of the Linnean Society* 82: 217–227.
- Eaton, J.G. 1990. Stratigraphic revision of Campanian (Upper Cretaceous) rocks in the Henry Basin, Utah. *Mountain Geologist* 27: 27–38.
- Eaton, J.G. 1993. Therian mammals from the Cenomanian (Upper Cretaceous) Dakota Formation, southwestern Utah. *Journal of Vertebrate Paleontology* 13: 105–124.
- Eaton, J.G. 1995. Cenomanian and Turonian (early Late Cretaceous) multituberculate mammals from southwestern Utah. *Journal of Vertebrate Paleontology* 15: 761–784.
- Eaton, J.G., and R.L. Cifelli. 2001. Multituberculate mammals from near the Early–Late Cre-

- taceous boundary, Cedar Mountain Formation, Utah. *Acta Palaeontologica Polonica* 46: 453–518.
- Eaton, J.G., R.L. Cifelli, J.H. Hutchison, J.I. Kirkland, and J.M. Parrish. 1999. Cretaceous vertebrate faunas from the Kaiparowits Plateau. In D.D. Gillette (editor), *Vertebrate paleontology in Utah: 345–354*. Salt Lake City: Utah Geological Survey, Miscellaneous Publication 99–1.
- Eaton, J.G., H. Munk, and M.A. Hardman. 1998. A new vertebrate fossil locality within the Wahweap Formation (Upper Cretaceous) of Bryce Canyon National Park and its bearing on the presence of the Kaiparowits Formation on the Paunsaugunt Plateau. Technical Reports, National Park Service 98/1: 36–40.
- Fox, R.C. 1969. Studies of Late Cretaceous vertebrates. III. A triconodont mammal from Alberta. *Canadian Journal of Zoology* 47: 1253–1256.
- Fox, R.C. 1971a. Early Campanian multituberculates (Mammalia: Allotheria) from the upper Milk River Formation, Alberta. *Canadian Journal of Earth Sciences* 8: 916–938.
- Fox, R.C. 1971b. Marsupial mammals from the early Campanian Milk River Formation, Alberta, Canada. In D.M. Kermack and K.A. Kermack (editors), *Early mammals*. *Zoological Journal of the Linnean Society* 50, supplement 1: 145–164.
- Fox, R.C. 1972. An Upper Cretaceous symmetrodont from Alberta, Canada. *Nature* 239: 170–171.
- Fox, R.C. 1974. *Deltatheroides*-like mammals from the Upper Cretaceous of North America. *Nature* 249: 392.
- Fox, R.C. 1975. Molar structure and function in the Early Cretaceous mammal *Pappotherium*: evolutionary implications for Mesozoic Theria. *Canadian Journal of Earth Sciences* 12: 412–442.
- Fox, R.C. 1976. Additions to the mammalian local fauna from the upper Milk River Formation (Upper Cretaceous), Alberta. *Canadian Journal of Earth Sciences* 13: 1105–1118.
- Fox, R.C. 1979a. Mammals from the Upper Cretaceous Oldman Formation, Alberta. I. *Alphadon* Simpson (Marsupialia). *Canadian Journal of Earth Sciences* 16: 91–102.
- Fox, R.C. 1979b. Mammals from the Upper Cretaceous Oldman Formation, Alberta. II. *Pedionomys* Marsh (Marsupialia). *Canadian Journal of Earth Sciences* 16: 103–113.
- Fox, R.C. 1980. *Picopsis pattersoni*, n. gen. and sp., an unusual therian from the Upper Cretaceous of Alberta, and the classification of primitive tribosphenic mammals. *Canadian Journal of Earth Sciences* 17: 1489–1498.
- Fox, R.C. 1981. Mammals from the Upper Cretaceous Oldman Formation, Alberta. V. *Eodelphis* Matthew, and the evolution of the Stagodontidae. *Canadian Journal of Earth Sciences* 18: 350–365.
- Fox, R.C. 1982. Evidence of new lineage of tribosphenic therians (Mammalia) from the Upper Cretaceous of Alberta, Canada. *Géobios, Mémoire Spécial* 6: 169–175.
- Fox, R.C. 1984. *Paranyctoides maleficus* (new species), an early eutherian mammal from the Cretaceous of Alberta. *Special Publication, Carnegie Museum of Natural History* 9: 9–20.
- Fox, R.C. 1985. Upper molar structure in the Late Cretaceous symmetrodont *Symmetrodontoides* Fox, and a classification of the Symmetrodonta. *Journal of Paleontology* 59: 21–26.
- Fox, R.C. 1987a. An ancestral marsupial and its implications for early marsupial evolution. In P.J. Currie and E.H. Koster (editors), *Fourth Symposium on Mesozoic Terrestrial Ecosystems: 101–105*. Drumheller: Tyrrell Museum.
- Fox, R.C. 1987b. Palaeontology and the early evolution of marsupials. In M. Archer (editor), *Possums and opossums: studies in evolution: 161–169*. Sydney: Surrey Beatty and the Royal Zoological Society of New South Wales.
- Fox, R.C. 1997a. Evolution of Cretaceous and Palaeocene mammals in western Canada. *Alberta* 1: 184–201.
- Fox, R.C. 1997b. Upper Cretaceous and Tertiary stratigraphy and paleontology of southern Saskatchewan. In L. McKenzie-McAnally (editor), *Canadian paleontology conference, field trip guidebook No. 6: 70–85*. St. Johns: Geological Association of Canada.
- Goldberg, P. 2000. Faunal composition, non-marine vertebrates, of the upper Cedar Mountain Formation (Cretaceous: Albian–Cenomanian), central Utah, 243 pp. Ph.D. dissertation, University of Oklahoma, Norman.
- Gradstein, F.M., F.P. Agterberg, J.G. Ogg, J. Hardenbol, P. Van Veen, J. Thierry, and Z. Huang. 1995. A Triassic, Jurassic and Cretaceous time scale. In W.A. Berggren, D.V. Kent, M.-P. Aubrey, and J. Hardenbol (editors), *Geochronology, time scales and global stratigraphic correlation: 95–126*. Tulsa: SEPM (Society for Sedimentary Geology) Special Publication 54.
- Hershkovitz, P. 1995. The staggered marsupial third lower incisor: hallmark of cohort Didelphimorphia, and description of a new genus and species with staggered i3 from the Albian (Lower Cretaceous) of Texas. *Bonner Zoologische Beiträge* 45: 153–169.
- Huxley, T.H. 1880. On the application of the laws

- of evolution to the arrangement of the Vertebrata and more particularly of the Mammalia. Proceedings of the Zoological Society of London 43: 649–662.
- Illiger, C. 1811. *Prodromus systematis mammalium et avium additis terminis zoographicis utriusque classis*. Berlin: C. Salfeld.
- Jacobs, L.L., and D.A. Winkler. 1998. Mammals, archosaurs, and the Early to Late Cretaceous transition in north-central Texas. In Y. Tomida, L.J. Flynn, and L.L. Jacobs (editors), *Advances in vertebrate paleontology and geochronology*. National Science Museum Monographs 14: 253–280.
- Jacobs, L.L., D.A. Winkler, and P.A. Murry. 1989. Modern mammal origins: evolutionary grades in the Early Cretaceous of North America. Proceedings of the National Academy of Sciences USA 86: 4992–4995.
- Jenkins, F.A., Jr., and A.W. Crompton. 1979. Triconodonta. In J.A. Lillegraven, Z. Kielan-Jaworowska, and W.A. Clemens (editors), *Mesozoic mammals: the first two-thirds of mammalian history*: 74–90. Berkeley: University of California Press.
- Jenkins, F.A., Jr., and C.R. Schaff. 1988. The Early Cretaceous mammal *Gobiconodon* (Mammalia, Triconodonta) from the Cloverly Formation in Montana. *Journal of Vertebrate Paleontology* 8: 1–24.
- Johanson, Z. 1996a. New marsupial from the Fort Union Formation, Swain Quarry, Wyoming. *Journal of Paleontology* 70: 1023–1031.
- Johanson, Z. 1996b. Revision of the Late Cretaceous North American marsupial genus *Alphadon*. *Palaeontographica Abteilung A* 242: 127–184.
- Kielan-Jaworowska, Z., and R.L. Cifelli. 2001. Primitive boreosphenidan mammal (?Deltatheroidea) from the Early Cretaceous of Oklahoma. *Acta Palaeontologica Polonica* 46: 377–391.
- Kielan-Jaworowska, Z., and D. Dashzeveg. 1989. Eutherian mammals from the Early Cretaceous of Mongolia. *Zoologica Scripta* 18: 347–355.
- Kielan-Jaworowska, Z., J.G. Eaton, and T.M. Bown. 1979. Theria of metatherian-eutherian grade. In J.A. Lillegraven, Z. Kielan-Jaworowska, and W.A. Clemens (editors), *Mesozoic mammals: the first two-thirds of mammalian history*: 182–191. Berkeley: University of California Press.
- Kielan-Jaworowska, Z., and L.A. Nessov. 1990. On the metatherian nature of the Deltatheroidea, a sister group of the Marsupialia. *Lethaia* 23: 1–10.
- Kirkland, J.I., B. Britt, D.L. Burge, K.C. Carpenter, R.L. Cifelli, F. DeCourten, S. Hasiotis, and T. Lawton. 1997. Lower to middle Cretaceous dinosaur faunas of the central Colorado Plateau: a key to understanding 35 million years of tectonics, sedimentology, evolution and biogeography. *Brigham Young University Geology Studies* 42: 69–103.
- Kirkland, J.I., R.L. Cifelli, B.B. Britt, D.L. Burge, F.L. DeCourten, J.G. Eaton, and J.M. Parrish. 1999. Distribution of vertebrate faunas in the Cedar Mountain Formation, east-central Utah. In D.D. Gillette (editor), *Vertebrate paleontology in Utah*: 201–218. Salt Lake City: Utah Geological Survey, Miscellaneous Publication 99–1.
- Krause, D.W. 1992. *Clemensodon megaloba*, a new genus and species of Multituberculata (Mammalia) from the Upper Cretaceous Type Lance Formation, Powder River Basin, Wyoming. *PaleoBios* 14: 1–8.
- Krishtalka, L., and R.K. Stucky. 1983. Paleocene and Eocene marsupials of North America. *Annals of the Carnegie Museum* 52: 229–263.
- Lillegraven, J.A. 1969. Latest Cretaceous mammals of upper part of Edmonton Formation of Alberta, Canada, and review of marsupial-placental dichotomy in mammalian evolution. *University of Kansas Paleontological Contributions* 50: 1–122.
- Lillegraven, J.A., Z. Kielan-Jaworowska, and W.A. Clemens (editors). 1979. *Mesozoic mammals: the first two-thirds of mammalian history*. Berkeley: University of California Press.
- Lillegraven, J.A., and M.C. McKenna. 1986. Fossil mammals from the “Mesaverde” Formation (Late Cretaceous, Judithian) of the Bighorn and Wind River basins, Wyoming, with definitions of Late Cretaceous North American land-mammal “ages”. *American Museum Novitates* 2840: 1–68.
- Luo, Z.-X., Z. Kielan-Jaworowska, and R.L. Cifelli. 2002. In quest for a phylogeny of Mesozoic mammals. *Acta Palaeontologica Polonica* 47: 1–78.
- MacLarnon, A.M. 1989. Applications of the Reflex instruments in quantitative morphology. *Folia Primatologica* 53: 33–49.
- Marsh, O.C. 1889a. Discovery of Cretaceous Mammalia. *American Journal of Science* 38: 81–92.
- Marsh, O.C. 1889b. Discovery of Cretaceous Mammalia. Part II. *American Journal of Science* 38: 177–180.
- Marshall, L.G., J.A. Case, and M.O. Woodburne. 1990. Phylogenetic relationships of the families of marsupials. *Current Mammalogy* 2: 433–502.
- Marshall, L.G., and Z. Kielan-Jaworowska. 1992. Relationships of the dog-like marsupials, del-

- tatheroidans and early tribosphenic mammals. *Lethaia* 25: 361–374.
- Matthew, W.D. 1916. A marsupial of the Belly River Cretaceous. *Bulletin of the American Museum of Natural History* 35: 477–500.
- McKenna, M.C., and S.K. Bell. 1997. *Classification of mammals above the species level*. New York: Columbia University Press.
- Montellano, M. 1992. Mammalian fauna of the Judith River Formation (Late Cretaceous, Judithian), northcentral Montana. *University of California Publications in Geological Sciences* 136: 1–115.
- Muizon, C. de, and R.L. Cifelli. 2001. A new basal “didelphoid” (Marsupialia, Mammalia) from the early Paleocene of Tiupampa (Bolivia). *Journal of Vertebrate Paleontology* 21: 87–97.
- Muizon, C. de, R.L. Cifelli, and R. Céspedes. 1997. The origin of dog-like marsupials and the early evolution of Gondwanian marsupials. *Nature* 389: 486–489.
- Nessov, L.A. 1985. New mammals from the Cretaceous of Kyzylkum. *Vestnik Leningradskogo Universiteta* 17: 8–18. [In Russian]
- Nessov, L.A. 1997. Cretaceous non-marine vertebrates of northern Eurasia. Sankt Petersburg: University of Sankt Petersburg, Institute of Earth Crust. [In Russian]
- Nessov, L.A., D. Sigogneau-Russell, and D.E. Russell. 1994. A survey of Cretaceous tribosphenic mammals from middle Asia (Uzbekistan, Kazakhstan and Tajikistan), of their geological setting, age and faunal environment. *Palaeovertebrata* 23: 51–92.
- Obradovich, J. 1993. A Cretaceous time scale. In W.G.E. Caldwell and E.G. Kauffman (editors), *Evolution of the Western Interior Basin*. Geological Association of Canada, Special Paper 39: 379–396.
- Patterson, B. 1956. Early Cretaceous mammals and the evolution of mammalian molar teeth. *Fieldiana: Geology* 13: 1–105.
- Reig, O.A., J.A.W. Kirsch, and L.G. Marshall. 1987. Systematic relationships of the living and neocenozoic American “opossum-like” marsupials (suborder Didelphimorphia), with comments on the classification of these and of the Cretaceous and Paleogene New World and European metatherians. In M. Archer (editor), *Possums and opossums: studies in evolution*: 1–89. Sydney: Surrey Beatty and the Royal Zoological Society of New South Wales.
- Rougier, G.W., J.R. Wible, and M.J. Novacek. 1998. Implications of *Deltatheridium* specimens for early marsupial history. *Nature* 396: 459–463.
- Sahni, A. 1972. The vertebrate fauna of the Judith River Formation, Montana. *Bulletin of the American Museum of Natural History* 147: 321–412.
- Simpson, G.G. 1927. Mesozoic Mammalia. VIII. Genera of Lance mammals other than multituberculates. *American Journal of Science* 14: 121–130.
- Simpson, G.G. 1929. American Mesozoic Mammalia. *Memoirs of the Peabody Museum of Yale University* 3: 1–235.
- Simpson, G.G. 1933. Paleobiology of Jurassic mammals. *Palaeobiologica* 5: 127–158.
- Simpson, G.G. 1945. The principles of classification and a classification of mammals. *Bulletin of the American Museum of Natural History* 85: 1–350.
- Slaughter, B.H. 1968. Earliest known marsupials. *Science* 162: 254–255.
- Slaughter, B.H. 1971. Mid-Cretaceous (Albian) therians of the Butler Farm local fauna, Texas. In D.M. Kermack and K.A. Kermack (editors), *Early mammals*. *Zoological Journal of the Linnean Society* 50, supplement 1: 131–143.
- Szalay, F.S. 1982. A new appraisal of marsupial phylogeny and classification. In M. Archer (editor), *Carnivorous marsupials*: 621–640. Sydney: Royal Zoological Society of New South Wales.
- Szalay, F.S. 1994. *Evolutionary history of the marsupials and an analysis of osteological characters*. Cambridge: Cambridge University Press.
- Szalay, F.S., and B.A. Trofimov. 1996. The Mongolian Late Cretaceous *Asiatherium*, and the early phylogeny and paleobiogeography of Metatheria. *Journal of Vertebrate Paleontology* 16: 474–509.
- Trofimov, B.A., and F.S. Szalay. 1994. New Cretaceous marsupial from Mongolia and the early radiation of the Metatheria. *Proceedings of the National Academy of Sciences USA* 91: 12569–12573.
- Turnbull, W.D. 1971. The Trinity therians: their bearing on evolution in marsupials and other therians. In A.A. Dahlberg (editor), *Dental morphology and evolution*: 151–179. Chicago: University Chicago Press.
- Winkler, D.A., P.A. Murry, and L.L. Jacobs. 1990. Early Cretaceous (Comanchean) vertebrates of central Texas. *Journal of Vertebrate Paleontology* 10: 95–116.
- Woodward, A.S. 1916. On a mammalian mandible from an Upper Cretaceous formation in Alberta, Canada. *Proceedings of the Zoological Society of London* 158: 525–528.