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 schmidti, 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). 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 Lanceland 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).
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 40Ar/39Ar 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 Mussentuchit 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 (talonid 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 screenwashing 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).
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 (floodplain, 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, supra-generics allocations of Cretaceous taxa within Marsupialia are problematic and will likely remain unsatisfactory until the known fossil
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 pleisiomorphic 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 (Krishthaka 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 pleisiomorphic 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.

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 protocrista 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; stylar shelf with weaker, less cuspidate rim; M3 with
TABLE 5.1
Dental Measurements of Adelodelphys muizoni

<table>
<thead>
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*Estimated measurement.

Postmetacrista directed labially (not postero-olabially), 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 linguually 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 Alphodon 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 schmidti, 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 genus 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.

Hyopodium: The type, and OMNH 30582 (M1); 30587 (M1?); 30388 (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.

**Location**: 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 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 cuspate 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, stylcone larger and 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 cuspate), 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.
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, x
TABLE 5.2
Dental Measurements of Sinbadelphys schmidti

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= 0.61, CV = 0.10, N = 4; Sinbadelphys schmidti, range = 0.75–0.98, x = 0.83, CV = 0.08, N= 12; CV of pooled samples = 15.2). Except for the stylocone, stylar cusps are lacking, with only a narrow rim present at the labial margin of the stylar shelf (minor stylar 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 lingually 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 paracone 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 paracoonde 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).

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 paracoonde keel is encountered among some early eutherians such as Paranyctoides (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

<table>
<thead>
<tr>
<th>ID</th>
<th>Tooth</th>
<th>AP</th>
<th>ANW</th>
<th>POW</th>
</tr>
</thead>
<tbody>
<tr>
<td>OMNH 33076</td>
<td>m1</td>
<td>2.65*</td>
<td>1.58*</td>
<td>1.64</td>
</tr>
<tr>
<td>OMNH 33971</td>
<td>m2 or 3</td>
<td>3.31*</td>
<td>1.65</td>
<td>1.34</td>
</tr>
<tr>
<td>OMNH 33072</td>
<td>m4</td>
<td>3.19</td>
<td>1.82</td>
<td>1.42</td>
</tr>
</tbody>
</table>

*Estimated 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 Kielen-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 cuspule is present on the paraconid keel. This cuspule 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 (Kielen-Jaworowska and Cifelli, 2001; Luo et al., 2002). On other specimens (e.g., OMNH 33971), the anterolingual cuspule 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, Papotherium*), early eutherians (e.g., *Prokennalestes*, see Kielen-Jaworowska and Dashzeveg, 1989; *Murtolestes*, see Averianov and Skutschas, 2000, and Averianov and Skutschas, 2001; *Otlestes*, see Nessov, 1985, and Nessov et al., 1994; *Montanalestes*, see Cifelli, 1999b), and deltatheriodans (Kielen-Jaworowska and Nessov, 1990; Marshall and Kielen-Jaworowska, 1992; Rougier et al., 1998; Kielen-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 stylar 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 conceivable, but currently within the realm of conjecture. At least two3 possible marsupials have been described from the Late Cretaceous of Asia: Asiatherium, from the Maas- trichtian of Mongolia (Trofimov and Szalay, 1994; Szalay and Trofimov, 1996); and Mar- sasia, 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-

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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

<table>
<thead>
<tr>
<th>% marsupial diversity</th>
<th>Mussentuchit (Albian-Cenomanian)</th>
<th>Dakota (late Cenomanian)</th>
<th>Aquilan (Santonian-Campanian)</th>
<th>Judithian (Campanian)</th>
<th>Lancian (late Maasrichtian)</th>
</tr>
</thead>
<tbody>
<tr>
<td>All mammals</td>
<td>17</td>
<td>38</td>
<td>36</td>
<td>44</td>
<td>41</td>
</tr>
<tr>
<td>Tribosphenic mammals</td>
<td>50</td>
<td>67</td>
<td>63</td>
<td>70</td>
<td>55</td>
</tr>
<tr>
<td>Non-multituberculate</td>
<td>27</td>
<td>60</td>
<td>55</td>
<td>70</td>
<td>55</td>
</tr>
<tr>
<td>Multituberculates</td>
<td>44</td>
<td>100</td>
<td>100</td>
<td>117</td>
<td>120</td>
</tr>
<tr>
<td>Number of mammal taxa</td>
<td>24</td>
<td>16</td>
<td>28</td>
<td>16</td>
<td>29</td>
</tr>
</tbody>
</table>


The Mussentuchit 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.

ACKNOWLEDGMENTS

I am pleased and honored to participate in this tribute to Malcolm McKenna, whose support and encouragement were instrumental in turning my research program to Mesozoic mammals some 20 years ago. I thank the Judd family of Castle Dale, Utah, for their enthusiastic, unwavering help in field activities. I also acknowledge with heartfelt thanks the many colleagues, former students, and friends who cheerfully shared the burden of field and lab activities, principal among them: E. M. Larson, S. K. Madsen, R. L. Nydam, and K. S. Smith. Scanning electron micrographs shown in figures 5.3–5.6 were taken by T. Rippy. I am grateful to J. G. Eaton for advice in the field program, and for arranging the loan of MNA specimens to me. Partial support for this research was provided by NGS grants 4761–91 and 5021–92, and NSF grants BSR-8906992, DEB-9401094, and DEB-9870173.

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