FIRST FOSSIL MAMMALS FROM THE UPPER CRETACEOUS EAGLE FORMATION (SANTONIAN, NORTHERN MONTANA, USA), AND MAMMAL DIVERSITY DURING THE AQUILAN NORTH AMERICAN LAND MAMMAL AGE

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Davis, B.M., Cifelli, R.L., and Cohen, J.E. 2016. First fossil mammals from the Upper Cretaceous Eagle Formation (Santonian, northern Montana, USA), and mammal diversity during the Aquilan North American Land Mammal Age. *Palaeontologia Polonica* **67**, 101–126.

Mammalian faunas in North America experienced dramatic change during the Cretaceous, with earlier faunas characterized by eutriconodontans, symmetrodontans, and unspecialized therians giving way to a major diversification of therian lineages by the Campanian–Maastrichtian. The Aquilan North American Land Mammal Age (NALMA), originally based on the well-studied fauna of the Milk River Formation (Santonian) of southern Alberta, records the start of this transition. Notable are first appearances of pediomyoid marsupialiforms and the eutherian *Paranyctoides*, and last occurrences of eutriconodontans and symmetrodontans. The Campanian Wahweap Formation has yielded a similar fauna, but until now the John Henry Member of the Straight Cliffs Formation was the only other unit of known Santonian age from which fossil mammals have been recovered, leaving this transitional interval represented by limited sampling. The Eagle Formation in central and northern Montana is considered to be laterally equivalent to the Milk River Formation, with northernmost exposures correlated to the upper Santonian, based on palynomorphs and magnetostratigraphy. Here, we describe the first fossil mammals known from the Eagle Formation. A relatively small rock sample yielded a rich, diverse assemblage including two genera of spalacotheriid symmetrodonts, several "alphadontid" marsupialiforms and the large pediomyoid *Aquiladelphis*, and at least two eutherians including *Paranyctoides*. Multituberculates, to be described separately, are also abundant and diverse. The Eagle Formation assemblage is broadly similar in composition to that from the Milk River Formation, but shares the spalacotheriid *Spalacotheridium* with older units, including the Straight Cliffs Formation from southern Utah. These initial results provide another biostratigraphic data point linking Santonian faunas across a broad latitudinal range, and encourage reevaluation of the Aquilan NALMA.

Key words: Mammalia, Late Cretaceous, Symmetrodonta, Tribosphenida, Aquilan, Eagle Formation.

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Received 15 June 2015, accepted 10 November 2015.

http://dx.doi.org/10.4202/pp.2016.67_101

INTRODUCTION

Late Cretaceous terrestrial faunas are unquestionably the most thoroughly studied and best known assemblages of the North American Mesozoic. In particular, numerous studies documenting the diversity and ultimate turnover of communities at the K-Pg event have given us incredibly fine-scale details of the rise and fall of dinosaurs and mammals (Archibald and Fastovsky 2004; Cifelli *et al.* 2004; Wilson 2005, 2013, 2014; Sprain *et al.* 2015). Slightly older assemblages of Campanian age (83.6–72.1 Mya, Gradstein *et al.* 2012) are also well represented; in particular, faunas of the Kaiparowits (Utah) and Dinosaur Park (Alberta) formations have been heavily sampled (see reviews in Currie and Koppelhus 2005 and Titus and Loewen 2013, and references therein). Among therian mammals, the Campanian–Maastrichtian interval documents a substantial diversification event. Marsupialiform groups such as pediomyoids and "alphadontids" become highly diverse and are by far the most abundant therians in the latter part of the Late Cretaceous (Clemens 1966; Lillegraven 1969; Montellano 1992; Johanson 1996; Kielan-Jaworowska *et al.* 2004; Davis 2007; Williamson *et al.* 2012; Eaton and Cifelli 2013). Eutherians, on the other hand, exhibited little known diversity during the Early Cretaceous (Cifelli 1999a; Davis and Cifelli 2011; Cifelli and Davis 2015) and disappeared from the record before reemerging in the Santonian (Fox 1970) and reaching a moderate diversity by the close of the Period (Kielan-Jaworowska *et al.* 2004; Archibald *et al.* 2011). Some recent molecular analyses (*e.g.*, Meredith *et al.* 2011) have proposed that this Cretaceous diversity included the origin of crown Placentalia.

The mammalian record for the entire Early Cretaceous of North America is represented by only a handful of assemblages, many of which await full description. Of these, the best known are the historically important fauna from the Trinity Group of Oklahoma and Texas, and the contemporaneous Cloverly Formation in Montana and Wyoming (Patterson 1956; Butler 1978; Jenkins and Schaff 1988; Cifelli 1999a; Davis and Cifelli 2011, references therein; Cifelli and Davis 2015). The therian mammals are generally plesiomorphic; though these faunas are characterized by the classic "Theria of metatherian-eutherian grade" (Patterson 1956), it is likely that both metatherians and eutherians achieved unappreciated morphological and taxonomic diversity by the Albian (Cifelli and Davis 2015). Spalacotheriid symmetrodontans are present but poorly known in the Early Cretaceous of North America (Patterson 1955; Cifelli *et al.* 2014); they would explode in number and diversity by the Cenomanian, as evident in the well-sampled Cedar Mountain Formation in southern Utah (Cifelli and Madsen 1999), and persist as uncommon faunal elements until the early Campanian (Cifelli and Madsen 1986). Eutriconodontans were also diverse during the Early Cretaceous, represented by *Gobiconodon* and numerous alticonodontine triconodontids (Patterson 1951; Jenkins and Schaff 1988; Cifelli *et al.* 1998, 1999); this group is rare during the Late Cretaceous (Fox 1969; Cifelli and Madsen 1998), and is last recorded in the Santonian (Fox 1976; Eaton 2013).

The composition of North American mammalian faunas changed dramatically during the Cretaceous. Unfortunately, sampling during the first part of the Late Cretaceous (Cenomanian–Santonian) is uneven and generally poor, resulting in an incomplete understanding of this transition. Nearly all of our knowledge of this interval comes from sites in southern Utah (see summaries in Kielan-Jaworowska *et al.* 2004; Eaton and Cifelli 2013), with the best-studied faunas hailing from the Cedar Mountain and Dakota formations (Albian–Cenomanian and upper Cenomanian, respectively). Of note are the diversity of metatherians (Cifelli and Eaton 1987; Cifelli 1993, 2004; Eaton 1993, 1995, 2009; Cifelli and Muizon 1997) and the apparent absence of eutherians, a pattern in contrast with that observed in Asia (Archibald and Averianov 2005; Chester *et al.* 2010). Small, sparse samples of Turonian–Coniacian age are known from the Straight Cliffs Formation (Cifelli 1990a; Eaton 1995, 2006a; Cifelli and Gordon 1999), with the therians either largely indeterminate or unstudied. Eutriconodontans, which are diverse in the Cedar Mountain Formation, are not recorded again until the Santonian, while spalacotheriid symmetrodontans are present but rare. The fossil record from the Santonian is appreciably better, but sampling is still quite limited. A small but diverse fauna has been recovered from the Iron Springs Formation (Eaton 1999; Eaton *et al.* 2014), but the age of the unit is poorly constrained and could range from Cenomanian to early Campanian. Otherwise, knowledge of Santonian mammals from North America is currently limited to fossils from the John Henry Member of the Straight Cliffs Formation in southern Utah (Eaton 2006b, 2013) and the Milk River Formation in southern Alberta (R. C. Fox references, see below). Metatherian diversity is very high, with the appearance of pediomyoids and several "alphadontid" genera alongside more generalized forms, and eutherians are recorded for the first time since the Albian.

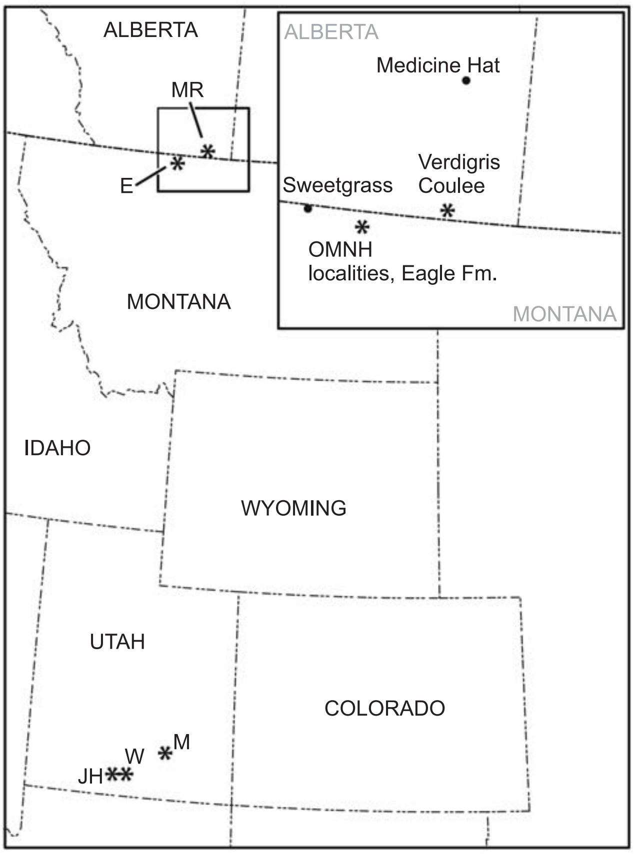

Fig. 1. Map of Aquilan North American Land Mammal Age localities (asterisks). Mammal localities from the John Henry Member of the Straight Cliffs Formation and Wahweap Formation are known on both the Paunsaugunt and Kaiparowits plateaus in southern Utah, and cannot be differentiated from one another at the scale of this map. Enlarged section shows Verdigris Coulee (Milk River Formation) and OMNH localities described in this paper (Eagle Formation). Abbreviations: E, Eagle Formation; JH, John Henry Member of Straight Cliffs Formation; M, Masuk Formation; MR, Milk River Formation; W, Wahweap Formation.

The mammalian fauna of the Milk River Formation, from a few localities in Verdigris Coulee, has been extensively studied by Richard C. Fox, resulting in a long series of publications (Fox 1968, 1969, 1970, 1971a, b, 1972a, b, 1976, 1980, 1982, 1984a, b, 1985, 1987; Montellano-Ballesteros *et al.* 2013; Montellano-Ballesteros and Fox 2015). This fauna records a number of notable first appearances, such as pediomyoids (*Aquiladelphis*), the stagodontid *Eodelphis*, and the eutherian *Paranyctoides*, as well as the last occurrence of eutriconodontans (*Alticonodon*). Because of these important differences with regard to older assemblages, the Milk River fauna was designated as the type for the Aquilan North American Land Mammal Age (NALMA) by Lillegraven and McKenna (1986). The Aquilan was expanded by Cifelli *et al.* (2004) to include a similar fauna from the early–middle Campanian Wahweap Formation and the faunule from a stratigraphically correlative unit, the Masuk Formation, both in southern Utah. While slightly older than the Milk River assemblage, the mammalian fauna from the upper part of the John Henry Member of the Straight Cliffs Formation is also broadly similar (Eaton and Cifelli 2013); for convenience of faunal comparisons, we provisionally refer it to the Aquilan (see the Discussion, below). Problems with the definition of the Aquilan, specifically with regard to the correlation of the Wahweap Formation, have been pointed out by several authors (Eaton 2013; Eaton and Cifelli 2013; Jinnah 2013); this issue will be explored below in the Discussion.

The Milk River Formation has a stratigraphic correlate exposed in central and northern Montana, the Eagle Formation (considered to be almost entirely Santonian in age, see Geologic Setting section, below). While the under- and overlying marine units contain invertebrate fossils and shark teeth, only palynomorphs have been recovered and studied from the Eagle Formation (Payenberg *et al.* 2002); no vertebrate fossils have been unambiguously described from the unit. Somewhat problematic dinosaur material, described by Marsh (1890) as the types of *Ornithomimus tenuis* and *O. grandis*, is possibly from the Eagle Formation. Marsh (1890, p. 85) states that these specimens were recovered from the same horizon but gives no locality details. In their thorough treatment of the fossils and geology in the Missouri Breaks region, Stanton and Hatcher (1905, p. 87) list the younger Judith River Formation as provenance for *O. tenuis* but claim unequivocally that the *O. grandis* material is from sandstones of the older Eagle Formation. Unfortunately, the type of *O. grandis* is lost (Gilmore 1920).

Field parties from the OMNH explored exposures of the Eagle Formation in the Sweet Grass Hills in northeastern Toole County, Montana in 2004 and 2005 (Fig. 1). Screen washing of small rock samples yielded abundant vertebrate fossils (see Methods and Conventions section, below), including fragmentary remains of osteichthyians, chondrichthyans, chelonians, lissamphibians, lacertilians, crocodilians, dinosaurs, and mammals. In addition to the symmetrodontan and therian fossils described in this paper, the OMNH collection from the Eagle Formation also includes relatively abundant and diverse multituberculate material, constituting nearly half of the informative mammalian specimens in the available sample. The multituberculates, which present their own unique challenges, are excluded from this paper and will be the focus of a subsequent study.

This paper is in tribute to the late Professor Zofia Kielan-Jaworowska, in recognition of her foundational work on mammals from the Cretaceous of central Asia. Of particular relevance to this present work are her discovery, description, and interpretation of wonderfully complete eutherian specimens from Campanian units in Mongolia (Kielan-Jaworowska 1969, 1975, 1977, 1978, 1984a–c). This series of publications placed the focus of early eutherian diversification squarely on the Asian landmass and provided vital points of morphological comparison for later studies of therian evolution and dispersal.

Institutional abbreviations. — AMNH, American Museum of Natural History, New York, New York, USA; MNA, Museum of Northern Arizona, Flagstaff, Arizona, USA; OMNH, Oklahoma Museum of Natural History, Norman, Oklahoma, USA; UALVP, University of Alberta Laboratory for Vertebrate Paleontology, Edmonton, Alberta, Canada; UCMP, University of California Museum of Paleontology, Berkeley, California, USA; and UMNH, Utah Museum of Natural History, Salt Lake City, Utah, USA.

Acknowledgements. — We would like to thank Kyle L. Davies and Cynthia L. Gordon (both OMNH) for assistance with collection in the field. We are especially grateful to Dave and Lenora McEwen and Bryan and Cathy Ratzburg (Galata, Montana, USA) for their hospitality during the 2004 and 2005 field seasons. Alyson Brink (Texas Tech University, Lubbock, TX, USA) and an anonymous reviewer provided useful comments on the manuscript.

GEOLOGIC SETTING

The Upper Cretaceous Eagle Formation was deposited along the margin of the Western Interior Foreland Basin. The unit was first described as the Eagle Sandstone by Weed (1889), and later divided into three members by Bowen (1914; see Rice 1980; Meijer-Drees and Mhyr 1981 for summaries of early work on the unit). The unit is generally regarded as representing a progradational clastic wedge situated stratigraphically between two transgressive shale wedges (the Niobrara Formation below and the Claggett Formation above; Fig. 2). The Eagle Formation and the laterally equivalent Milk River Formation (see below) have been thoroughly studied due to their role as reservoirs of large amounts of biogenic gas (*e.g.*, Rice 1980; Ridgley 2000; Payenberg and Braman 2003). Thick, cliff-forming sandstones within the Eagle Formation (specifically the Virgelle Member) are responsible for the characteristic white bluffs of the Missouri Breaks region along the Missouri River in north-central Montana; the stratigraphic section is best exposed in this area and has received most attention. Farther north near the Canadian border, the Eagle Formation is exposed very locally along the flanks of a local uplift called the Sweet Grass Hills, a series of buttes (some of which are nearly 1000 m tall) in northern Toole and Liberty counties. These exposures yielded the fossils in this study.

The Eagle Formation sits conformably on the Telegraph Creek Formation, a sequence of dark, sandy shales that is thought to represent the transition from the open marine deposition of the Niobrara Formation to the shoreface and fluvial environments recorded by the Eagle Formation (Rice 1980; Payenberg and Braman 2003). The Eagle Formation is divided into three lithostratigraphic members (Fig. 2), the lowest of which is the Virgelle Member (the transition from the Telegraph Creek Formation is defined by the absence of shale beds). This predominately sandstone unit is generally massive, resistant, and cliff-forming, weathering at its top into small hoodoos. The lower portion preserves hummocky and swaley cross-stratification, which suggests storm-dominated deposition along the shoreface (Leckie and Cheel 1986; Meyer *et al.* 1998); upper portions of the member are more tabular. The overlying Deadhorse Coulee Member is entirely non-marine in origin, containing alternating mudstones, siltstones, and sandstones with occasional thin coal

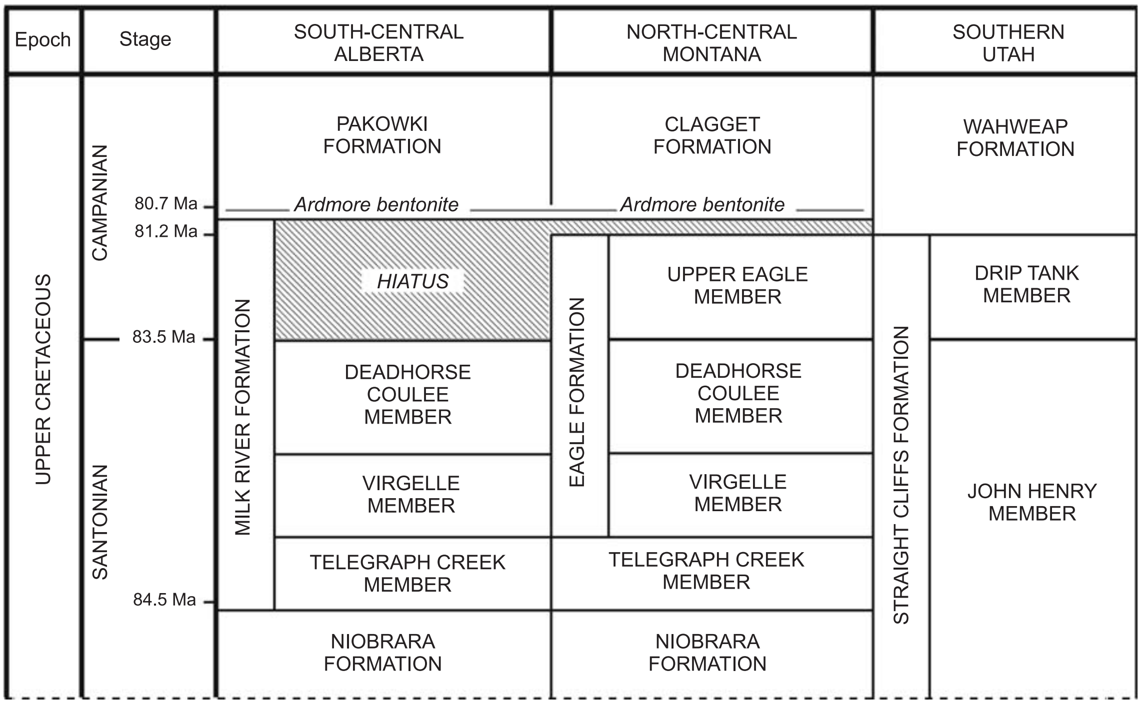

Fig. 2. Chronostratigraphic column correlating rock units of Santonian–Campanian age in south-central Alberta, north-central Montana, and southern Utah. Modified from Payenberg *et al.* (2003, fig. 3).

seams (fluvial channels and crevasse splays, as well as coastal plain deposits related to a prograding deltaic system). Exposures are often banded in color. The Deadhorse Coulee Member is separated from the Upper Eagle Member by a minor transgressive event, marked by a sudden appearance of mud-rich sandstones with a marine influence (Payenberg and Braman 2003). The presence of flaser bedding and invertebrate ichnofossils suggests a protected tidal environment, perhaps a bay or lagoon. The Upper Eagle Member thins northward through Montana and is not present in a studied section of the laterally equivalent Milk River Formation (see below) in Writing-On-Stone Provincial Park (WOSPP), southern Alberta (Payenberg *et al.* 2002). The contact between the Eagle Formation and the overlying Claggett Formation is unconformable and distinctly marked by a dark chert pebble bed, termed the Eagle Shoulder.

Age estimates for the Eagle Formation have varied with respect to the Santonian–Campanian boundary, with different data sources collected at different latitudes yielding alternate placements of the unit. However, refinements of the age of the boundary itself have driven some of this instability. For the sake of clarity, only the most recent work, by Brahman (2001) and Payenberg *et al.* (2002), will be summarized here (discussion of previous work can be found in these two papers). The lower age limit for the Eagle Formation is based on the assignment of the Telegraph Creek Formation near Shelby in far northern Montana to the *Desmoscaphites bassleri* ammonite zone (Cobban 1955). Obradovich (1993) dated the base of this zone at 84.5 Mya. U-Pb and ^{40}Ar-^{39}Ar dates from the Ardmore bentonite near the base of the Claggett-Pakowki transgression consistently date this event to ~81 Mya, throughout the latitudinal range of the unit from southern Alberta south to Wyoming (Hicks *et al.* 1995; Payenberg *et al.* 2002); this establishes an upper age limit to the sequence.

Leahy and Lerbekmo (1995) identified the 34n–33r reversal in the Deadhorse Coulee Member in southern Alberta; this paleomagnetic event is placed just below the Santonian–Campanian boundary by Montgomery *et al.* (1998). The boundary itself is defined biostratigraphically (last occurrence of the crinoid *Marsupites testudinanus*, Hancock and Gale 1996), and has been dated to 83.5 Mya (Obradovich 1993). It is therefore likely, based on current data, that all or nearly all of the Eagle Formation is late Santonian in age and was deposited between 84.5–83.5 Mya. However, this applies only to the unit where it occurs in northern and north-central Montana. In the Elk Basin in southern Montana/northern Wyoming, Hicks *et al.* (1995) placed the entire Eagle Formation within chron 33r and dated a bentonite in the Upper Eagle Member at 81.14 ± 0.51 Mya, only slightly older than the Claggett transgression. The Eagle Formation appears to be time transgressive, with the southern-most portions of the unit being almost entirely Campanian in age.

Vertebrate fossils were recovered from four closely-spaced localities (within a few hundred meters laterally and no more than ten vertical meters), two of which yielded mammals and will be the focus of this paper (OMNH V1409 and V1412; specific coordinates are on file at the OMNH and are available to qualified investigators upon request). The exposures are within the Sweet Grass Hills in northeastern Toole County, Montana and consist of horizontal but laterally variable lenses of mudstones, sandstones, siltstones, and some very thin coal beds. No clear stratigraphic boundaries within the section were observed, and the tops and flanks of the exposures are grass-covered, hampering lateral correlation with any other exposures. The most productive microvertebrate locality (OMNH V1409) occurs in a fine, dull white sandstone containing dispersed invertebrate shell fragments, though an occasional complete but unarticulated pelecypod valve or gastropod steinkern is present. This sandstone sits on a structureless gray green mudstone, fines upward into a gray sandy mudstone, and is capped by another structureless gray green mudstone. Immediately lateral to this is a well indurated, approximately 0.8 m sandstone lens. OMNH V1412 occurs in a slumped, heavily weathered block of drab varicolored mudstone in shades of tan, green, and gray. This mudstone contains dispersed pebble- to small cobble-sized sideritic nodules. Exact stratigraphic context is impossible to determine, but it appears that the block slumped from lower in the section than V1409. The OMNH localities derive from vertically limited (10–15 m) exposures of the Eagle Formation; lithology throughout this section is characteristic of Deadhorse Coulee Member. While placement within the Upper Eagle Member cannot be entirely ruled out, this member is dominantly marine and thins northward, being absent at WOSPP; it is unknown if the Upper Member is present in the study area in northern-most Montana. The OMNH localities are only ~20 km southeast of WOSPP and preserve terrestrial and freshwater vertebrates, lending strong support to their stratigraphic placement within the Deadhorse Coulee Member.

CORRELATION WITH THE MILK RIVER FORMATION

The Eagle and Milk River formations are lithologically very similar and are divided laterally by nothing more than the international border. The Milk River Formation has been extensively studied in southern Alberta in and around WOSPP (Meijer-Drees and Mhyr 1981; McCrory and Walker 1986; Cheel and Leckie 1990; Payenberg *et al.* 2002; Meyer and Krause 2006). In Alberta, the Telegraph Creek Formation is included as the lowermost member of the Milk River Formation, with the Virgelle and Deadhorse Coulee members equivalent in status to their counterparts in the Eagle Formation (Fig. 2). Similarities in palynoflora between the Virgelle and Deadhorse Coulee members of the Milk River Formation in WOSPP and the same members of the Eagle Formation in north-central Montana (near the Missouri River) suggest that these units are time-equivalent in these areas (Payenberg *et al.* 2002). An equivalent to the Upper Eagle Member is absent from exposures of the Milk River Formation in WOSPP, but the Deadhorse Coulee Member is capped by the same chert pebble bed which marks the top of the Eagle Formation in Montana. A hiatus of some 2.5 Ma is interpreted between the end of Milk River deposition and the Pakowki marine transgression (equivalent to the Claggett Formation), based on the presence of the 34n–33r reversal in the upper Deadhorse Coulee Member (Leahy and Lerbekmo 1995) and radiometric dates from the Ardmore bentonite in the Pakowki Formation (Hicks *et al.* 1995); this, presumably, was when the Upper Eagle Member was deposited in central and southern Montana (Payenberg *et al.* 2002). East of WOSPP and further basin-ward, the Alderson Member of the marine Lea Park Formation is likely time-equivalent with the Upper Eagle Member (Ridgley 2000). As summarized above, additional data from ammonites and magnetostratigraphy (Hicks *et al.* 1995) suggest that the entire Eagle Formation in southern Montana and Wyoming is lower Campanian in age and likely younger than exposures to the north, including most or all of the Milk River Formation. A complex picture thus emerges for the dynamic western shoreline of the Western Interior Seaway during the Santonian–Campanian.

The OMNH localities in the Eagle Formation are some 150 km away from the nearest studied section of the unit (along the Missouri Breaks in north-central Montana), making them difficult to place, both stratigraphically and chronologically, within the time transgressive latitudinal variation identified in the Eagle Formation. Considering the relative proximity of the OMNH localities to exposures of the Milk River Formation, the best correlation is likely with the Deadhorse Coulee Member in southern Alberta. As will be discussed below, the mammalian fauna overlaps broadly with that known from the Milk River Formation. It is on this basis that we tentatively assign a latest Santonian age to the OMNH localities in the Eagle Formation.

METHODS AND CONVENTIONS

Over the course of two field seasons (2004 and 2005), the OMNH processed 1100–1400 kg of sediment from OMNH V1409 and V1412 through underwater screen washing, following standard microvertebrate recovery techniques (Cifelli *et al.* 1996). Approximately 170 mammalian specimens from these localities have been catalogued to date. Scanning electron micrographs of specimens (polyurethane resin casts) were obtained at the OMNH using a Denton Vacuum Desk II (gold/palladium) sputter coater and a LEO 1450VP SEM. Tooth measurements (all in millimeters) were taken with a Reflex Microscope (see MacLarnon 1989, Consultantnet Ltd, 94 High Street, Linton, Cambridge, CB21 4JT, UK), as defined by Lillegraven and McKenna (1986) and Lillegraven and Bieber (1986): AP, mesiodistal length of tooth, in approximate anatomical orientation (including the clingulid for symmetrodontan lower molars); ANW, anterior (mesial) width (trigonid width on lower molars; distance from edge of stylar shelf, buccal to paracone, to line going through protocone, parallel to line defined by apices of paracone and metacone on uppers); POW, posterior (distal) width (talonid width on lower molars; distance from distal stylar shelf [metastylar corner] to line going through protocone, parallel to line defined by apices of paracone and metacone on uppers). Measurements are given in Table 1 (specimens omitted from Table 1 were too incomplete to be measured). Specimens for which tooth position cannot be determined are denoted with "X" (*e.g.*, MX or mx). Tooth terminology and conventions follow Kielan-Jaworowska *et al.* (2004).

SYSTEMATIC PALEONTOLOGY

Superlegion **Trechnotheria** McKenna, 1975

Family **Spalacotheriidae** Marsh, 1887

Genus ***Spalacotheridium*** Cifelli, 1990a

Spalacotheridium mckennai Cifelli, 1990a

(Fig. 3A)

Locality and horizon: OMNH V1409, Deadhorse Coulee Member of the Eagle Formation (Santonian, Upper Cretaceous), Toole County, Montana, USA.

Referred material. — OMNH 66376, left m5.

Description. — OMNH 66376 is a very small spalacotheriid lower molar (Table 1). It is moderately worn and nearly complete, missing the mesiolingual corner of the cingulid and the tip of the paraconid. The protoconid is the tallest cusp, and though somewhat abraded it was only ~50% taller than the metaconid. The preserved base of the paraconid suggests that it was likely subequal in height to the metaconid; this is supported by the roughly equal height of the notches in the protocristid and paracristid. The paraconid and metaconid are positioned close to one another but are slightly divergent, forming a trigonid angle of 35°. The cingulid is complete buccally, with the lingual portion highest between the roots and dipping farthest distally to the swollen but low heel.

Comments. — Subequal height of the paraconid and metaconid (or, as a proxy, the height of the notches in the protocristid and paracristid) indicates referral of this specimen to *Spalacotheridium.* Its small size is most consistent with *S. mckennai* from the slightly older Smoky Hollow Member of the Straight Cliffs Formation (Turonian, southern Utah). The only well-preserved specimens of this species that have been previously described (MNA V5792, Cifelli 1990a, fig. 1; MNA V6046 and V6756, Cifelli and Gordon 1999, fig. 6) are somewhat smaller still. The best-preserved of these, MNA V5792 and V6046, have a less acute trigonid angle and a lingual cingulid that is relatively horizontal instead of distally sloping as in OMNH 66376. However, these differences are likely attributable to tooth position, with the Eagle Formation specimen representing a more distal molar (see Cifelli and Madsen 1999, fig. 6). In addition to a smaller species from the older Cedar Mountain Formation (*S. noblei*, Cifelli and Madsen 1999), isolated lower molars of *Spalacotheridium* are known from the upper Santonian John Henry Member of the Straight Cliffs Formation (Eaton 2006b, 2013). While these specimens are larger still than OMNH 66376, they agree well in morphol-

Table 1. Dental measurements (mm) of mammals from the Eagle Formation (upper Santonian), Montana, USA. Specimens for which no complete standard measurements could be obtained are omitted.

Taxon	Tooth	ID (OMNH)	AP	ANW	POW
Spalacotheridium mckennai	m5	66376	0.73	0.93	–
Symmetrodontoides canadensis	p2	66373	1.55	0.45	–
	p4	66370	1.96	0.85	–
	m2	66371	1.06	1.21	–
	m5	66372	0.69	1.48	–
Varalphadon wahweapensis	M2	66379	1.79	1.74	1.87
	M3	66357	1.92	2.10	2.23
	M3	66358	1.99	–	–
Varalphadon sp.	dp3	66367	1.46	0.65	0.66
	m1	66362	1.70	0.86	0.86
	m2	66361	1.68	0.89	0.98
	m3	66388	1.92	1.15	1.13
Alphadon halleyi	M3	66382	–	–	2.25
	m2 or 3	66387	2.02	1.15	1.16
Albertatherium primus	M1	66378	2.15	–	–
	M2	66377	2.25	–	–
	m2 or 3	66380	2.14	1.24	1.20
Aquiladelphis incus	M3	66351	5.64	5.69	5.92
Aquiladelphis minor	m2	66353	3.83	2.63	2.20
Leptalestes sp.	mx	66366	–	–	0.65
Metatheria indet.	dp3 or m1	66341	1.38	0.64	0.73
Tribosphenida indet.	upper molariform	64165	2.67	2.94	2.56

ogy with material referred to the genus. Improved samples will be needed to determine if more than one species of *Spalacotheridium* is present in the Turonian–Santonian interval.

Genus ***Symmetrodontoides*** Fox, 1976

Symmetrodontoides canadensis Fox, 1976

(Fig. 3B–E)

Locality and horizon: All OMNH V1409, Deadhorse Coulee Member of the Eagle Formation (Santonian, Upper Cretaceous), Toole County, Montana, USA.

Referred material. — OMNH 66373, right p2; OMNH 66370, right p4; OMNH 66371 right m2; 66372 left m5.

Description. — Two lower premolars from the Eagle Formation are here referred to a single spalacotheriid taxon. OMNH 66370 closely resembles UALVP 12086 from the Milk River Formation, which Fox (1976, fig. 4) identified as an m1 of *Symmetrodontoides canadensis* (we follow Cifelli 1999b in regarding this specimen as a p4). OMNH 66370 (Fig. 3C) differs only in having a slightly broader cingulid at the mesial extent of the crown, and a slightly taller distal heel cusp; the tooth is well preserved except for some minor abrasion to the buccal cingulid and tip of the protoconid, and wear along the main distal crest. OMNH 66373 (Fig. 3B) matches the expected size and morphology of a premolar one or two positions mesial to OMNH 66370, and we provisionally identify this specimen as a p2 of *S. canadensis* based on the patterns for spalacotheriid premolars proposed by Cifelli (1999a). The specimen is mesiodistally elongate and is missing the mesial-most part of the crown, so the presence or size of a paraconid is unknown. The protoconid is positioned mesial to the presumed mid-point of the crown, and is slightly lower as compared to the p4 protoconid. Its mesial slope is steep, with the distal slope broadly worn and bearing a low metaconid and an additional small cusp at the terminus of the main crest. The distal heel is similarly developed as on the p4, though it is positioned directly above the root instead of projecting distally. A narrow cingulid encircles the entire preserved portion of the crown.

OMNH 66371 (Fig. 3D), identified here as a complete but rather worn right m2, is identical to the second preserved tooth in the holotype of *Symmetrodontoides canadensis* (UALVP 8588; Fox 1972b, 1976). It has a trigonid angle of 35°. We follow Cifelli and Madsen (1999), who interpreted UALVP 8588 as preserving the m1–m3 (instead of m3–m5) based on comparisons with abundant spalacotheriid material from the Cedar Mountain Formation of Utah. Finally, OMNH 66372 (Fig. 3E) resembles an isolated molar identified by Fox

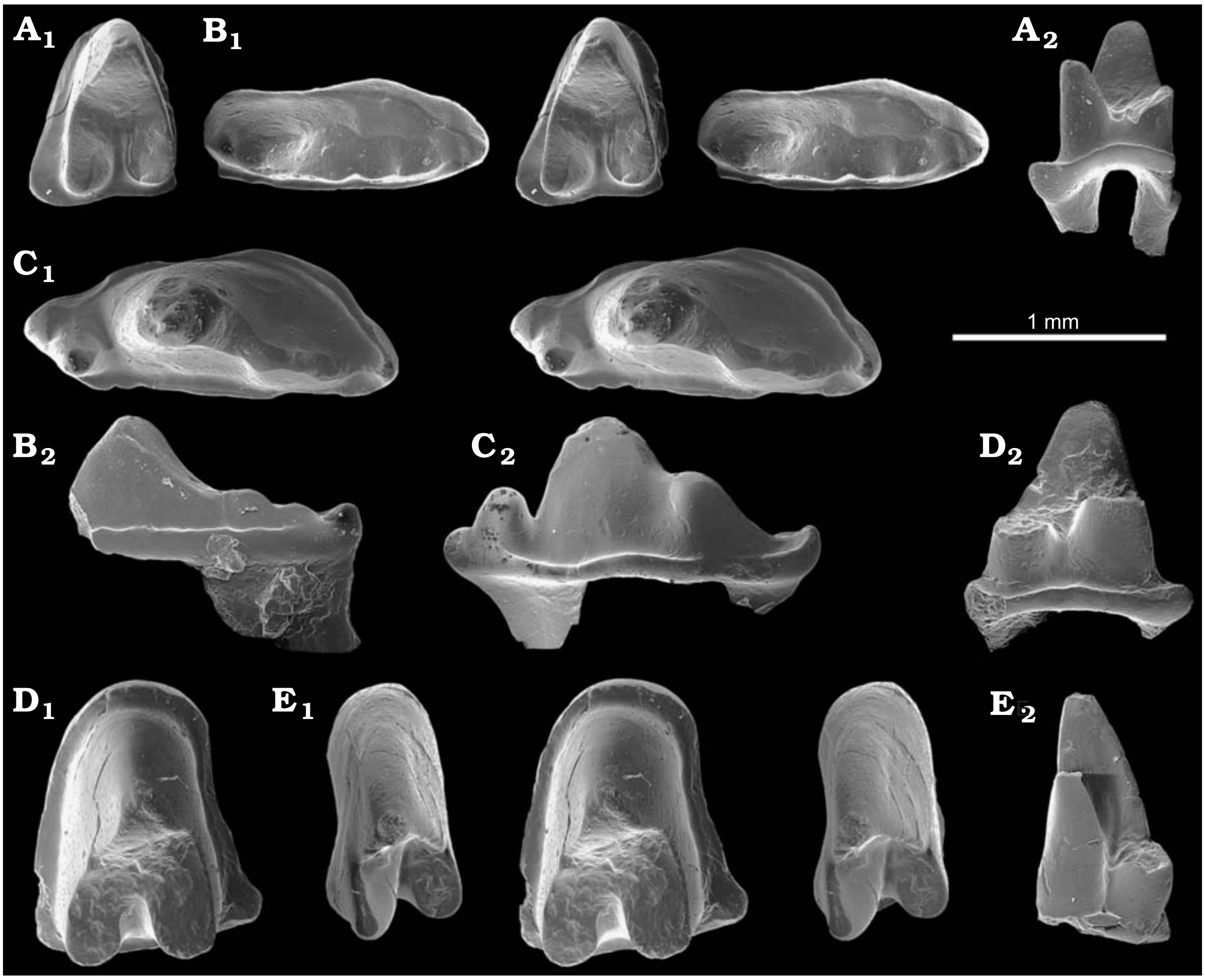

Fig. 3. Spalacotheriid symmetrodontans from the Eagle Formation (all OMNH locality V1409, Upper Cretaceous, Santonian, Montana). **A**. *Spalacotheridium mckennai*, OMNH 66376, left m5 in occlusal (A_1, stereopair) and lingual (A_2) views. **B–E**. *Symmetrodontoides canadensis*. **B**. OMNH 66373, right p2 in occlusal (B_1, stereopair) and lingual (B_2) views. **C**. OMNH 66370, right p4 in occlusal (C_1, stereopair) and lingual (C_2) views. **D**. OMNH 66371, right m2 in occlusal (D_1, stereopair) and lingual (D_2) views. **E**. OMNH 66372, left m5 in occlusal (E_1, stereopair) and lingual (E_2) views.

(1976, fig. 5, UALVP 12087) as the m6. The base of the crown is broken on the OMNH specimen, such that the cingulid and heel are missing, and the tip of the paraconid is damaged. The tooth is tall yet strongly mesiodistally compressed (trigonid angle 31°), and was likely only slightly narrower than the m2. The paraconid appears to have been considerably lower than the metaconid, which is slightly recurved and somewhat heavier in comparison to UALVP 12087. Due to damage and incomplete knowledge of the molar series of *Symmetrodontoides*, it is difficult to determine with certainty which position OMNH 66372 represents. Its morphology is consistent, however, with the antepenultimate molar in reference to spalacotheriids from the Cedar Mountain Formation and we tentatively identify it as an m5.

Comments. — Symmetrodontans are distinctive but rather rare components of the Eagle fauna, comprising roughly 4% of the catalogued mammalian specimens. By comparison, this group accounts for nearly a third of mammalian species, and nearly 40% of specimens identified to species level, in the Albian–Cenomanian Mussentuchit local fauna in the Cedar Mountain Formation (Cifelli and Madsen 1999; Cifelli *et al.* 2016 this volume).

Subclass **Tribosphenida** McKenna, 1975

Infraclass **Metatheria** Huxley, 1880

Family “**Alphadontidae**” Marshall, Case, *et* Woodburne, 1990

Genus ***Varalphadon*** Johanson, 1996

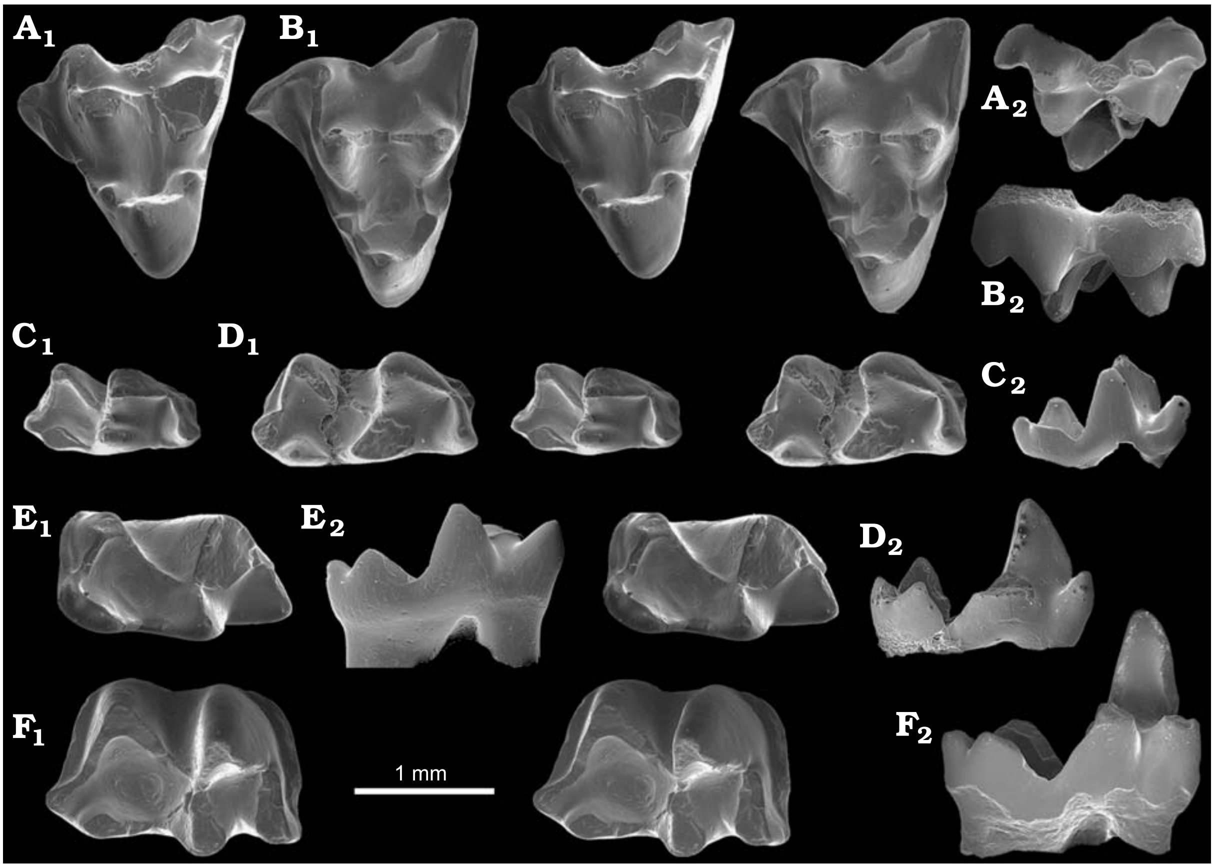

Fig. 4. The "alphadontid" marsupialiforms *Varalphadon wahweapensis* and *Varalphadon* sp. from the Eagle Formation (Upper Cretaceous, Santonian, Montana). **A–B**. *Varalphadon wahweapensis* (all OMNH locality V1409). **A**. OMNH 66379, left M2 in occlusal (A_1, stereopair) and buccal (A_2) views. **B**. OMNH 66357, left M3 in occlusal (B_1, stereopair) and buccal (B_2) views. **C–F**. *Varalphadon* sp. **C**. OMNH 66367 (OMNH locality V1409), left dp3 in occlusal (C_1, stereopair) and lingual (C_2) views. **D**. OMNH 66362 (OMNH locality V1409), left m1 in occlusal (D_1, stereopair) and lingual (D_2) views. **E**. OMNH 66361 (OMNH locality V1409), left m2 in occlusal (E_1, stereopair) and lingual (E_2) views. **F**. OMNH 66388 (OMNH locality V1412), left m3 in occlusal (F_1, stereopair) and lingual (F_2) views.

Varalphadon wahweapensis (Cifelli, 1990b)

(Fig. 4A, B)

Locality and horizon: All OMNH V1409, Deadhorse Coulee Member of the Eagle Formation (Santonian, Upper Cretaceous), Toole County, Montana, USA.

Referred material. — OMNH 66379, left M2; OMNH 66357, left M3; OMNH 66358, left M3 missing protoconal region (not illustrated).

Description. — Two upper molars from the Eagle Formation are referred to *Varalphadon wahweapensis*. OMNH 66379 (Fig. 4A) is a slightly damaged left M2, missing most of the metacone and bearing abrasion to the tips of the paracone and stylar cusps. The metacone has a broader base than the paracone, but the relative height of the cusps is impossible to determine. While not connected at their bases, the two cusps are not widely spaced. The centrocrista is straight. The protocone is large but uninflated and unexpanded, with the lingual half of the crown somewhat narrow. The conules are well developed, bear very weak internal cristae, and are positioned close to the protocone; they flank a deep trigon basin. The preprotocrista continues past the paraconule to connect to the parastyle, while the postprotocrista does not extend buccally past the metacone. The preparacrista is short, notched, and travels to a large stylocone situated very close to the paracone. The postmetacrista is relatively short and oblique; it does not bear a substantial notch, and terminates at a low metastyle. The parastyle is about half the height of the stylocone and is connected to it by a weak crest. Stylar cusps are present at the C and D positions, but both are damaged. Cusp C is situated at the center of the shallow ectoflexus and, judging from what is left of its base, it was low and roughly conical. Cusp D is larger and more elongate, aligned with the ectocingulum and positioned directly buccal to the metacone.

OMNH 66357 (Fig. 4B) is a well-preserved left M3, agreeing very closely with other material in the OMNH collection referred to *Varalphadon wahweapensis*. The metacone is broader than the paracone but is subequal in height. The protoconal region is wider transversely than the M2, with conules farther spaced from the protocone and bearing stronger internal cristae. The stylocone is better separated buccally from the paracone, but the parastylar lobe is still narrower than the metastylar lobe and the ectoflexus is shallow. The postmetacrista is longer and oriented in a more directly buccal fashion. A tiny cuspule is present just mesial to the center of the ectoflexus, but a developed stylar cusp C is absent.

Comments. — These two specimens closely resemble material from the coeval John Henry Member of the Straight Cliffs Formation and younger Wahweap and Kaiparowits formations (Cifelli 1990b, c; Eaton 2013). Upper molars of *Varalphadon wahweapensis* are differentiated from those of *V. creber* in relative narrowness of the parastylar lobe; this is most apparent on M3 (Johanson 1996). The referred upper molars here show variation in development of stylar cusp C, a particularly labile character among specimens referred to this genus.

Varalphadon sp.

(Fig. 4C–F)

Locality and horizon: OMNH V1409 and V1412 (only OMNH 66388), Deadhorse Coulee Member of the Eagle Formation (Santonian, Upper Cretaceous), Toole County, Montana, USA.

Referred material. — OMNH 66367, left dp3; OMNH 66362, left m1; OMNH 66361, left m2; OMNH 66388, left m3.

Description. — OMNH 66367 (Fig. 4C) is small and low crowned, with a widely open trigonid and low, procumbent paraconid—all features typical of metatherian deciduous lower premolars (*e.g.*, Clemens 1966; Cifelli and Muizon 1998). The tip of the protoconid is broken, but this cusp was heavier but only slightly taller than the metaconid. The paraconid is widely spaced from the metaconid but positioned directly mesial to it (on a line passing through the entoconid and metaconid). Cusp f is developed as an oblique shelf, while only a faint vertical keel is present in the position of cusp e along the mesial edge of the paraconid. The talonid is wider than the trigonid. The hypoconid is the largest talonid cusp; the entoconid is somewhat broad and strongly twinned with the hypoconulid. The cristid obliqua meets the trigonid below the protocristid notch, and there is a strong buccal postcingulid.

OMNH 66362 (Fig. 4D) is larger with a more acute trigonid, but otherwise shares many similarities with the dp3. The paraconid is low and procumbent; the metaconid is broken but was clearly much taller, and this cusp pinches distally into a sharp crest descending to meet the entocristid at a notch. The talonid is subequal to slightly wider than the trigonid, and shows the same morphology as the dp3 except that the entoconid is somewhat less elongate and more conical. The relatively low-crowned trigonid coupled with a wide talonid suggest this is a first molar.

OMNH 66361 (Fig. 4E) agrees with the other two lower molars in general morphology except that it is slightly larger, with a larger paraconid (though still lower than the metaconid). The protoconid is broken at its base, but the tooth is otherwise complete. The metaconid is relatively heavy. The talonid matches the other specimens in morphology, and is slightly wider than the trigonid. The base of the talonid is lower than the base of the trigonid in buccal view, suggesting that this tooth is from the middle of the molar series, probably m2.

OMNH 66388 (Fig. 4F) is slightly larger than OMNH 66361 and differs in morphology, consistent with a tooth from one position farther distal. The trigonid cusps form a more acute angle, and the talonid is slightly narrower in comparison to the trigonid. Otherwise, this specimen agrees well with the others assigned to *Varalphadon*: the paraconid is lower than the metaconid, and the entoconid is broad.

Comments. — As highlighted recently by Eaton (2013), there is a paucity of diagnostic lower molar characters for many generally primitive "alphadontid"-grade taxa; in her revision of the group, Johanson (1996) focused primarily on upper molar morphology. There are currently no described lower molars for *Apistodon*, known from the Milk River and Straight Cliffs formations (Fox 1971a; Davis 2007; Eaton 2013) and expected to occur (though not yet recognized) in the Eagle Formation. *Apistodon* does not differ tremendously from *Varalphadon* in upper molar morphology and should be expected to possess lower molars which are also very similar and perhaps difficult to distinguish with certainty. It is possible that future discoveries of more complete material and larger sampling will necessitate reevaluation of lower molars currently assigned to *Varalphadon* and similar taxa.

Genus ***Alphadon*** Simpson, 1927

Alphadon halleyi Sahni, 1972

(Fig. 5A, B)

Locality and horizon: OMNH V1409, Deadhorse Coulee Member of the Eagle Formation (Santonian, Upper Cretaceous), Toole County, Montana, USA.

Referred material. — OMNH 66382, left M3 missing mesiobuccal corner; OMNH 66387, left m2 or m3.

Description. — OMNH 66382 (Fig. 5A) is identified as M3 based on the width of the distal stylar shelf relative to the lingual portion of the crown and the buccal orientation of the postmetacrista. The parastylar lobe is missing. The paracone and metacone are rounded, subequal in height, and well separated at their bases. The protocone is large and slightly inflated; the conules are accordingly well developed with strong internal cristae. Stylar cusps C and D are both moderately developed, with D slightly larger than C. The ectoflexus appears to have been rather shallow, with cusp C positioned distal to its midpoint. The postprotocrista does not extend buccally past the metacone.

OMNH 66387 (Fig. 5B) is likely from the middle of the lower molar series, as suggested by the relative heights of the bases of the trigonid and talonid in buccal view. It compares very well with specimens assigned to *Alphadon halleyi* from the Judith River Formation (particularly UCMP 131267, Montellano 1992). The tooth is well worn along the crests, with the hypoconid particularly worn and probably damaged. The paraconid is slightly lower than the metaconid, somewhat procumbent, and positioned slightly buccal to the metaconid—features typical of *Alphadon* lower molars. The talonid is slightly wider than the trigonid. Other aspects of its morphology are typical, and do not warrant full description.

Comments. — The upper molar from the Eagle Formation (OMNH 66382) agrees well with species of *Alphadon* (as opposed to *Varalphadon*) in having well-separated paracone and metacone and more robust protoconal region, while the lower molar has a relatively wider talonid. Referral to *Albertatherium* is unlikely, as stylar cusp C is small and positioned distal to the center of a shallow ectoflexus; the lower molar is smaller than specimens referred to *Albertatherium*, with weaker crests and a relatively taller protoconid. A lower molar from the John Henry Member (Santonian) of the Straight Cliffs Formation, described by Eaton (2006b), was left in open nomenclature but closely allied to *Alphadon halleyi*. Otherwise, this species is distributed broadly during the Judithian, from the Dinosaur Park (Fox 1979a), Judith River (Sahni 1972; Montellano 1992), Kaiparowits (Cifelli 1990b), and Aguja (Cifelli 1994) formations. Both Eagle Formation specimens are within the size range of molars referred to *A. halleyi*, and are smaller than molars referred to *A. sahnii* (see Montellano 1988; Montellano 1992; Cifelli 1994).

Genus ***Albertatherium*** Fox, 1971a

Albertatherium primus Fox, 1971a

(Fig. 5C, D)

Locality and horizon: All OMNH V1409, Deadhorse Coulee Member of the Eagle Formation (Santonian, Upper Cretaceous), Toole County, Montana, USA.

Referred material. — OMNH 66378, right M1 missing protoconal region; OMNH 66377, left M2 missing protoconal region; OMNH 66391, fragmentary left M4.

Description. — OMNH 66378 is heavily worn and broken, but differs from OMNH 66377 only in morphology expected of a mesial molar (parastyle lingual in position and in line with the paracone and metacone, and a slightly more oblique postmetacrista). It is accordingly not illustrated here. OMNH 66377 (Fig. 5C) is missing the lingual portion of the crown, including the protocone and paraconule. It is identified as M2 based on the slightly narrower parastylar lobe as compared to the metastylar lobe (nearly equal in width on M3). The paracone and metacone are subequal in height with the metacone slightly broader. Crests are all well developed; the postmetacrista is long and mainly buccal in orientation, but not particularly tall nor notched. The preparacrista bows mesially before doubling back toward the apex of the very large stylocone (the preparacrista runs toward the parastyle in some specimens referred to *Albertatherium*, see Fox 1971a; Johanson 1994). A sharp, slightly notched crest connects the apices of the stylocone and parastyle, the latter of which bears a strong mesial keel which would likely have overlapped the preceding molar. Stylar cusps C and D are also large; cusp C is conical and positioned at or just distal to the center of a deep, somewhat wide ectoflexus. Cusp D is not connected to cusp C, though it has several short crests descending from

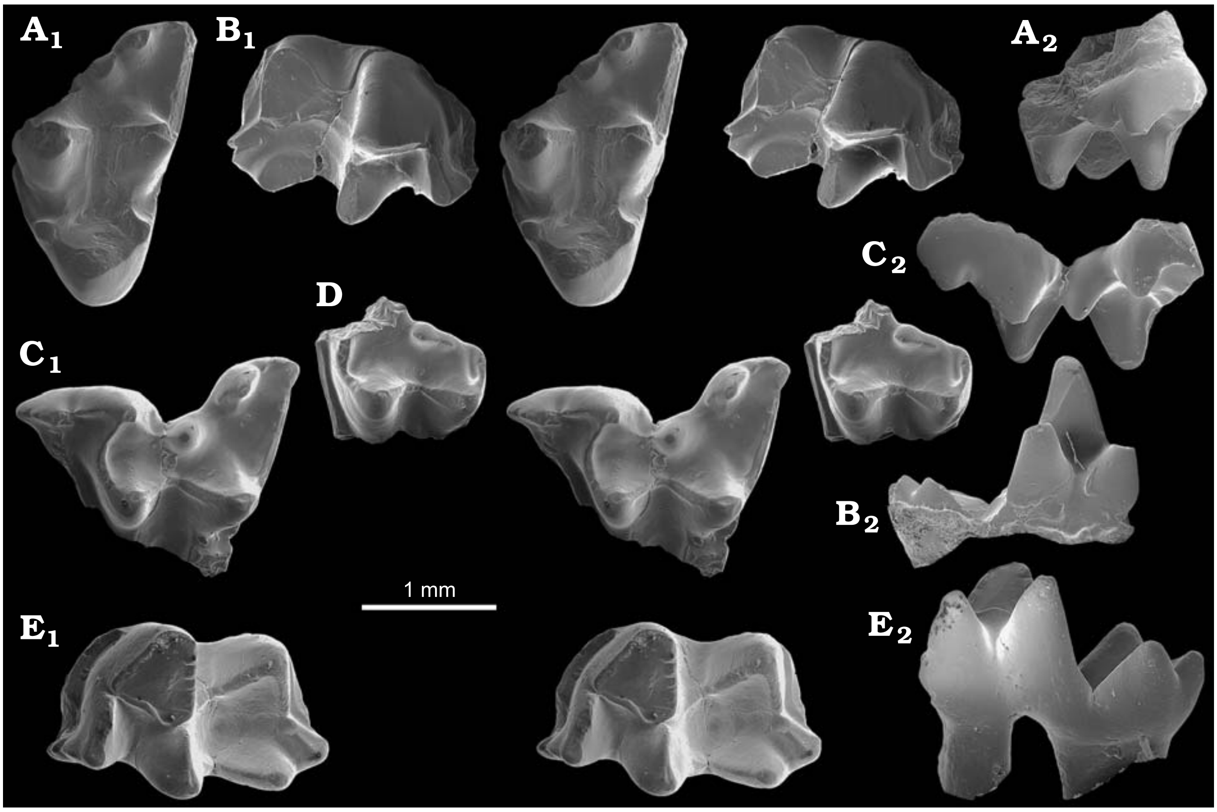

Fig. 5. The "alphadontid" marsupialiforms *Alphadon halleyi*, *Albertatherium primus* and *Albertatherium* sp. from the Eagle Formation (all OMNH locality V1409, Upper Cretaceous, Santonian, Montana). **A**, **B**. *Alphadon halleyi*. **A**. OMNH 66382, left M3 in occlusal (A_1, stereopair) and buccal (A_2) views. **B**. OMNH 66387, left m2 or m3 in occlusal (B_1, stereopair) and lingual (**B**2) views. **C**, **D**. *Albertatherium primus*. **C**. OMNH 66377, left M2 in occlusal (C_1, stereopair) and buccal (C_2) views. **D**. OMNH 66391, left M4 in occlusal (stereopair) view. **E**. *Albertatherium* sp., OMNH 66380, right m2 or m3 in occlusal (E_1, stereopair) and lingual (E_2) views.

its apex. Part of the metaconule is preserved, and internal conular cristae were present. The postprotocrista does not extend buccally past the metacone.

OMNH 66391 (Fig. 5D) has the reduced metacone and metastylar lobe typical of ultimate molars. The parastylar lobe and lingual half of the crown are missing. The paracone agrees well in size and shape with OMNH 66377, and the preserved part of the tooth is morphologically appropriate for referral to the same taxon. The preparacrista is strong and notched, and stylar cusp C is large and centrally positioned. Though short, the postmetacrista is also well developed.

Comments. — The spellings of the species names for *Albertatherium* were incorrectly emended by Kielan-Jaworowska *et al.* (2004) to *A. primum* and *A. secundum*. As the original species names were derived from Latinized nouns, it is not required that they agree with the gender of the generic name (ICZN 1999); therefore, we retain the original spellings here.

Albertatherium sp.

(Fig. 5E)

Locality and horizon: OMNH V1409, Deadhorse Coulee Member of the Eagle Formation (Santonian, Upper Cretaceous), Toole County, Montana, USA.

Referred material. — OMNH 66380, right m2 or m3.

Description. — OMNH 66380 is a moderately worn lower molar, well preserved except for breakage of the protoconid. The cusps and crests are rather robust, and it is of appropriate size for referral to *Albertatherium*. The paraconid and metaconid are erect and of similar size at their bases, with the paraconid slightly shorter and positioned slightly buccal. The paracristid is quite strong and bears a well-developed notch. The protocristid is also notched. The mesial keel on the paraconid is very sharp and cuspidate along its height. The talonid is subequal in width to the trigonid. The cusps are all well developed, with the hypoconulid recumbent and the smallest of the three. A notch is present at the base of each crest connecting the cusps, including the entocristid and cristid obliqua, which rises to meet the protocristid notch. This lower molar is probably from the middle of the series.

Comments. — Johanson (1994) named a second species of *Albertatherium* from the Milk River Formation, *A. secundus*, on the basis of two upper molars which differed from those of the type species only in lacking stylar cusp C. The variability of this cusp among other "didelphid"-like taxa raises caution as to its taxonomic utility when employed alone, but perhaps a future larger sample will bolster diagnostic support of two species of *Albertatherium*. Johanson (1994) proposed no diagnostic characters for lower molars to separate these two species, and simply referred all lower molars from Verdigris Coulee to *A. primus*. We take a more conservative approach and leave the lower molar from the Eagle Formation in open nomenclature.

Superfamily **Pediomyoidea** Simpson, 1927

Family **Aquiladelphidae** Davis, 2007

Genus ***Aquiladelphis*** Fox, 1971a

Aquiladelphis incus Fox, 1971a

(Fig. 6A)

Locality and horizon: OMNH V1409, Deadhorse Coulee Member of the Eagle Formation (Santonian, Upper Cretaceous), Toole County, Montana, USA.

Referred material. — OMNH 66351, left M3.

Description. — OMNH 66351 is a very large (Table 1), distinctive upper molar unquestionably belonging to *Aquiladelphis incus*, originally described from the Milk River Formation. The parastylar lobe is nearly as wide as the metastylar lobe (though the entire stylar shelf is narrow, a feature common to pediomyids and their relatives, Davis 2007), and the parastyle is buccal to the paracone; these features suggest that this specimen is an M3. The crown has heavy, somewhat low cusps with a very broad trigon basin and strong, cuspidate crests. The paracone and metacone are widely separated, with the paracone being the taller of the two. The preparacrista is weak, notched, and runs to a relatively low, broad stylocone positioned very close to the paracone. A series of cuspules trails distally along a crest from the apex of the stylocone. The ectocingulum is strong and cuspidate along the entire buccal margin of the crown. The dominant feature of the stylar shelf is the massive cusp C, positioned distal to the center of the very shallow ectoflexus. A number of crests descend from the apex of this pyramidal cusp, one of which reaches the base of the centrocrista. The abraded base of a small cusp corresponding to cusp D is present on the distal flank of cusp C. The postmetacrista is low. Crenulated cingula flank both sides of the low, broad protocone. The conules are blunt and bear weak internal cristae, one feature in which this specimen differs from others referred to this taxon. The postprotocrista extends buccally past the metacone, but does not reach the metastylar area.

Aquiladelphis minor Fox, 1971a

(Fig. 6B, C)

Locality and horizon: OMNH V1409, Deadhorse Coulee Member of the Eagle Formation (Santonian, Upper Cretaceous), Toole County, Montana, USA.

Referred material. — OMNH 66352, left MX preserving only mesiobuccal corner; OMNH 66353, right m2.

Description. — OMNH 66352 (Fig. 6B) is a worn and fragmentary mesiobuccal corner of an upper molar. It agrees well in general morphology with OMNH 66351 except for its much smaller size, which is appropriate for *Aquiladelphis minor*. The paracone is fairly low and robust. The stylocone is small and the parastylar lobe quite narrow, and what remains of the ectocingulum is cuspidate.

OMNH 66353 (Fig. 6C) is a worn but complete lower molar. It is fairly low crowned with robust cusps and crests; this, together with its size and the buccal attachment of the cristid obliqua to the trigonid, indicates referral to *Aquiladelphis* (the paraconid is lower than the metaconid, which precludes stagodontid affinity). The specimen is very similar to UALVP 5534 from the Milk River Formation (see Davis 2007, fig. 22B), and likely represents the same locus (m2).

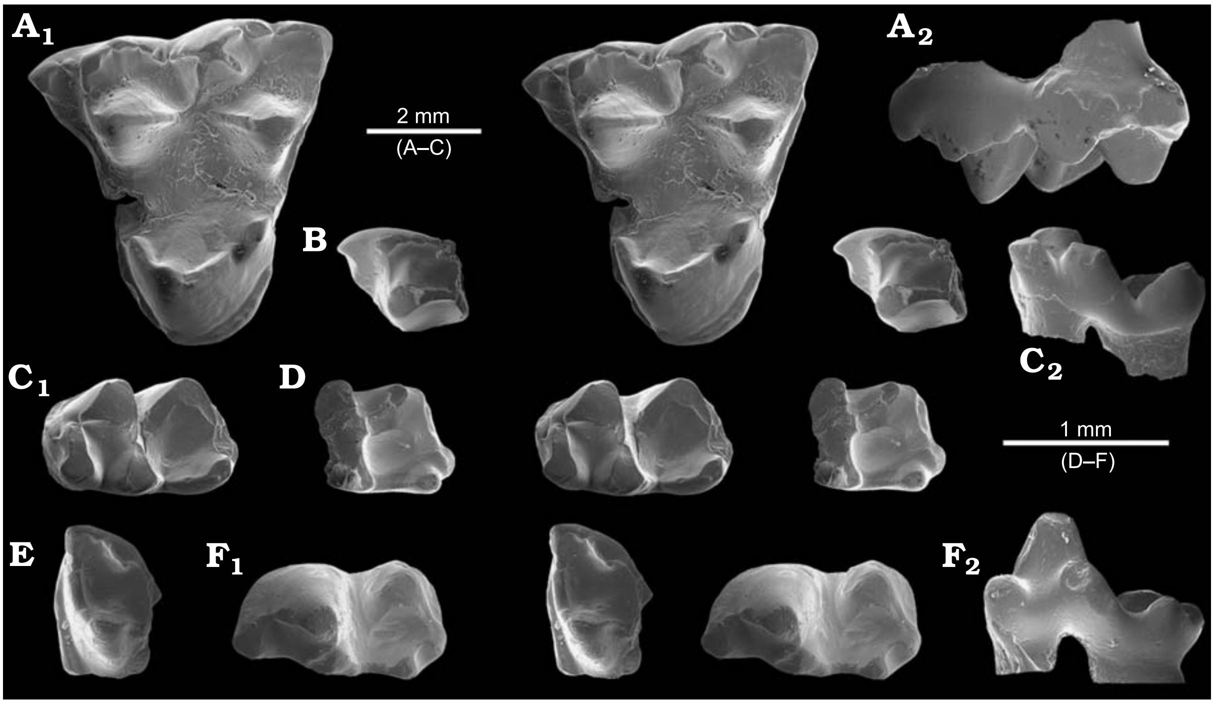

Fig. 6. The pediomyoid marsupialiforms *Aquiladelphis* and *Leptalestes*, and basal metatherians from the Eagle Formation (all OMNH locality V1409, Upper Cretaceous, Santonian, Montana). **A**. *Aquiladelphis incus*, OMNH 66351, left M3 in occlusal (A_1, stereopair) and buccal (A_2) views. **B**–**C**. *Aquiladelphis minor*. **B**. OMNH 66352, left MX in occlusal (stereopair) view. **C**. OMNH 66353, right m2 in occlusal (C_1, stereopair) and lingual (C_2) views. **D**. *Leptalestes* sp., OMNH 66366, right mx in occlusal (stereopair) view. **E**. *Iqualadelphis lactea*, OMNH 66347, Right MX in occlusal (stereopair) view. **F**. Metatheria indet., OMNH 66341, right dp3 or m1 in occlusal (F_1, stereopair) and lingual (F_2) views.

Comments. — Molars of *Aquiladelphis* are highly distinctive and readily identifiable. This taxon is somewhat broadly distributed, with a probable additional Aquilan occurrence in the John Henry Member of the Straight Cliffs Formation (unidentified pediomyids in Eaton *et al.* 1999, fig. 3C, D), as well as records in younger units (Judithian Fruitland Formation, Rigby and Wolberg 1987; and "Edmontonian" Williams Fork Formation, Diem 1999). A similar species (*A. laurae*) was described from a Campanian locality in Cedar Canyon, southwestern Utah, possibly in the Wahweap Formation or an equivalent unit (Eaton 2006a).

Family **Pediomyidae** Simpson, 1927

Leptalestes sp. Davis, 2007

(Fig. 6D)

Locality and horizon: OMNH V1409, Deadhorse Coulee Member of the Eagle Formation (Santonian, Upper Cretaceous), Toole County, Montana, USA.

Referred material. — OMNH 66366, right mx preserving talonid only.

Description. — OMNH 66366 is a very small, fragmentary, and abraded lower molar missing all of the trigonid except the bases of the protoconid and metaconid. However, enough is preserved to permit brief description and comparisons. The talonid is subequal in width to the trigonid; the hypoconid is leveled by wear, but in distal view the base of this cusp is substantially lower than the lingual base of the talonid. The entoconid is quite tall and conical, and strongly twinned with the hypoconulid. The cristid obliqua is short and, based on its orientation, appears likely to have met the trigonid wall at a point buccal to the protocristid notch.

Comments. — This specimen, though poorly preserved, compares quite well with small pediomyids from younger rock units. Coupled with its very small size and delicate construction, the strong twinning of the talonid cusps, tall entoconid, and general buccal sloping of the talonid are all shared by the Judithian *Leptalestes prokrejcii* (Fox 1979b). While the preserved morphology of the specimen is a very close match, specific referral is left open due to the limited available material.

Family incertae sedis

Iqualadelphis lactea Fox, 1987

(Fig. 6E)

Locality and horizon: OMNH V1409, Deadhorse Coulee Member of the Eagle Formation (Santonian, Upper Cretaceous), Toole County, Montana, USA.

Referred material. — OMNH 66347, right MX preserving only distobuccal corner.

Description. — OMNH 66347 is an upper molar fragment preserving only the distobuccal corner of the crown. The metacone is slender and angular, with a strong postmetacrista that is oriented buccally. A small but well-defined and elongate cusp D is present on the stylar shelf, and the postprotocrista extends buccally almost to the edge of the crown. In these regards (as well as size), the specimen is very similar to molars referred to *Iqualadelphis lactea* from the Milk River Formation (see Johanson 1993).

Infraclass **Metatheria** indet.

(Fig. 6F)

Locality and horizon: OMNH V1409, Deadhorse Coulee Member of the Eagle Formation (Santonian, Upper Cretaceous), Toole County, Montana, USA.

Referred material.—OMNH 66341 right dp3 or m1.

Description.—OMNH 66341 is a small metatherian lower molariform representing a taxon not yet clearly known by other materials. Trigonid structure suggests a molar from the front of the series or, possibly, a deciduous premolar. The paraconid is low, procumbent, and positioned near the midline of the crown, making the trigonid quite open lingually. The metaconid is damaged but appears to have been low with a gentle distal slope towards the talonid, which is wider than the trigonid. The molar cusps are generally low and somewhat inflated. There is no clear development of a precingulid. A distinct neck is present at the distal root-crown junction, possible evidence that this tooth may have been in the process of root resorption and subsequent shedding of the crown. It is similar in size but quite different in morphology from the dp3 referred here to *Varalphadon*. The specimen is smaller than but otherwise very similar to UMNH VP 6793 from the Wahweap Formation (Eaton 2013, fig. 15.13B), tentatively referred to *Iugomortiferum*, a metatherian genus of uncertain affinities otherwise known from the Wahweap Formation (Cifelli 1990c). A larger sample is needed before a confident referral of this specimen can be made.

Infraclass **Eutheria** Gill, 1872

Incertae sedis

Paranyctoides sp. Fox, 1979c

(Fig. 7A)

Locality and horizon: OMNH V1409, Deadhorse Coulee Member of the Eagle Formation (Santonian, Upper Cretaceous), Toole County, Montana, USA.

Referred material. — OMNH 66346, right MX preserving only protoconal region.

Description. — OMNH 66346 is the lingual half of an upper molar that agrees in size and preserved morphology with *Paranyctoides*, known from various Late Cretaceous occurrences, including the Milk River and Oldman formations (Fox 1979c, 1984a). The protocone is angular and leans mesially. Though the metaconule is missing it is clear that the paraconule was positioned higher on the crown. Internal conular cristae and the pre- and postprotocristae are very strong and sharp. Broad cingula flank both sides of the protocone at its base. The trigon basin is narrow and deep.

Comments. — *Paranyctoides* is also known from the early Campanian Wahweap Formation and several other units (Cifelli 1990d ; Kielan-Jaworowska et al. 2004). Older records from the Turonian–Coniacian of Asia have been referred to this genus (see review in Averianov and Archibald 2013), but the validity of Asiatic *Paranyctoides* has recently been questioned (Montellano-Ballesteros *et al.* 2013). Eutherians are rare components of the Eagle fauna, with only two specimens that can be referred with confidence: a single specimen of *Paranyctoides* and an indeterminate upper molar fragment described below. It is likely that further sampling will yield additional material — *Paranyctoides*, for example, is known by many more specimens in the comparatively much better sampled Milk River Formation (Fox 1984a; Montellano-Ballesteros *et al.* 2013).

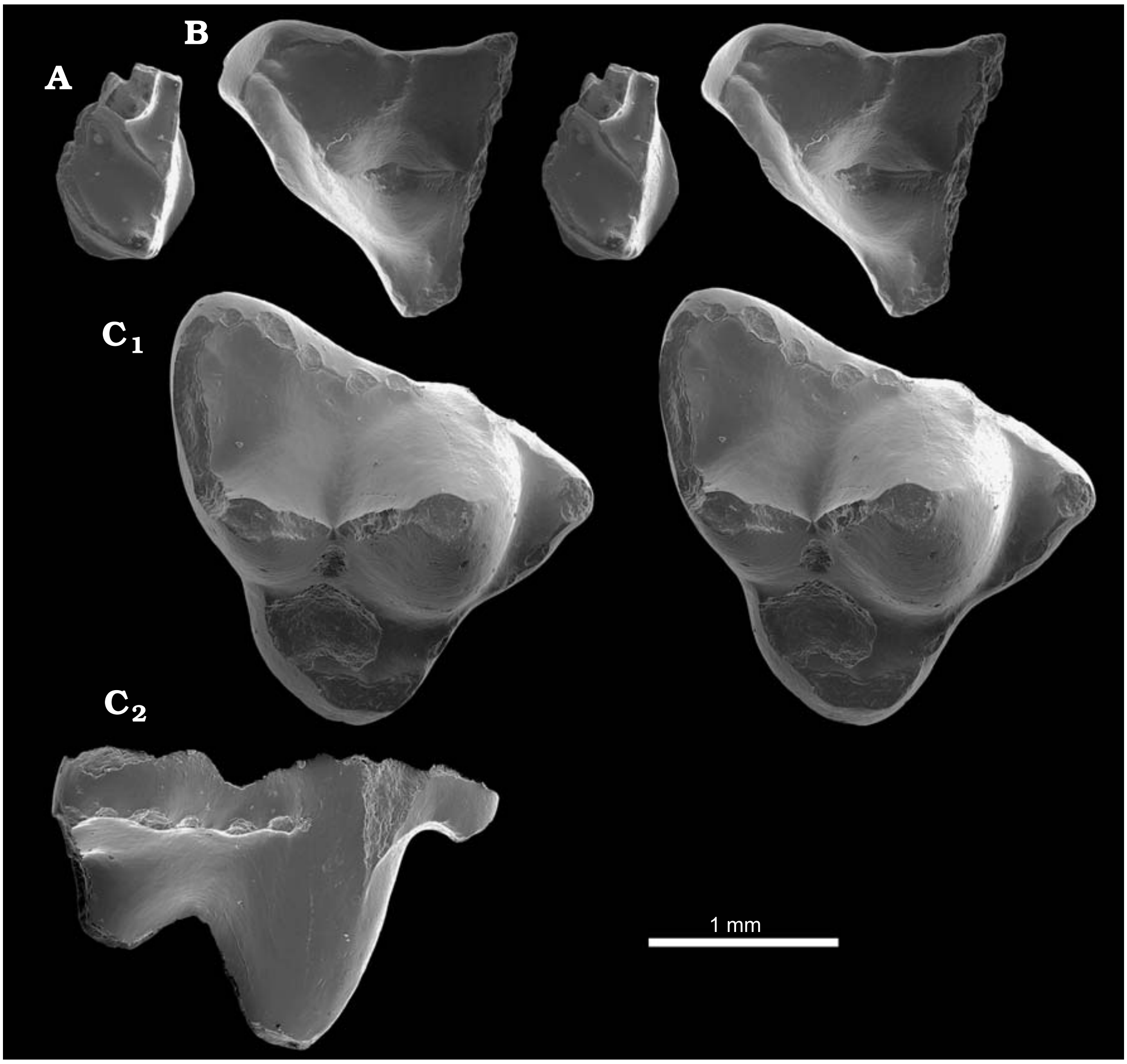

Fig. 7. Eutherians and Tribosphenida indet. from the Eagle Formation (Upper Cretaceous, Santonian, Montana). **A**. *Paranyctoides* sp., OMNH 66346 (OMNH locality V1409), right MX in occlusal (stereopair) view. **B**. Eutheria indet., OMNH 66344 (OMNH locality V1409), left MX in occlusal (stereopair) view. **C**. Tribosphenida indet., OMNH 64165 (OMNH locality V1412), right upper molariform in occlusal (C_1, stereopair) and buccal (C_2) views.

Infraclass **Eutheria** indet.

(Fig. 7B)

Locality and horizon: OMNH V1409, Deadhorse Coulee Member of the Eagle Formation (Santonian, Upper Cretaceous), Toole County, Montana, USA.

Referred material. — OMNH 66344, left MX preserving only mesiobuccal corner.

Description. — OMNH 66344 is an upper molar fragment preserving only the mesiobuccal corner of the tooth. This specimen is identified as eutherian based on favorable comparisons with taxa known by relatively complete material (in particular, *Aspanlestes*, see Archibald and Averianov 2012, fig. 7). The paracone is robust and rounded, with a weak preparacrista oriented mesiobuccally. The preparacrista terminates just mesial to the apex of the parastyle, which is positioned far buccal and mesial to the paracone. The stylocone is absent or is represented by one or two small cuspules along the ectocingulum buccal to the paracone. A preparastyle is lingual to and in close proximity with the parastyle, and while the mesial cingulum in this region is broad, the preprotocrista is discontinuous at the level of the paracone. Nothing is preserved of the lingual portion of the tooth. The parastylar lobe is narrow but an ectoflexus was present and the stylar shelf appears to be widening distally at the broken margin of the crown, suggesting that this is not an ultimate molar.

Comments. — The preserved morphology of OMNH 66344 compares favorably to zhelestids, with its rounded paracone, crenulations along its ectocingulum, and a narrow parastylar lobe, although not quite as narrow as seen in *Aspanlestes* and *Parazhelestes* (Archibald and Averianov 2012). Some specimens referred to these taxa show a similar interruption in the preprotocrista. The buccal separation between the paracone and parastyle coupled with the interpreted width of the distal stylar shelf are most consistent with M2. Unfortunately, the limited portion of the crown preserved precludes taxonomic referral and further comparisons.

Subclass **Tribosphenida** indet.

(Fig. 7C)

Locality and horizon: OMNH V1412, Deadhorse Coulee Member of the Eagle Formation (Santonian, Upper Cretaceous), Toole County, Montana, USA.

Referred material. — OMNH 64165, right upper molariform.

Description. — OMNH 64165 is a complete upper molariform tooth with peculiar morphology. The swollen paracone is the dominant feature on the crown; its conical base occupies much of the occlusal surface. The metacone is closely appressed to the paracone and less than half its height. It is connected to the paracone by a well-worn, straight centrocrista. The postmetacrista is long, very well developed and is heavily worn; the enamel at the base of the metacone is pinched, suggesting the possible presence of a notch along the postmetacrista. The crest is oriented buccally and forms a 90° angle with the centrocrista. The only trace of a preparacrista is a faint mesiobuccal crest that blends with an abraded portion of the ectocingulum; this crest does not clearly reach the apex of the paracone. A stylocone is absent. The parastyle is low and positioned on a broad flange well separated from the paracone. A straight line can be formed through the apices of the parastyle, paracone, and metacone. The tooth has a nearly flat buccal margin with no development of an ectoflexus, and while stylar cusps are not clearly developed, a series of abraded cuspules are present along the ectoflexus, the largest of which is in the position of stylar cusp D. The protoconal region is low, somewhat flat, and small. Much of the enamel is missing from this part of the tooth, but the protocone appears to be poorly developed and somewhat mesiodistally long. Conules are not obvious; the area of the metaconule is damaged, and a very tiny cuspule is present in the position of the paraconule. The trigon basin is developed as a shallow, horizontal trough. The postprotocrista terminates at the lingual base of the metacone without wrapping distally; the preprotocrista is interrupted briefly near the lingual base of the paracone but continues to the parastyle. Wear facets are developed in the embrasure formed by the centrocrista and along the postmetacrista, but no facets are visible on the mesial face of the paracone or flanking the protocone.

Comments. — The unusual morphology exhibited by this tooth suggests a number of interesting possible affinities, none of which is completely convincing. Broadly similar fossils from the Cedar Mountain Formation (Cenomanian, Utah, USA) are described elsewhere in this volume (Cifelli *et al.* 2016 this volume), and we offer complementary comments here. OMNH 64165 invites comparison with deciduous upper premolars of metatherians. However, a stylocone is commonly present on dP3 of metatherians, and features of the protoconal region (such as conules and the pre- and postprotocristae) would be expected to be better developed (see Clemens 1966). The DP3 is unknown for *Aquiladelphis*, which is represented by two species in this assemblage. As in OMNH 64165, the stylocone of *Aquiladelphis* is reduced and the parastylar lobe is narrow to absent in this and related pediomyoid taxa (Davis 2007), but the lingual half of the tooth is very broad and the postcingulum is well developed. If OMNH 64165 were a DP3 of *Aquiladelphis*, these features should be present (albeit in reduced form). Additionally, the postmetacrista on this specimen is oriented directly buccally, while this crest is oblique in known Cretaceous metatherian DP3s.

Some features of OMNH 64165 can be interpreted as plesiomorphic for tribosphenidan molars in general: the relative proportions of the paracone and metacone and the very small protocone are reminiscent of the aegialodontid *Kielantherium* (Lopatin and Averianov 2006). Similarly, the Eagle specimen is a close match for some specimens referred by Fox (1980) to cf. *Picopsis* sp. from the Milk River Formation. *Picopsis pattersoni* was originally proposed as a basal tribosphenidan most closely allied with aegialodontids (including *Kielantherium*). The holotype of *P. pattersoni* is damaged, but it most likely instead represents a metatherian deciduous upper premolar: the metacone is well separated from the paracone and is not much smaller, the postmetacrista is oriented obliquely, and a large stylar cusp is present in the C or D position (Fox 1980, fig. 1; specimen better illustrated in Scott and Gardner 2013, fig. 3A,B). Though poorly preserved, the material informally referred by Fox (1980) to cf. *Picopsis* sp. appears to depart from a typical metatherian DP3 and likely does not represent the same taxon as the holotype of *P. pattersoni*. The same can be said of OMNH 64165, yet the affinities of these specimens are still unclear.

A second primitive-grade tribosphenidan was recently described from the same locality that yielded *Picopsis* in the Milk River Formation, *Tirotherium aptum* Montellano-Ballesteros *et* Fox, 2015. Some features of the upper molars compare well with OMNH 64165, such as the inflated paracone, absence of a stylocone, and well-developed, buccally-oriented postmetacrista (on some specimens). However, the protocone and conules of *Tirotherium* are strong and rounded, with sharp internal cristae, flanking a deep trigon basin. The postprotocrista extends buccally to the level of the metacone. In these regards, *Tirotherium* is more derived than *Picopsis* (sensu lato) and the Eagle specimen or, more likely, *Tirotherium* more closely resembles a metatherian DP3. Further discussion of this taxon is beyond the scope of this paper, but see Cifelli *et al.* (2016 this volume) for more thorough comments on *Picopsis*-like taxa.

The loss of the stylocone and mesial stylar shelf on OMNH 64165 can also be regarded as derived features relative to the primitive therian condition. The strong emphasis on postvallum shearing and structural neglect of the protocone are characteristic of advanced deltatheroidans, among these in particular the Lancian *Nanocuris* (Fox *et al.* 2007; Wilson and Riedel 2010; Rougier *et al.* 2015). OMNH 64165 is superficially very similar to AMNH 59451, identified as ?*Nanocuris* sp. (Wilson and Riedel 2010, fig. 4). The Eagle specimen is about a third smaller. The protocone is better developed and transversely wider in *Nanocuris*, but is still quite small and (like OMNH 64165) lacks conules. The paracone and metacone have similar relative proportions, and in both specimens the postprotocrista lacks buccal extension, the mesial stylar shelf is narrow to absent, and the preparacrista is very poorly developed. The Eagle specimen is comparatively narrower transversely, and the complete absence of the stylocone and extreme swelling of the paracone are inconsistent with known deltatheroidans. The enlarged paracone lacking a stylocone and the poorly developed protoconal region are, however, characteristic of some semi-molariform eutherian premolars. The same upper molar referred to ?*Nanocuris* sp. by Wilson and Riedel (2010) was originally described by Clemens (1973, p. 71), with discussion of possible identity as a DP3 of an unknown cimolestid. While OMNH 64165 does bear some superficial similarities to known Paleocene cimolestids (*e.g.*, Williamson *et al.* 2011), the length and orientation of the postmetacrista and narrow protocone do not compare favorably. Further comparison must await additional specimens representing other tooth positions of this enigmatic mammal from the Eagle Formation.

DISCUSSION

The discovery of fossil mammals in the Eagle Formation is significant not only in that it brings to light unrecognized, highly productive paleontological potential in a rock unit within the United States Western Interior, but because it also contributes data to improve our understanding of an important interval in the evolution of modern mammalian faunas in North America. Knowledge of mammal evolution on this continent during the first ~60 Ma of the Cretaceous (Berriasian–Santonian) is generally poor, punctuated by a few well-sampled assemblages that rarely form an overlapping or continuous record (see the following and references within: Kielan-Jaworowska *et al.* 2004; Davis and Cifelli 2011; Eaton and Cifelli 2013; Cifelli *et al.* 2014; Cifelli and Davis 2015; Cifelli *et al.* 2016 this volume). Consequently, there are no widely-recognized NALMAs for faunas older than Aquilan (Cifelli *et al.* 2004). It is not until the Santonian–Campanian that sampling and taxonomic resolution are sufficient to permit the recognition of a broad biostratigraphic framework for correlating local faunas. The Aquilan NALMA was originally defined on the basis of the fauna from the Milk River Formation (Lillegraven and McKenna 1986), and later expanded to include assemblages from the Wahweap and Masuk formations (Cifelli *et al.* 2004). Characteristic first occurrences are the neoplagiaulacid multituberculate *Mesodma*, the stagodontid *Eodelphis*, and the eutherian *Paranyctoides*. The first pediomyoids also appear, including the large and distinctive *Aquiladelphis*.

It should be no surprise that the known components of the mammalian fauna from the Eagle Formation are broadly similar to that of the contemporary and geographically proximal Milk River Formation (Table 2). Of the taxa described here, three are absent from Verdigris Coulee: *Alphadon halleyi* (several isolated lower molars from the Milk River Formation were initially assigned to *Alphadon*, but later intimated to

Table 2. Mammal taxa (excluding multituberculates and some taxa left in open nomenclature) from units currently assigned to the Aquilan North American Land Mammal Age (NALMA), and occurrences in older (Turonian–Coniacian) and younger (Judithian NALMA) assemblages. Inclusion of the upper John Henry Member of the Straight Cliffs Formation in the Aquilan is best regarded as provisional. Abbreviations: E, Eagle Formation; J, Judithian (includes Judith River, Dinosaur Park, and Kaiparowits formations); JH, John Henry Member of Straight Cliffs Formation; MR, Milk River Formation; SH, Smoky Hollow Member of Straight Cliffs Formation; W, Wahweap Formation. Compiled from Kielan-Jaworowska *et al.* (2004) and Eaton and Cifelli (2013).

		Aquilan					
		SH	E	MR	JH	W	J
Eutriconodonta	*Alticonodon lindoei*			×			
	Alticonodon sp.				cf.		
“Symmetrodonta”	*Spalacotheridium mckennai*	×	×				
	Spalacotheridium sp.				×		
	Symmetrodontoides canadensis		×	×			
	Symmetrodontoides foxi					×	
	Symmetrodontoides oligodontos	×			cf.		
	Symmetrodontoides sp.				×		
Tribosphenida indet.	*Potamotelses aquilensis*			×			
	Potamotelses sp.				×		
	Zygiocuspis goldingi					×	
	Picopsis pattersoni			×			
	Picopsis sp.			×	×		
	Tirotherium aptum			×			
Metatheria indet.	*Iugomortiferum thoringtoni*					×	
	Iqualadelphis lactea		×	×			
	Apistodon exiguus			×	cf.	cf.	
“Alphadontidae”	*Albertatherium primus*		×	×			
	Albertatherium secundus			×			
	Alphadon halleyi		×		cf.		×
	Alphadon sp.	×		×			×
	Varalphadon creber			×		cf.	
	Varalphadon crebreforme					×	
	Varalphadon wahweapensis		×	×		×	×
	Varalphadon sp.		×		×	cf.	
	Turgidodon russelli					cf.	×
	Turgidodon sp.					×	×
Pediomyoidea	*Aquiladelphis incus*		×	×			
	Aquiladelphis minor		×	×			×
	Leptalestes sp.		×		×		×
Stagodontidae	*Eodelphis* sp.			×	×		×
Eutheria	*Paranyctoides maleficus*			×			×
	Paranyctoides sp.		×			×	×

belong to either *Turgidodon praesagus* or a different genus, Fox 1979a), the pediomyid *Leptalestes*, and *Spalacotheridium mckennai*. The occurrence of *Spalacotheridium* is interesting in that this spalacotheriid genus is otherwise only known from southern Utah, including older assemblages in the Smoky Hollow Member of the Straight Cliffs Formation (Turonian) and the Cedar Mountain Formation (Albian–Cenomanian). The absence from the Eagle assemblage of certain other Aquilan taxa (*e.g.*, the distinctive eutriconodontan *Alticonodon*, the basal tribosphenidan *Potamotelses*, the basal metatherian *Apistodon*, and the stagodontid *Eodelphis*) could be attributed to the small sample so far attained from the unit.

The fauna from the upper part of the John Henry Member of the Straight Cliffs Formation is similar in age to the Eagle assemblage (Eaton 2006b, 2013), but current taxonomic resolution does not allow close comparison. The two units share many genera (including the geologically oldest record of the pediomyid *Leptalestes*, otherwise known from the Judithian–Lancian), but no taxa identified to the species level are in common. Some key taxa are shared between the John Henry and Milk River Formation, such as *Alticonodon*, *Potamotelses*, and *Apistodon*, so it is likely that additional collections (especially of more complete material) will permit formal inclusion of the John Henry assemblage into the Aquilan; for present purposes, we do so only provisionally.

The somewhat younger Wahweap Formation (and its lateral correlate, the Masuk Formation) has been included in the Aquilan based on taxa shared with the Milk River Formation, notably the multituberculates *Cimexomys antiquus* (though the Wahweap taxon is only conferred), *Cimolodon similis* and *C. electus*, the spalacotheriid *Symmetrodontoides*, and the marsupialiform *Varalphadon*. However, the presence of several other multituberculate taxa and the marsupialiform *Turgidodon* hint at closer ties with younger, Judithian assemblages (see Eaton and Cifelli 2013, table 14.1). The age of the Wahweap Formation has recently been adjusted based on a radiometric date from low in the unit (Jinnah *et al.* 2009); the Wahweap occupies a slice of time some ~3 Ma younger than the Milk River Formation, yet still several million years older than most Judithian assemblages (Jinnah 2013). Perhaps, as suggested by Eaton and Cifelli (2013), the Wahweap fauna should be housed in a separate biostratigraphic zone for the early–middle Campanian.

Whether the differences between the Milk River fauna in southern Alberta and those from southern Utah are related to slight differences in age or are due to differences in latitude or paleoenvironment remain open questions. Still, several trends emerge regarding patterns of mammal diversity during the Santonian–Campanian. Symmetrodontans make their final appearance during this interval, but they were reasonably diverse. At the same time, eutherians are beginning to diversify after a hiatus of ~25 Ma since their first (Albian) appearance on the continent (Cifelli and Davis 2015). The presence of *Paranyctoides* and an indeterminate zhelestid-like taxon (OMNH 66344, Eagle Formation) hint at the possibility of migration playing a role in seeding some of this diversity, as these groups are present in older rocks in central Asia (Archibald and Averianov 2005). Pediomyoid marsupialiforms also make their first appearance during the Aquilan. Though direct competition between extinct groups is difficult to evaluate, the demise of symmetrodontans may be related to the diversification of latest Cretaceous therian lineages (see also Grossnickle and Polly 2013). While zhelestids have broad, rather generalized molars, the Judithian records the appearance of therians with much more insectivorous or sectorial teeth, such as *Gypsonictops* and *Cimolestes*. Moreover, many pediomyid taxa are quite small (*e.g.*, *Leptalestes*) and likely occupied the same dietary niche as most symmetrodontans.

Finally, the first appearances of *Eodelphis* and *Aquiladelphis* are noteworthy in that these taxa are large and possess molars with heavy cusps and crests. These are not the first Cretaceous records of therians with such a modified dentition: the stagodontid *Pariadens* is known from the Cenomanian Cedar Mountain and Dakota formations (Cifelli and Eaton 1987; Cifelli 2004), and while poorly known, *Argaliatherium* from the Albian Cloverly Formation clearly has similar specializations (Cifelli and Davis 2015). However, the presence of this morphotype in the Aquilan suggests increased utilization of a dietary niche among marsupialiforms during the Late Cretaceous. Increased sampling and better taxonomic resolution, especially from promising but poorly explored units such as the Eagle Formation, is ultimately needed to further address questions of ecological specialization and the timing of events such as diversification or dispersal. The biostratigraphic definitions linking the geographically broad but discontinuous mammalian record are in need of refinement, and additional fossils will shed light on the major transitions evident among Cretaceous mammal faunas in North America.

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