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Earliest Cretaceous mammals from the western United States

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Mammalian diversity in North America shifted significantly during the Early Cretaceous, from archaic groups dominant in the well-sampled faunas of the Late Jurassic to advanced forms (including early members of modern clades) by the Albian–Cenomanian. However, the dynamics of this transition are poorly understood, since faunas of earliest Cretaceous age are unknown. Here we describe the first fossil mammals from exposures of the Lakota Formation in the Black Hills of South Dakota, a unit correlated with the upper Berriasian–lower Barremian and positioned stratigraphically between the underlying Morrison Formation and Aptian–Albian units exposed elsewhere in North America. The mammalian fauna from the Lakota Formation is transitional with regard to the North American fossil record, representing a broad spectrum of both Jurassic and Cretaceous lineages: present are “plagiaulacidan” multituberculates allied with Late Jurassic Allodontidae and Early Cretaceous Plagiaulacoidea; the geologically youngest dryolestoid(s) and “triconodontine” triconodontids (characteristic Late Jurassic taxa from the Morrison Formation); the oldest spalacotheriid “symmetrodont”; the first record of an amphitheriid-like stem zatherian from North America (abundant in the Middle Jurassic–earliest Cretaceous of Europe); and the oldest North American tribosphenic mammal (abundant and diverse on the continent by the end of the Early Cretaceous). Taxa making their first North American appearance in the Lakota Formation (Plagiaulacoidea, including a genus also known from the Purbeck of Britain; Spalacotheriidae, stem Zatheria, Tribosphenida) are also known from the Early Cretaceous of Western Europe, suggesting the possibility that they represent immigrants.

Key words: Mammalia, Multituberculata, Triconodontidae, Spalacotheriidae, Dryolestidae, Zatheria, Tribosphenida, Lakota Formation, Cretaceous, North America.

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Introduction

The Early Cretaceous represents an important interval in the evolutionary history of mammals. Across northern continents, the dominant groups of the Late Jurassic either decline dramatically in diversity (dryolestoids), are replaced by more advanced taxa, as happened to “plagiaulacidan” multituberculates and “triconodontine” eutriconodontans (see below for comments regarding the use of quotation marks around some taxa), or disappear entirely (docodonts). The known fossil record also documents the first appearance of dentally modern taxa (Tribosphenida) in the earliest Cretaceous of Europe and North Africa (Kermack et al. 1965;

Sigogneau-Russell 1991a, 1992; Sigogneau-Russell et al. 2001), although, if the reported age of *Juramaia* is correct, tribosphenidans may have originated as early as the beginning of the Late Jurassic in Asia (Luo et al. 2011) (we regard the tribosphenic-like Australosphenida of southern continents to be unrelated; see Rougier et al. 2007; Davis 2011a, and included references). By the end of the Early Cretaceous (Albian–Cenomanian boundary), significant radiations of tribosphenidans had occurred in North America (e.g., Butler 1978; Cifelli 1993, 1999a, 2004; Davis and Cifelli 2011) and Asia (e.g., Kielan-Jaworowska and Dashzeveg 1989; Ji et al. 2002; Luo et al. 2003; Lopatin and Averianov 2006a; Hu et al. 2010). Mammalian evolution followed a different path on southern continents, with monotremes making their first

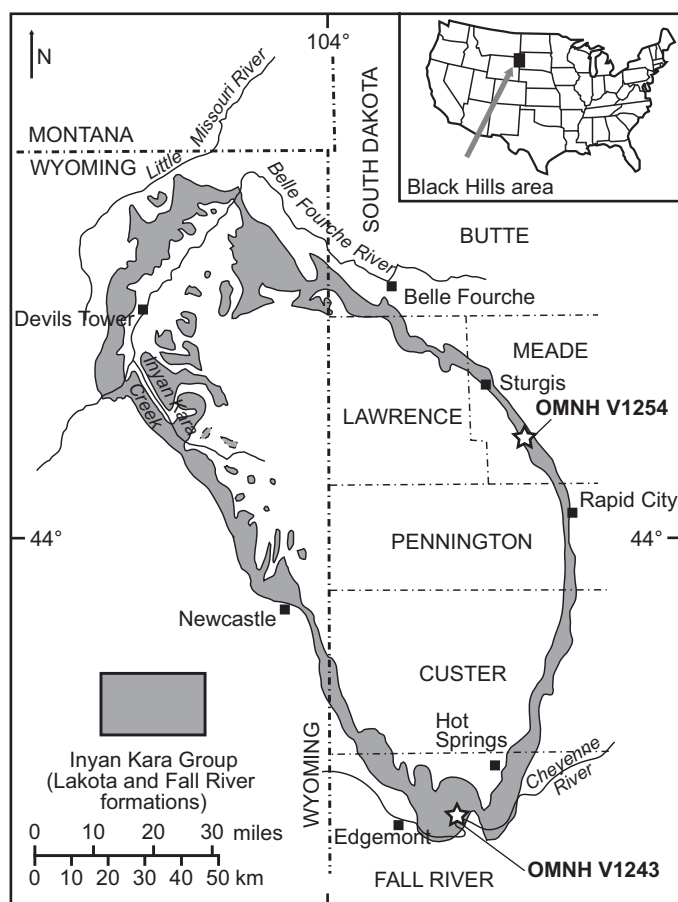


Fig. 1. Map of exposures of the Lower Cretaceous Inyan Kara Group in southwestern South Dakota and northeastern Wyoming (USA), which includes the Lakota Formation (Berriasian–Barremian). Stars indicate OMNH localities which yielded specimens described in this study. Modified from Sames (2011a), as based on Waagé (1959) and Sohn (1979).

appearance in the Aptian–Albian of Australia (Archer et al. 1985; Flannery et al. 1995). Also present are ausktribosphenids (Rich et al. 1997; Rich et al. 2001a, b), a dentally advanced group with uncertain affinities but possibly related to the pseudotribosphenic shuotheriids from the Jurassic of China and Britain (Chow and Rich 1982; Sigogneau-Russell 1998; Luo et al. 2001; see Luo et al. 2007). Increased sampling in recent decades has improved our understanding of portions of the Early Cretaceous, but most material dates from the Barremian or younger, leaving the earliest portions of the Epoch relatively unknown.

In North America, the Early Cretaceous has particular relevance. The Late Jurassic Morrison Formation (mainly Kimmeridgian–Tithonian, though time of deposition for the unit as a whole may also include the late Oxfordian and early Berriasian, see for example Kowallis et al. 1998; Miall et al. 2008) presents one of the best-known assemblages of early mammals anywhere in the world. However, the next oldest faunas on this continent are from the Cloverly, Antlers, and Arundel formations, collectively ranging from Aptian to Albian in age, leaving a considerable gap in the fossil record of some 35 Ma (here and throughout, we follow the times-

cale of Gradstein et al. 2012). Mammalian faunas in North America changed dramatically in composition during this interval. Thus, for example, major groups such as docodonts and dryolestoids went extinct, while tribosphenic mammals, undocumented prior to the Aptian–Albian, became abundant and diverse. Questions of whether this transition can be characterized as gradual or abrupt, and whether or not these lineages ultimately have different stratigraphic ranges in North America than elsewhere in the world, have until now been difficult or impossible to address.

We report here on the first fossil mammals discovered in earliest Cretaceous rocks in North America, from the Lakota Formation (upper Berriasian–lower Barremian) of South Dakota. Material was collected by OMNH field parties during the summers of 2001–2003, from two localities on the northeastern and southern margins of the Black Hills uplift (Fig. 1). This small but moderately diverse assemblage (Table 1) helps address the gap in our knowledge of mammalian evolution between the end of the Jurassic and the late Early Cretaceous in North America. We document stratigraphic range extensions for archaic groups such as allodontoid multituberculates, “triconodontine”-grade triconodonts, and dryolestoids; and new first occurrences of plagiaulacoid multituberculates, spalacotheriid “symmetrodonts”, and tribosphenidans. Also present is the first North American record of an amphitheriid-like stem zatherian.

Table 1. Mammals from the Lakota Formation (Lower Cretaceous: upper Berriasian–lower Barremian), South Dakota, USA. Terminal taxa appear in bold.

Class Mammalia Linnaeus, 1758
Order Multituberculata Cope, 1884
Suborder “Plagiaulacida” Ameghino, 1889
Superfamily Allodontoidea (Marsh, 1889)
Family indet.
<i>Passumys</i> gen. nov.
<i>Passumys angelli</i> sp. nov.
Superfamily Plagiaulacoidea (Gill, 1872)
Family Plagiaulacidae Gill, 1872
<i>Bolodon</i> Owen, 1871
<i>Bolodon hydei</i> sp. nov.
Order Eutriconodonta sensu Gaetano and Rougier (2011)
Family Triconodontidae Marsh, 1889
Gen. et sp. indet.
Family ?Triconodontidae Marsh, 1889
Gen. et sp. indet.
Superlegion Trechnotheria McKenna, 1975
Family Spalacotheriidae Marsh, 1887
<i>Infernolestes</i> gen. nov.
<i>Infernolestes rougieri</i> sp. nov.
Superorder Dryolestoida Butler, 1939
Family Dryolestidae Marsh, 1879a
<i>Lakotalestes</i> gen. nov.
<i>Lakotalestes luoi</i> sp. nov.
Superorder Zatheria McKenna, 1975
Family and genus indet.
Subclass Tribosphenida McKenna, 1975
Family and genus indet.

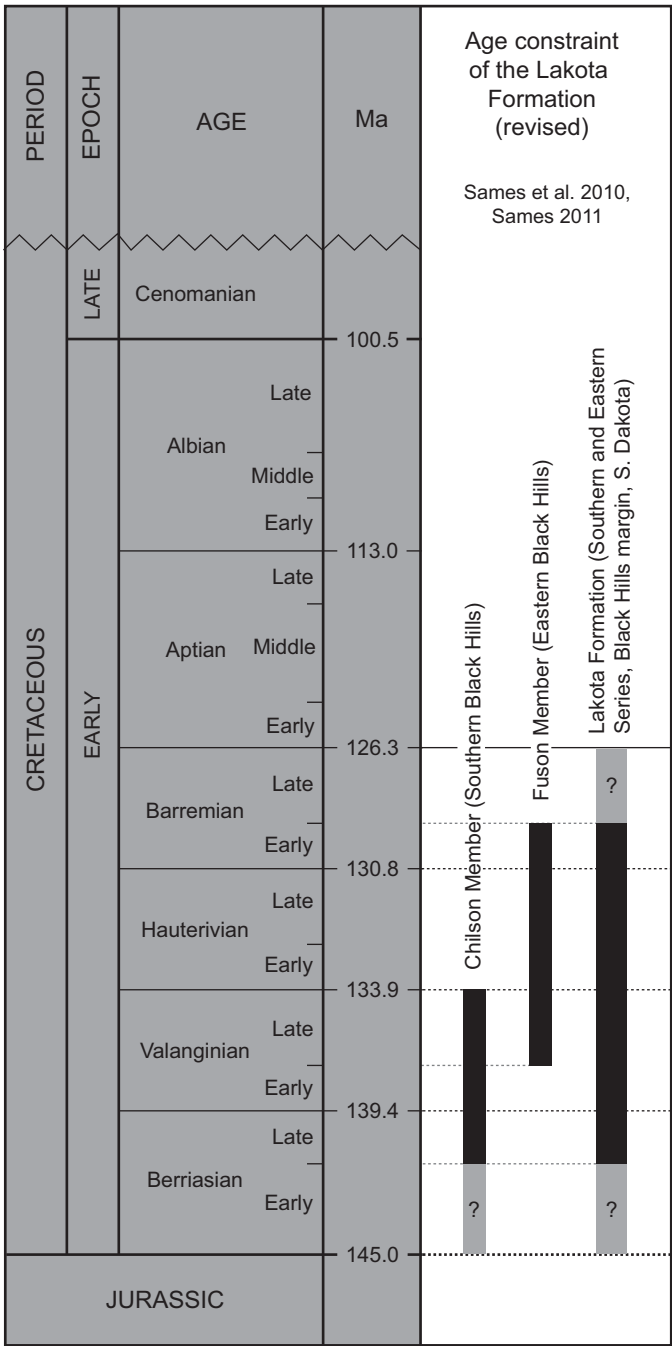


Fig. 2. Chronostratigraphy of the Lakota Formation (southern and eastern Black Hills). Absolute ages after Gradstein et al. (2012). Chronostratigraphic age constraints of the Lakota Formation follow results from ostracod correlations (Sames et al. 2010; Sames 2011a, b).

Institutional abbreviations.—OMNH, Oklahoma Museum of Natural History, Norman, Oklahoma, USA.

Other abbreviations.—L, mesiodistal length; Ma, millions of years; W, buccolingual width. Molars are abbreviated “M” or “m” to denote upper or lower dentition, respectively; premolars are abbreviated “P” or “p” to denote upper or lower dentition, respectively. Measurements in brackets are dimensions of incomplete specimens, and include only the preserved portion.

Material and methods

The specimens described in this study were collected and prepared following standard methods of microvertebrate sampling detailed by Cifelli (1996). Other vertebrate groups are also represented in the OMNH collection from the Lakota Formation, including various chondrichthyans, osteichthyans, amphibians, lepidosaurs, crocodilians, and dinosaurs (to be described elsewhere). Scanning electron micrographs of specimens were obtained at the OMNH using a Denton Vacuum Desk II (gold/palladium) sputter coater and a LEO 1450VP SEM. Tooth measurements were taken with a Reflex Microscope (see MacLarnon 1989), as defined by Lillegraven and Bieber (1986).

Geologic setting

Tectonic context.—The depositional area of the nonmarine Lower Cretaceous Lakota Formation of the Black Hills region (South Dakota and Wyoming) is situated in the Western Interior foreland basin (also known as the North American Cordilleran foreland basin or “Western Interior Basin”). The Western Interior foreland basin is the largest of its type known, extending from northeast Canada to central Mexico and occupying an area of more than five million square kilometers (e.g., Kauffman and Caldwell 1993). The basin began to develop in the Late Jurassic between the North American Cordilleran orogenic belt to the west and the North American craton to the east, in response to the subduction of oceanic plates of the Pacific domain (Kauffman and Caldwell 1993; DeCelles 2004). The orogenic belt and the foreland basin evolved contemporaneously (for about 100 Ma) until the Eocene in various types of process-response and feedback relationships. This includes the Sevier orogeny (“middle” to Late Cretaceous) and the Laramide orogeny (Late Cretaceous to Eocene). Sediment deposition during the Late (possibly as early as Middle) Jurassic to Early Cretaceous was strongly connected with the tectonic coevolution of both the proto-Cordillera and its associated foreland basin, causing alternating source, supply rate and depozones of the nonmarine sediments (Kauffman and Caldwell 1993). The Laramide event (Late Cretaceous to Eocene) later led to fracturing of the craton and partitioned a part of the foreland basin into a mosaic of smaller foreland basins and uplifts (DeCelles 2004; Dickinson 2004); the Black Hills uplift (Wyoming and South Dakota) represents the easternmost of these.

The lower boundary of nearly all Lower Cretaceous non-marine deposits throughout the Western Interior foreland basin is represented by an unconformity, although it is unclear whether this is synchronous or diachronous. This separates them from nonmarine Upper Jurassic (to possibly lower Berriasian) strata comprising the Morrison Formation in most of the US part of the basin. However, within the study area of the Black Hills Uplift, the Upper Jurassic is locally represented by either the Unkpapa Sandstone or the Morrison

Formation. The timespan represented by this unconformity remains controversial, is likely variable, and in need of refinement. Time intervals ranging from at least 15–20 up to 35 Ma have been given, according to maximum age estimates of Barremian (or possibly Hauterivian) to middle Albian for the respective Lower Cretaceous formations (see Sames et al. 2010 and references therein for a detailed review). The upper age constraint for most such units is simply given as pre-middle Albian, which represents the minimum age provided by well-dated, overlying deposits of the first of the major so-called mid-Cretaceous marine transgressions in North America. These ultimately led to the establishment, by the mid-Albian, of the Cretaceous Western Interior Seaway, extending from Canada to the Gulf of Mexico (DeCelles 2004). However, new results from ostracod correlations (Lakota Formation of South Dakota and Cedar Mountain Formation of Utah) strongly suggest older maximum ages, definitely pre-Aptian and possibly as early as late Berriasian (~142 Ma, Sames et al. 2010; Sames 2011a, b). A pre-Aptian age for the Lakota Formation (Fig. 2; Berriasian to Barremian) is generally supported by charophyte data, i.e., the occurrence of *Clavator grovesii grovesii* (Tithonian to early Valanginian) from the lowermost Lakota Formation (Martín-Closas et al. 2013).

Lakota Formation.—The Lakota Formation, which forms the lower part of the Inyan Kara Group (Fig. 1), lies in the distal (back-bulge) part of the Western Interior basin (e.g., DeCelles 2004; Miall et al. 2008). In general, the dominant lithologies of the Lakota Formation (mudstone, sandstone, and limestone) indicate deposition on floodplains and/or wetlands adjacent to rivers (Elliott et al. 2007, and references therein). The latter are represented by fluvial sandstone, which is particularly well developed in the southern Black Hills. Typically, the Lakota Formation is between 15–140 m thick, and has been variably subdivided into either the Chilson, Minnewaste Limestone, and Fuson members (Waagé 1959; Post and Bell 1961), or three informal lithostratigraphic intervals (L1, L2, and L3; Way et al. 1998) (Fig. 3).

Lithostratigraphic correlation within the Lakota Formation throughout the Black Hills margin is still under discussion. It is complicated by the strong lateral facies and thickness changes that characterize the unit, and by the fact that individual members are variably absent from the section. As Bolyard and McGregor (1966: 2227) commented: “The most outstanding characteristic of the Lakota is its marked variability, both in lithologic aspect and in thickness.” The Minnewaste Limestone Member, for example, is restricted to the southern Black Hills, and L1 strata (units of the Chilson Member), thickest and known in some detail in the southern Black Hills (e.g., Waagé 1959; Post and Bell 1961), are absent throughout much of the northern Black Hills (Zaleha 2006). To further complicate matters, parts of the Chilson and Fuson members are lithologically similar, leading to uncertainty or erroneous conclusions as to stratigraphic position, especially in areas with limited exposure.

Lithostratigraphic Subdivision of the Lakota Formation		Position of mammal horizons within the Lakota Formation
Way et al. 1998; Zaleha 2006	Waagé 1959; Post and Bell 1961; Dahlstrom and Fox 1995	
↑ ?	↑ ?	
Fall River Formation	Fall River Formation	
L3	Fuson Member (S4)	OMNH V1254
L2	Fuson Member (S3)	
	Minnewaste Limestone Member	
L1	Chilson Member (S2)	OMNH V1243
	Chilson Member (S1)	
Morrison Formation	Morrison Formation	

Fig. 3. Lithostratigraphic subdivision of the Lakota Formation (Black Hills margin, South Dakota and Wyoming) following the authors given in the heading. Subunits S1–S4 correspond to Post and Bell’s (1961) informal subdivisions and are equivalent to “fluvial units” 1–4 of Dahlstrom and Fox (1995). There are still conflicting discussions regarding parts of the lithostratigraphy, particularly the position of the Minnewaste Limestone Member, whether it forms the top and part of the L1 informal interval (as shown here) or the base and part of L2. The Lakota Formation is variably (and locally) underlain by the Morrison Formation or the Unkpapa Sandstone, as discussed in the text.

The Chilson Member has been subdivided into the informal units 1 and 2 by Post and Bell (1961), corresponding to fluvial unit 1 and fluvial unit 2 of Dahlstrom and Fox (1995: fig. 3), respectively (Fig. 3). Each unit varies in thickness from 0 to about 120 m. Unit 1, the stratigraphically lower of the two, is present in the southwestern and western Black Hills. Unit 2

overlaps unit 1 from the SE and can be readily distinguished only in the southeastern Black Hills (e.g., Edgemont, Flint Hill, Cascade Springs, and Hot Springs USGS 7.5' topographic quadrangles), where it completely replaces unit 1 in much of that area (Post 1967; Dahlstrom and Fox 1995).

The Minnewaste Limestone Member, which forms the upper part of the L1 interval (Zaleha 2006), is lacustrine and is restricted to scattered outcrops in the southern Black Hills. It consists of nearly pure limestone with a maximum thickness of 24 m but is typically between 3–6 m thick (Gott et al. 1974). The L1 and L2 intervals are separated by an unconformity which is locally angular to strongly angular (Way et al. 1998; Zaleha et al. 2001).

Like the Chilson Member, the uppermost part of the Lakota Formation, the Fuson Member, is largely of fluvial origin. Mappable units within the member include fluvial units 3 and 4, separated by a variegated sandstone and mudstone. Of these, “the variegated mudstone unit, which is interbedded with fluvial unit 3, is the most widespread informal unit of the Lakota Formation and has probable equivalents around the entire periphery of the Black Hills” (Dahlstrom and Fox 1995: S4), though it is locally truncated or missing (Gott et al. 1974).

Localities sampled.—Samples yielding the mammals discussed herein derive from two sites: one (OMNH locality V1243) in the southern and one (OMNH locality V1254) in the eastern sequences of the Lakota Formation, South Dakota (Fig. 1). As noted, the character, thickness, and representation (in terms of subdivisions) of the Lakota Formation differ substantially from place to place, and stratigraphic/biostratigraphic context must therefore be discussed individually for the two sites.

OMNH locality V1243 is situated near the mouth of Hell Canyon (Section 26, Township 8S, Range 4E; N43°19' W103°37'), about 17 km ENE of Edgemont, Fall River County, South Dakota (Fig. 1). The productive horizon, on a ledge between massive (and vertically exposed) sandstone beds, is a mudstone layer (ranging in thickness from 10–25 cm) with abundant indurated sandy lenses containing bone fragments and clayballs. Owing to slope cover and terrain, it proved impractical to measure a stratigraphic section through OMNH V1243. However, the geology of the area has been mapped in considerable detail (Post 1967; Bell and Post 1971). Unit 1 of the Chilson Member is missing in this area; the Minnewaste Limestone Member is exposed about 1.5 km to the NNW, and the Chilson-Fuson contact is readily distinguished. The underlying contact between the Unkpapa Sandstone and Lakota formations is also locally exposed. OMNH locality V1243 lies in the lower one-fourth of unit 2 of the Chilson Member (Fig. 3).

The lower Lakota Formation (specifically the lower part of Chilson Member unit 2) in the southern Black Hills has been comparatively well sampled micropaleontologically (e.g., Sohn 1979; Martín-Closas et al. 2013; Sames et al. 2010; Sames 2011a, b). Age constraints for this part of the

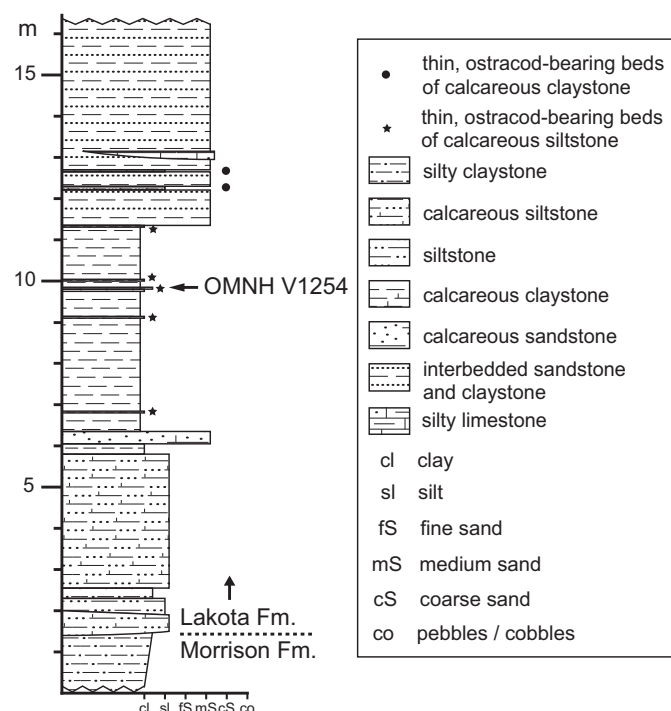


Fig. 4. Stage Barn Canyon Road section (measured by BS, containing OMNH location V1254), Fuson Member of the Lakota Formation.

section, and therefore for OMNH locality V1243, are late Berriasian–Valanginian (Fig. 2).

OMNH locality V1254 is situated in a roadcut along Stagebarn Canyon Road (Section 30, Township 3N, Range 7E; N44°12' W103°20'), about 24 km WNW of Rapid City, Meade County, South Dakota (Fig. 1). The Stage Barn Canyon Road section has been measured and sampled for ostracods in horizons bracketing and including OMNH locality V1254 (Fig. 4). We interpret this section to represent much of (and perhaps only) the Fuson Member, including fluvial units 3 and 4 (S3 and S4, after Dahlstrom and Fox 1995) of the Lakota Formation (Fig. 3). If this is correct, the mammal specimens derive from the lacustrine sandstone within the variegated mudstone intercalated between these fluvial units. The bone-yielding horizon lies at the base of this sandstone, and includes clayballs as well as vertebrate remains.

Owing to marked lateral facies changes and the highly reduced total thickness of the succession, explicit assignment of the Stage Barn Canyon Road sequence to either (part) of the Chilson Member (unit 2) and/or the Fuson Member remains open to question, and there is no consensus in the available geologic literature. In some parts of the Black Hills margin (as we interpret for the section including OMNH locality V1254), the Fuson Member rests directly on Jurassic deposits (the Morrison Formation or, locally, its equivalent, the Unkpapa Sandstone). The Stagebarn Canyon Road section is very close to, or potentially the same as, Sohn's (1979: 6–7) map and sample locality 8, therein assigned to the Chilson Member, “probably unit 2” (Sohn 1979). However, the ostracod assemblage recovered from the Stage Barn Canyon Road section is strongly different from those of the Chilson Member

(unit 2) in the southern sequence, noted above, and matches those recovered from other localities of the eastern sequences, in the presumed Fuson Member of the Lakota Formation (Sames 2011a: fig. 11; Sames 2011b: fig. 9). Therefore, the parts of section concerned here (at least those above 6.5 m, Fig. 4 herein, from where the mammal sample was collected) are assigned to the Fuson Member of the Lakota Formation. Estimated age constraints for the section including OMNH locality V1254, and other ostracod assemblages of the eastern sequences, are late Valanginian–early Barremian (Fig. 2).

Systematic paleontology

Class Mammalia Linnaeus, 1758

Order Multituberculata Cope, 1884

Suborder “Plagiaulacida” Ameghino, 1889

Remarks.—Two “groups” of Multituberculata are conventionally recognized. Hahn and Hahn (2004, 2006) regard the “Plagiaulacida” (the geologically older of the two, with assigned taxa ranging from the Middle Jurassic to Albian–Cenomanian) as a monophyletic group. However, “plagiaulacidans” are generally characterized by plesiomorphies and are often represented by isolated teeth; hence, diagnosis on the basis of synapomorphies is problematic. We conservatively follow the usage of Kielan-Jaworowska et al. (2004) in regarding the “Plagiaulacida” as a paraphyletic grade, pending a detailed phylogenetic analysis. A second group of multituberculates, the Cimolodonta (Albian–Cenomanian to Oligocene), are generally conceived as monophyletic (Simmons 1993; Kielan-Jaworowska and Hurum 2001; Weil and Krause 2008), though there is not universal agreement on this point (e.g., Hahn and Hahn 1999; Fox 2005). The primary distinctions between “plagiaulacidans” and cimolodontans lie in the incisors and premolar series (e.g., Clemens and Kielan-Jaworowska 1979), but molar characteristics have also proven useful in assessing relationships of taxa known by isolated teeth (e.g., Eaton and Cifelli 2001; Hahn and Hahn 2004; Cifelli et al. 2013). Among the “Plagiaulacida”, Kielan-Jaworowska and Hurum (2001; see also Kielan-Jaworowska et al. 2004) recognize three informal groupings: the allodontid (Allodontidae Marsh, 1889 and Zofiabaataridae Bakker, 1992, plus *Glirodon* Engelmann and Callison, 1999), paulchoffatiid (Paulchoffatiidae Hahn, 1969; Hahnodontidae Sigogneau-Russell, 1991b; and Pinheirodontidae Hahn and Hahn, 1999), and plagiaulacid (Plagiaulacidae Gill, 1872; Eobaataridae Kielan-Jaworowska, Dashzeveg, and Trofimov, 1987; and Albionbaataridae Kielan-Jaworowska and Ensom, 1992; plus *Janumys* Eaton and Cifelli, 2001) “lines”, with the Arginbaataridae Hahn and Hahn, 1983 considered incertae sedis. These “lines” were formalized (with some changes in content) as superfamilies by Hahn and Hahn (2004), who also placed the Arginbaataridae in their own superfamily.

We recognize two new multituberculates, each represented by an isolated molar, from the Lakota Formation.

Available data suggest that both are “plagiaulacidans”, each referable to a different superfamily, following the taxonomic arrangement of Hahn and Hahn (2004). Authorship for superfamilies listed below reflects Article 36.1 of the International Code of Zoological Nomenclature (ICZN 1999).

Superfamily Allodontoidea (Marsh, 1889)

Family indet.

Genus *Passumys* nov.

Type species: *Passumys angelli* sp. nov., monotypic; see below.

Etymology: From the Latin *passus*, open, in allusion to the broad central valley on the holotype.

Diagnosis.—As for the type and only species.

Passumys angelli sp. nov.

Fig. 5A.

Etymology: In honor of Jim Angell of Edgemont, South Dakota, in recognition of his scientific, logistic, and diverse other help to OMNH field parties through the years.

Holotype: OMNH 64191, right m1.

Type locality: OMNH V1243, Fall River County, South Dakota, USA.

Type horizon: Chilson Member, Lakota Formation (Lower Cretaceous: upper Berriasian–Valanginian).

Diagnosis.—Small multituberculate with m1 ovoid to subrectangular in occlusal view, having mesial and distal margins of the crown gently rounded and symmetrical instead of beveled; central valley broad buccolingually; cusps of lingual and buccal rows mesiodistally aligned, conical, and well separated, with valleys between cusps extending to the level of the central valley. Most closely similar to *Ctenacodon*, *?Psalodon* (we follow Simpson [1926] in questionably referring to *Psalodon* specimens preserving the lower dentition, as the genus was established on upper teeth only), and *Glirodon*, but differs in having well-separated first two cusps of the lingual row (with cusp 1 the largest), and a larger cusp 1 of the buccal row that is also subequal to the other cusps of that row.

Description.—The crown of OMNH 64191 is ovoid or subrectangular and nearly symmetrical in occlusal outline ($L = 1.41$ mm, $W = 1.12$ mm). It bears two rows of three cusps; the lingual cusp row is slightly higher than the buccal row. The cusp rows are offset, with the cusps of the buccal row lying slightly mesial to their counterparts of the lingual row (most apparent in occlusal view; Fig. 5A₁). The cusps of each row are well spaced; cusp 1 of each row has a flat distal face and cusp 2 has flat mesial and distal faces, but each cusp is subconical. The distal cusp of each row is entirely conical. No enamel ornamentation or crenulation is observed. The central valley is straight and broad, bearing light wear only. Light wear is also present on the internally-facing sides of the cusp rows. Very faint wear is present on the buccal faces of cusps 1 and 2 of the buccal cusp row. The tallest cusp is the mesial-most of the lingual row; it is twice as high as its counterpart on the buccal row. From the apex of this dominant cusp, a crest descends mesially and then buccomesially,

terminating at the mesial end of the central valley. Weak crests descend from the apices of the distal cusps of each row, rimming the distal end of the central valley.

Remarks.—The m1 of *Passumys* is clearly distinct from that of cimolodontans in being proportionately short, in bearing only three cusps in each row, in having well separated, conical cusps, and in lacking any sort of enamel ornamentation (Fig. 5A). Among “plagiaulacidans” known by m1, *Passumys* differs from the Paulchoffatoidea in lacking cingulids (mesially and distally) and enlargement of the second cusp in the buccal row; from the Plagiaulacoidea in having better separated, more conical cusps, in lacking enamel ornamentation, in being symmetrical in occlusal view (no beveling of mesial or distal borders); and in having only three cusps in the buccal row (*Eobaatar clemensi* Sweetman, 2009 is described as bearing three cusps on the buccal row; however, the distal-most of these is comprised of two cusps separated by a pit, giving the appearance of four cusps in this row); and from the Arginbaataroidea in having three (rather than two) cusps in the lingual row and in being symmetrical (not beveled mesially and distally) in occlusal view.

Among the Allodontoidea, *Passumys* is dissimilar to *Zofiabaatar pulcher* Bakker and Carpenter, 1990, which has an m1 that is sub-quadrate and that appears to have only two main cusps in each row, with additional, mesially-placed cusps united by a strong mesial cingulid (Kielan-Jaworowska et al. 2004: fig. 8.25G₂). *Passumys* compares most favorably with m1s referred to species of *Ctenacodon* Marsh, 1879b, *?Psalodon* Simpson, 1926, and *Glirodon* Engelmann and Callison, 1999. As noted in the diagnosis, *Passumys* differs in its more symmetrical occlusal outline, better separation of cusps in the lingual row (particularly cusps 1 and 2), and in having relatively larger first cusps of both rows. Like the lower dentition in general (Simpson 1929), m1s assigned to the various species of *?Psalodon* and *Ctenacodon* are rather similar, differing in minor details. All have a distinctly small first cusp in the buccal row; this cusp tends to be rapidly reduced or obliterated by wear. These species are also characterized by significant union (to about half their heights) and close appression of the first two cusps in the lingual row. Judged by the published illustration (Engelmann and Callison 1999: fig. 25), the m1 of *Glirodon grandis* Engelmann and Callison, 1999 appears to be more similar to that of *Passumys* than are those of *?Psalodon* and *Ctenacodon*, though it appears to differ in that the cusp rows converge mesially.

Stratigraphic and geographic range.—Lower Cretaceous (upper Berriasian–Valanginian), South Dakota, USA. Currently known only from the type locality and horizon.

Superfamily Plagiaulacoidea (Gill, 1872)

Family Plagiaulacidae Gill, 1872

Genus *Bolodon* Owen, 1871

Type species: *Bolodon crassidens* Owen, 1871, Durlston Bay, Purbeck Group (Berriasian: England).

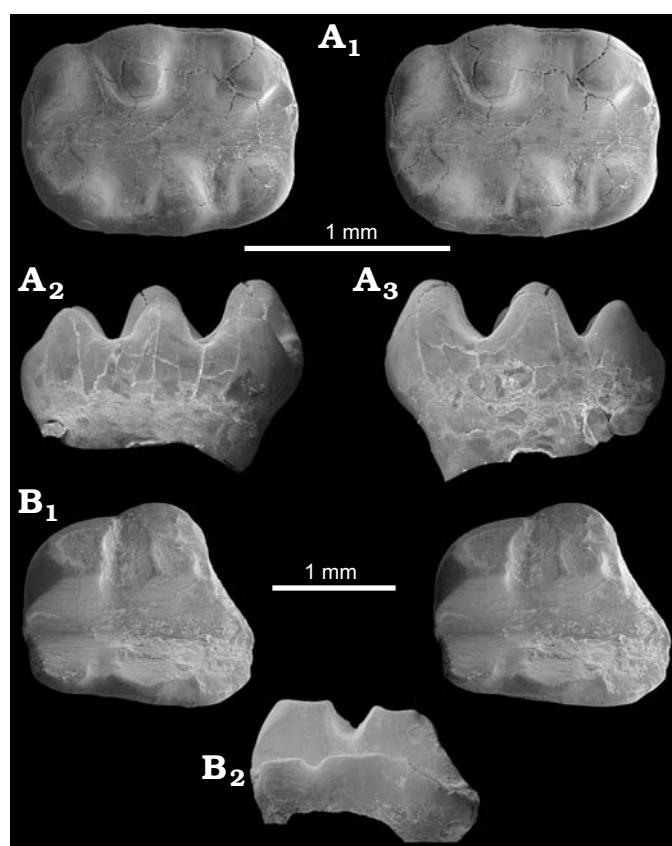


Fig. 5. “Plagiaulacidan” multituberculate mammals from OMNH locality V1243, Lakota Formation (Lower Cretaceous: upper Berriasian–Valanginian), South Dakota, USA. **A.** The allodontoid *Passumys angelli* gen. et sp. nov., OMNH 64191 (holotype), right m1 in occlusal (A₁, stereopair), buccal (A₂), and lingual (A₃) views. **B.** The plagiaulacoid *Bolodon hydei* sp. nov., OMNH 62670 (holotype), right M2 in occlusal (B₁, stereopair) and oblique lingual (B₂) views.

Bolodon hydei sp. nov.

Fig. 5B.

Etymology: In honor of Dayton Hyde, founder of the Institute of Range and the American Mustang, for his support and cooperation on the part of the Institute.

Holotype: OMNH 62670, a right M2.

Type locality: OMNH V1243, Fall River County, South Dakota, USA.

Type horizon: Chilson Member, Lakota Formation (Lower Cretaceous: upper Berriasian–Valanginian).

Diagnosis.—Small multituberculate most comparable to *Bolodon osborni* but differing in that the second cusp of the lingual row is larger than the other two, the buccal ridge is less developed, mesiolingual corner of the crown extends farther mesially, and the distal margin of the crown is more squared-off (less pointed).

Description.—OMNH 62670 is complete and in a good state of preservation, except that it is heavily worn (L = 2.04 mm, W = 1.74 mm). Much of the enamel is missing, and the original extent of ornamentation is unclear. The presence of some ornamentation is suggested by two ridges that ascend mesially from the apex of cusp 1 in the buccal row, enclos-

ing a small basin on the mesial flank of that cusp (Fig. 5B); a second small basin is present mesiobuccal to the apex of buccal cusp 1. The buccal cusp row bears two large, subequal cusps, while the lingual cusp row appears to have had three cusps (abrasion of the mesial part of the lingual cusp row leaves interpretation open). The buccal ridge is heavily worn; it appears to have been buccolingually widest at the level of cusp 1 in the buccal row. The ridge extends distally to cusp 2 of the buccal cusp row as only a narrow ridge. The crown is therefore broadest at the level of cusp 1 of the buccal row. The crown tapers mesiolingually, with cusp 1 of the lingual row placed farther mesially than cusp 1 of the buccal row. The remaining cusps are relatively in-line transversely (as they are in *Iberica hahni* Badiola, Canudo, and Cuenca-Bescós, 2011). Buccal and lingual cusp rows are subequal in height but the buccal cusps are significantly broader-based. Adjacent faces of the buccal cusps (distal face of cusp 1, mesial face of cusp 2) are flat; both cusps have a semi-pyramidal appearance (buccal and lingual faces have flat wear facets). The lingual cusps have been substantially reduced by wear, but it is clear that they were joined to form a ridge (not developed as separate, conical cusps), with cusps separated by narrow, shallow grooves rather than deep valleys. Cusp 2 of the lingual row appears to have been the largest. Cusps 1 and 3 of the lingual row were probably subequal, but breakage of cusp 1 makes absolute size difficult to determine. The central valley is straight-sided and is worn into a broad V. Substantial wear is also present on the buccal face of the buccal cusp row, extending to and nearly obliterating the buccal ridge.

Remarks.—Individual molar characteristics often have perplexing distributions among the “Plagiaulacida” and basal Cimolodonta, and character polarities are not well understood in some cases; the following comments are based on the recent treatment of Cifelli et al. (2013). *Bolodon hydei* sp. nov. is probably plesiomorphic in a number of features, such as the presence of only two buccal and three lingual cusps, lack of separation between the mesial cingulum and first cusp of the buccal row, slight development of (and lack of cusps on) the mesiobuccal ridge, length relative to width, proportions of the cusps in the buccal row, and mesiodistal alignment of all cusps in the lingual row (Fig. 5B). The mesial margin of OMNH 62670 is sinuous, with a pronounced, mesially-projecting “spout” at the central valley. Polarity of this feature is uncertain; the condition occurs within various groups of “Plagiaulacida” and basal Cimolodonta. Derived conditions seen in *Bolodon hydei* include the probable presence of enamel ornamentation, sub-pyramidal outline of cusps in the buccal row, and joining of lingual cusps into a ridge, with narrow grooves (rather than well developed valleys) between cusps.

We compared *Bolodon hydei* with all “plagiaulacids” and basal cimolodontans (“*Paracimexomys* group”; Kielan-Jaworowska and Hurum 2001) for which M2 is known. The foregoing combination of characters, together with apomorphies of individual taxa, distinguishes *B. hydei* from basal Cimolodonta, Allodontoidea, Arginbaataroidea, Paulchoffatoidea, and Eobaataridae. On the other hand, we found the

comparison with *B. osborni* Simpson, 1929 (Plagiaulacidae) so compelling that we consider the species congeneric. The holotype and referred M2 (see Kielan-Jaworowska and Ensom 1992) demonstrate some intraspecific variability in *B. osborni*, notably in the fact that enamel ornamentation (in the form of ribbing and pitting) is better developed on the referred specimen. Both differ from OMNH 62670 in having less difference in size between cusps of the lingual row, in having a more prominent mesiobuccal rim, and in having a distal margin that is more rounded, with the lingual side projecting farther distally.

Stratigraphic and geographic range.—Lower Cretaceous (upper Berriasian–Valanginian), South Dakota, USA. Currently known only from the type locality and horizon.

Order Eutriconodonta Kermack, Mussett, and Rigney, 1973 (sensu Gaetano and Rougier 2011)

Family Triconodontidae Marsh, 1887

Remarks.—Cusp terminology follows that of Crompton and Jenkins (1968).

Gen. et sp. indet.

Fig. 6A–C.

Material.—OMNH 62800, a right lower molar from OMNH 1254, Fuson Member, Lakota Formation (Lower Cretaceous: upper Valanginian–lower Barremian), Meade County, South Dakota, USA.

Description.—OMNH 62800 is a very small ($L = [0.96 \text{ mm}]$, $W = 0.39 \text{ mm}$), heavily abraded right lower molariform with three cusps definitively present, arranged in a mesiodistal line. The tooth closely resembles triconodontids such as *Priacodon* Marsh, 1887 and *Triconodon* Owen, 1859 in being low-crowned and mesiodistally long, with vertical cusps. Evidence of the roots is visible, though this region of the specimen is heavily abraded. In occlusal view (Fig. 6A), the crown tapers distally to a point occupied by cusp d. The tallest preserved cusp is identified as cusp a; it was likely substantially taller than the other cusps, though its absolute height is difficult to judge due to abrasion. In this regard, OMNH 62800 more closely resembles *Priacodon* than *Triconodon* or *Trioracodon* Simpson, 1928; in the latter two taxa, the principal cusps are more nearly subequal in height. Cusp b is missing but was most likely present, since the apex of cusp a is positioned above the notch between the roots, suggesting that the crown likely extended mesially well beyond the preserved margin. Cusp c is well separated from and about half the height of cusp a, and bears a ridge descending its lingual face. Cusp d is half again lower, and is positioned close to cusp c yet still distal to (i.e., overhanging) the distal root. There is an enamel ridge running down the buccal face of each preserved cusp (Fig. 6C). In occlusal view, the crests connecting the apices of the cusps run closer to the buccal margin of the crown. The lingual cingulid is connected to the apex of cusp d, but it is obliterated by abrasion lingual to cusp

c. An oval scar is present on the distal face of cusp d, likely from contact with the succeeding molar. Small wear facets are visible on the distobuccal faces of each preserved cusp.

Remarks.—OMNH 62800 possesses features which are characteristic of “triconodontine” triconodontids (Marsh 1887): the molar is low-crowned with vertical cusps, and cusp d is small and overhangs the distal root. In alticonodontines such as *Astroconodon* Patterson, 1951 and *Jugulator* Cifelli and Madsen, 1998, the main cusps are recumbent and cusp d is situated directly above the distal root (see, for example, Kielan-Jaworowska et al. 2004: figs. 7.15, 7.16). “Triconodontines”, as defined by Simpson (1928) to include the Late Jurassic–Early Cretaceous genera *Priacodon* Marsh, 1887, *Triconodon* Owen, 1859, and *Trioracodon* Simpson, 1928, are paraphyletic in all recent phylogenetic analyses of eutriconodontans (Montellano et al. 2008; Kusuhashi et al. 2009; Gaetano and Rougier 2011), and are therefore more appropriately treated as a structural grade lacking the specializations of alticonodontines. Also of note is the absolute size of OMNH 62800; though damaged, it is substantially smaller than all described triconodontids, with the exception of the purported triconodontid *Victoriaconodon* Montellano, Hopson, and Clark, 2008 from the Lower Jurassic La Boca Formation of Mexico (Montellano et al. 2008). While the m1 is the only molariform preserved in *Victoriaconodon*, it differs substantially from OMNH 62800 and other described triconodontids (instead resembling amphilestids much more closely).

?Triconodontidae Marsh, 1887

Gen. et sp. indet.

Fig. 6D.

Material.—OMNH 62855, right mesial lower premolar from OMNH 1254, Fuson Member, Lakota Formation (Lower Cretaceous: upper Valanginian–lower Barremian), Meade County, South Dakota, USA.

Description.—The crown of OMNH 62855 is comparatively long mesiodistally ($L = 1.04$ mm) and low-crowned, as is the case with mesial premolars of triconodontids (see Simpson 1928). Both roots of the tooth are broken and appear to have been buccolingually compressed, but the distal root was clearly larger than the mesial root. Between the roots, the inferior margin of the crown has a pronounced dorsal flexure. The crown is well preserved, with light apical wear on cusps a and c; cusp b appears to be damaged, but was clearly placed lower on the crown than cusp c. Cusp a is slightly recumbent distally, with sharp crests descending mesially and distally from its apex. The buccal face of cusp a is convex. Mesially, the crown is broad buccolingually; a faint bulge is present near the mesio-buccal base of the tooth, suggesting the presence of cusp f, but this region of the tooth is abraded and no further details are available. Distally, the crown tapers buccolingually; a stronger bulge is present at the distal base of the crown, though no cusp is developed. There is no evidence of a buccal cingulid.

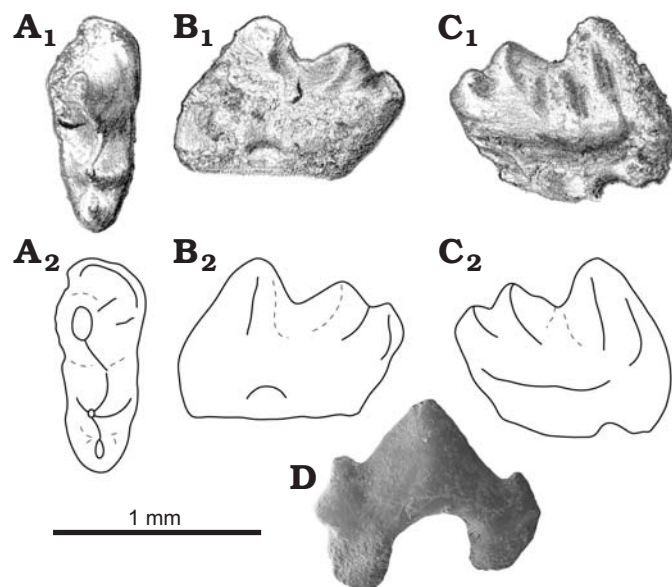


Fig. 6. Triconodontid eutriconodontan mammals from OMNH locality V1254, Lakota Formation (Lower Cretaceous: upper Valanginian–lower Barremian), South Dakota, USA. **A–C.** Camera lucida drawings (**A₁–C₁**) and interpretive illustrations (**A₂–C₂**) of OMNH 62800, right lower molar in occlusal (**A**), lingual (**B**), and buccal (**C**) views. **D.** OMNH 62855, right lower premolar in buccal view. **A–C** courtesy of Nicholas J. Czaplewski.

Remarks.—OMNH 62855 is embedded in a rock fragment; it is fully exposed in lateral view, and the crown is visible in occlusal view. The principal cusp is slightly asymmetrical in lateral view, with the apex tilted toward the presumed distal end (a supposition supported by the relative heights of the flanking cusps: presumed cusp c is placed higher on the flank of the central cusp than presumed cusp b, as is generally the case in mesial premolars of triconodontids). In this view, the central cusp has a convex lateral face, but a cingulid is entirely lacking. This supports our conclusion that this tooth represents a lower right premolar. Though larger than the species represented by OMNH 62800, this premolar represents another species smaller than all previously described triconodontid taxa.

Superlegion Trechnotheria McKenna, 1975

Family Spalacotheriidae Marsh, 1887

Genus *Infernolestes* nov.

Type species: *Infernolestes rougeri* sp. nov., monotypic; see below.

Etymology: From the Latin *infernus*, hell, in reference to Hell Canyon, from which the holotype was discovered, and to the conditions endured at the type locality.

Diagnosis.—As for the type and only species.

Infernolestes rougeri sp. nov.

Fig. 7.

Etymology: In honor of Guillermo Rougier, for his contributions to knowledge of Mesozoic mammals.

Holotype: OMNH 62671, right lower molar, identified as m1.

Type locality: OMNH V1243, Fall River County, South Dakota, USA.

Type horizon: Chilson Member, Lakota Formation (Lower Cretaceous: upper Berriasian–Valanginian).

Diagnosis.—Moderate-sized spalacotheriid differing from other spalacotheriids except *Heishanolestes* in having an m1 with an obtuse trigonid angle, in having the paraconid/metaconid closely appressed to the protoconid (crown transversely narrow), and in possessing a wide, flat lingual cingulid; differs from other spalacotheriids except *Yaverlestes* in possessing a long mesial shelf; differs from other spalacotheriids except *Spalacotherium evansae* and *Yaverlestes* in bearing an incomplete buccal cingulid; differs from other spalacotheriids except *Spalacotheridium*, *Symmetrodontoides*, and *Heishanolestes* in possessing a flat (not dorsally flexed) lingual cingulid; differs from other spalacotheriids except *Spalacotheridium* and *Spalacolestes* in having a relatively shorter metaconid; differs from *Heishanolestes* in having a less obtuse trigonid angle and less robust trigonid cusps (especially the paraconid).

Description.—OMNH 62671 is a small molar ($L = 1.25$ mm, $W = 0.71$ mm) from the mesial end of the tooth row, probably representing the m1. It is preserved in a small fragment of dentary, but no traces of alveoli remain mesial or distal to this tooth. The three trigonid cusps form an obtuse angle (111°), with the protoconid by far the most robust and tallest cusp. The crown is virtually unworn, with the exception of slight apical wear on the metaconid and some breakage of the tip of the paraconid. The protoconid has an almost flat lingual face, and the cusp reclines distally so that its apex is closer to the metaconid than to the paraconid. The paraconid and metaconid originate very close to the base of the protoconid, with the paraconid roughly half the height of the metaconid. The paraconid is conical, and its apex is connected to the apex of the protoconid by a weak paracristid. The metaconid is also conical, and is slightly more than half the height of the protoconid. The metaconid is closely appressed to the protoconid, such that the protocristid is substantially higher than the paracristid; the postvallid shearing surface is also better developed than the prevallid surface. The lingual cingulid is very broad and bears two tiny cuspules mesial to the midpoint. This cingulid is also approximately horizontal in lingual view and roughly straight in occlusal view (i.e., not concave; Fig. 7A). There is a wide mesial shelf bearing a small but abraded cusp e, situated in a mesiodistal line with the paraconid and metaconid. Distally, cusp d is larger than cusp e but is still a small cusp. It is connected to the base of the metaconid by a weak crest, but this crest does not climb the distal face of the metaconid. The buccal cingulid is strong distally, weaker mesially, and incomplete at the midpoint of the crown (Fig. 7C), though it is possible the gap in the cingulid is a result of preservation. The cingulid flexes ventrally at the midpoint, the apex of this arch corresponding to the hiatus in the cingulid. The buccal margin of the crown is set substantially lower (ventral) relative to the lingual side. The obtuse angle formed by the trigonid cusps and the great height differential between the paraconid and metaconid lead us to suggest that OMNH 62671 represents an m1.

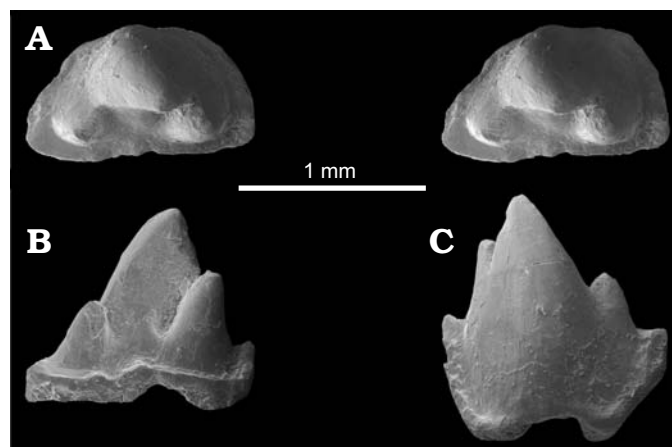


Fig. 7. The spalacotheriid “symmetrodont” mammal *Infernolestes rougieri* gen. et sp. nov. from OMNH locality V1243, Lakota Formation (Lower Cretaceous: upper Berriasian–Valanginian), South Dakota, USA. OMNH 62671 (holotype), right lower molar in occlusal (A, stereopair), lingual (B), and buccal (C) views.

Remarks.—*Infernolestes* gen. nov. is placed within the Spalacotheriidae based on the presence of derived characters and the absence of features typical of the Tinodontidae Marsh, 1887 and Zhangheotheriidae Hu, Wang, Luo, and Li, 1997 (see Rougier et al. 2003; Tsubamoto et al. 2004; Li and Luo 2006). *Infernolestes* differs from tinodontids and zhangheotheriids (and resembles spalacotheriids) in the marked difference in height at the alveolar margin of the crown, with the buccal side extending farther ventrally. There is also substantial height difference between the paraconid and metaconid and the accompanying placement of the paracristid and protocristid, with the metaconid and protocristid much higher. The primary shearing crest on the crown, formed by the protocristid, is developed flush with the distal face of the trigonid; this crest functions as the leading edge of postvallid shear, which is present and developed at eruption in Spalacotheriidae (apomorphy). The paracristid is, in contrast, much more poorly developed. There appears to be a slight displacement of the mesial face of the trigonid, with a groove present between the paraconid and protoconid extending to the base of the cusps (Fig. 7A). Unfortunately, the tooth is unworn (other than some apical wear) and evidence of occlusal contact at these surfaces is absent. It is not entirely clear if the morphology seen in *Infernolestes* represents an intermediate condition between the development of shearing surfaces in plesiomorphic groups, which require remodeling through wear (see Crompton and Jenkins 1968; Cifelli et al. 1998; Luo and Ji 2005), and the derived spalacotheriids, which have a functional surface present at eruption (see Cifelli and Madsen 1999). However, the balance of character evidence supports placement of this taxon within the Spalacotheriidae.

Infernolestes does differ from nearly all spalacotheriids (and instead resembles tinodontids and zhangheotheriids) in the obtuse angle of the trigonid and the relatively poor transverse development of the trigonid (especially the short length of the pre- and postvallid shearing surfaces; Fig. 7A). Howev-

er, a close point of comparison exists with the morphology of the m1 in *Heishanolestes* Hu, Fox, Wang, and Li, 2005 (Hu et al. 2005: fig. 4B), which is clearly a spalacotheriid based on the remainder of the molar series. These two taxa also share a wide lingual cingulid (to the exclusion of all other described spalacotheriids), but *Inferolestes* lacks the specialized, robust cusps of the m1 in *Heishanolestes* and, in general proportions, more closely resembles the m1 of other North American spalacotheriids (such as *Spalacolestes* Cifelli and Madsen, 1999 and *Spalacotheridium* Cifelli, 1990; see Cifelli and Madsen 1999). Currently, the oldest known spalacolestine spalacotheriid is *Yaverlestes* (Sweetman 2008), from the Barremian of Britain. However, mesial lower molars (the only material available for *Inferolestes*) are generally not informative as to subfamilial relationships, and we therefore conservatively refer the Lakota taxon to the Spalacotheriidae only.

Two additional specimens referred to spalacotheriid taxa bear mention in this context. Fox (1976) described *Symmetrodontoides canadensis* Fox, 1976 on the basis of a dentary fragment preserving three molars, which he identified as the m3–5. He referred a second dentary fragment bearing a single, low-crowned molariform tooth to the same species, identifying this tooth as the m1 (Fox 1976: fig. 4). The cusps form a severely obtuse angle (much more so than in *Inferolestes*), while the distal molars are more typical of a spalacotheriid. However, this specimen more likely represents a deciduous premolar (see discussion in Cifelli 1999b), and the holotype of *Symmetrodontoides canadensis* can be reinterpreted with confidence to contain the m1–3. Gill (2004: fig. 4A, B) referred an isolated molariform from Cliff End (Valanginian of Britain) to *Spalacotherium* cf. *tricuspidens*; it is unclear if this specimen actually represents the m1 of a species of *Spalacotherium* Owen, 1854, but it does bear close resemblance to the m1 of *Heishanolestes* (Hu et al. 2005: fig. 4B). The specimen is lower-crowned and has a more obtuse trigonid angle than *Inferolestes*, with bulbous cusps and a paraconid set more mesially (as in *Heishanolestes*). The mesial shelf is very short and cusp d is apparently lacking; this, coupled with very weak cingulids may suggest that this low-crowned tooth represents a different iteration of a spalacotheriid deciduous premolar.

Stratigraphic and geographic range.—Lower Cretaceous (upper Berriasian–Valanginian), South Dakota, USA. Currently known only from the type locality and horizon.

Superorder Dryolestoidea Butler, 1939

Family Dryolestidae Marsh, 1879b

Remarks.—We follow the synonymies recognized by Martin (1999) but retain usage of separate names in cases where synonyms were suggested but not formally proposed (see below).

Genus *Lakotalestes* nov.

Type species: *Lakotalestes luoi* sp. nov., monotypic; see below.

Etymology: Named for the Lakota Formation, from whence the ho-

lotype and only known specimen of the type species was collected; and the Greek *lestes*, robber or plunderer, a commonly-used suffix for genera of small, presumably faunivorous mammals.

Diagnosis.—As for the type and only species.

Lakotalestes luoi sp. nov.

Fig. 8A.

Etymology: In honor of Zhe-Xi Luo, for his contributions to knowledge of Mesozoic mammals.

Holotype: OMNH 62673, right upper molar from the distal part of the series, perhaps M5.

Type locality: OMNH V1243, Fall River County, South Dakota, USA.

Type horizon: Chilson Member, Lakota Formation (Lower Cretaceous: upper Berriasian–Valanginian).

Diagnosis.—Small dryolestid; upper molars differing from those of *Dryolestes*, *Krebsotherium*, and *Laolestes* in having stylocone placed mesially, adjacent to parastyle and buccal terminus of relatively straight paracrista, rather than in a more median position; differs from all Dryolestidae except *Portopinheirodon* (which differs in having median ridge mesially placed and closely paralleling paracrista), *Kurtodon pusillus* (which differs in lacking the metacone) and *Amblotherium nanum* (which differs in having a weaker median ridge) in lacking cusp “C”. Most similar to *Miccylyotyrans minimus*, differing in: slightly larger size, broader ectoflexus, lacking cusp “C” and parastylar hook; and in having a stronger, continuous (from paracone to median cusp) median ridge; well-developed, tall median cusp; and broad-based central cusp placed on median ridge.

Description.—OMNH 62673 is a small (L = 0.86 mm, W = 1.40 mm) right upper molar with light wear, missing the apex and part of the lingual face of the paracone, and the stylocone-parastyle; the enamel is slightly damaged in the regions of metastyle and metacone, but the presence of these structures is clear. In occlusal profile the crown is buccolingually wide, a well-marked ectoflexus is present, and the parastylar lobe projects mesiobuccally rather than mesially, suggesting that the tooth represents a distal locus in the maxilla (Fig. 8A₁). Comparison to the most morphologically similar species, *Miccylyotyrans minimus* Simpson, 1927, *Amblotherium pusillum* (Owen, 1866), *A. gracile* Marsh, 1879a, and *Kurtodon pusillus* Osborn, 1887, indicates that OMNH 62673 is M5 or, less likely, M6. Like other dryolestids, three roots are present. Of these, the lingual root is notably robust, being as broad mesiodistally as the two buccal roots combined (Fig. 8A₂). A groove is present on the buccal face of the lingual root, which bends mesially toward the tip—another indication that the tooth occupied a distal position in the molar series.

The paracone has a rounded (not angular) lingual profile; its mesial face is vertical whereas the distal face slopes slightly, so that the paracone appears to be tilted mesially. The apex of this cusp is missing, but it was clearly the tallest cusp on the tooth. The paracrista and metacrista form sharp, raised crests to enclose a trigon basin. Enamel is missing from part of the metacrista, but a distinct swelling shows that the metacone was

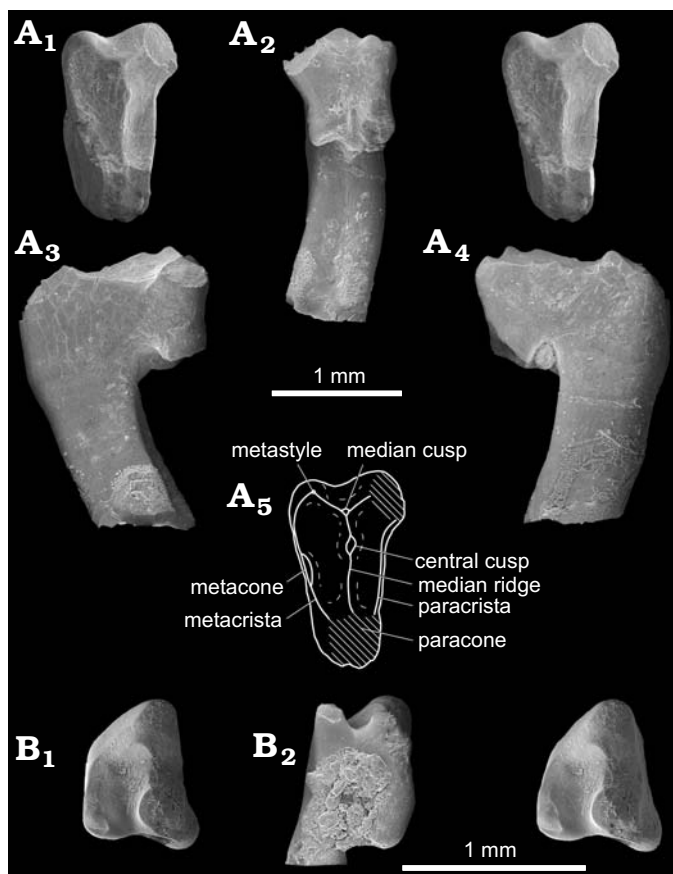


Fig. 8. Dryolestid mammals from the Lakota Formation (Lower Cretaceous: upper Berriasian–lower Barremian), South Dakota, USA. **A.** *Lakotalestes luoi* gen. et sp. nov., OMNH 62673 (holotype), from OMNH locality V1243; right upper molar in occlusal (A_1 , stereopair), buccal (A_2), mesial (A_3), and distal (A_4) views, with interpretive illustration (A_5) of occlusal view. **B.** cf. *Lakotalestes luoi*, OMNH 62854, from OMNH locality V1254; right lower molar (trigonid only) in occlusal (B_1 , stereopair) and lingual (B_2) views.

buccolingually elongate and well developed. Cusp “C”, usually present on upper molars of dryolestids (Prothero 1981), is lacking, but the metastyle is developed as a distinct cusp (well seen in buccal view; Fig. 8 A_2) at the buccal margin of the stylar shelf, just mesial to the buccodistal corner of the tooth.

A well-marked median ridge extends buccally from the paracone, terminating in a distinct, mesiodistally developed median cusp that is situated at the deepest part of the ectoflexus, somewhat lingual to the buccal margin of the tooth. The most distinctive feature of the upper molar of *Lakotalestes luoi* gen. et sp. nov. is the presence of another cusp, herein termed the central cusp, on the median ridge about two-thirds of the distance from paracone to median cusp. The central cusp is nearly as tall as the median cusp and is much broader-based, occupying the greater part of the trigon basin.

The paracrista extends buccally from the paracone for about two-thirds of the crown width, terminating at the distolingual base of the parastylar lobe. The stylocone is not preserved, but its presence may be inferred from the upward curvature of preserved adjacent enamel and by the presence

of a crest that joined the stylocone to the more distally-lying median cusp (Fig. 8 A_3). The parastyle is also missing; judged by the parastylar lobe that remains toward the base of the crown, the parastyle did not form a hook-like structure.

Remarks.—*Lakotalestes luoi* gen. et sp. nov. appears structurally closest to *Miccylyotyrans minimus* (from the Kimmeridgian–Tithonian Morrison Formation, USA at Como Quarry 9; Simpson 1927), and, to a lesser extent, *Kurtodon pusillus* and *Amblotherium* spp. (known by upper dentitions from the Berriasian Purbeck Limestone Group, UK at Durlston Bay; Simpson 1928; *Amblotherium* is well represented by lower dentitions from the Morrison as well). Both *Miccylyotyrans* and *Kurtodon* may be based on upper dentitions belonging to species of *Amblotherium* (Martin 1999) and were tentatively recognized as such by Kielan-Jaworowska et al. (2004). We have retained usage of separate names in order to promote specificity in the differential diagnosis and comparisons. *Lakotalestes* is similar to *Miccylyotyrans* in that the paracrista terminates at the base of the stylocone, whereas in *Kurtodon* and *Amblotherium* spp. the crest ascends the flank of the cusp, generally terminating at its apex. Like *Lakotalestes*, *Miccylyotyrans* has a median cusp (though it is smaller and placed just distal to the small ectoflexus), also reportedly present, in diminutive form, in *Amblotherium nanum* (Owen, 1871) and *Kurtodon pusillus* (see Simpson 1928). A strong, complete median ridge is present in *Lakotalestes*. A complete median ridge is also variably present in *Miccylyotyrans*; the ridge is present but incomplete buccally in *Kurtodon*, faint to absent (depending on tooth position) in *Amblotherium nanum*, and lacking in *A. pusillum*. Also variable in their presence among these taxa are cusps on the metacrista: *Lakotalestes* has a metacone but no cusp “C”; both cusps are present in *Miccylyotyrans* and *Amblotherium pusillum* but lacking in *A. nanum* and *Kurtodon*. *Lakotalestes* is unique in the development of a broad-based central cusp (Fig. 8 A_1 , A_2). A cusp is also present in this position on the single known upper molar of the dryolestoid *Donodon perscriptoris* Sigogneau-Russell, 1991c, described and placed in its own monotypic family by Sigogneau-Russell (1991c). *Donodon* does not otherwise invite close comparison.

In his cladistic analysis of relationships among Dryolestidae (including only taxa known by both upper and lower dentitions), Martin (1999) recognizes a basal dichotomy of included genera; *Amblotherium* lies in a clade with the Iberian *Krebsotherium* Martin, 1999 and *Crusafontia* Henkel and Krebs, 1969. *Krebsotherium* (monotypic), represented by *K. lusitanicum* Martin, 1999, is known from the early Kimmeridgian of Guimarota, Portugal (Martin 1999). The type of *Crusafontia*, *C. cuencana* Henkel and Krebs, 1969, is known from lower Barremian horizons at Galve and Uña, Spain (Henkel and Krebs 1969; Krebs 1993); a referred species, *C. amoae* Cuenca Bescós, Badiola, Canudo, Gasca, Moreno-Azanza, 2011, was recovered from a slightly older (Hauterivian–Barremian) horizon of the El Castellar Formation at Galve (Cuenca Bescós et al. 2011). Both the clade *Krebsotherium* (*Crusafontia* (*Amblotherium*)) and its con-

stituents are diagnosed by apomorphies of the lower molars (Martin 1999). As inferred for *Lakotalestes*, these taxa are primitive relative to other dryolestids in retaining a stylocone that is small; the stylocone is somewhat more distally placed in *Krebsotherium* than in *Crusafontia* or *Lakotalestes*, but variably retains connection to the paracrista (the paracrista extends to the apex of the stylocone in both species of *Crusafontia* whereas it terminates at the base of that cusp in *Lakotalestes*). In addition to its distally placed stylocone, *Krebsotherium* is dissimilar to *Lakotalestes*, *Amblotherium* spp., *Miccylotyrens*, *Kurtodon*, and *Crusafontia* in having a mesiodistally broader paracone profile and in lacking an ectoflexus. Cusp “C” and the metacone are variably present, at least, on molars of *C. amoe*; the condition in *C. cuencana* is uncertain because of wear on the only known upper molar. The median cusp is absent from the known upper molar of *C. cuencana* and variably present in *C. amoe*; a median ridge is lacking from known specimens of both species.

In their recent description of a highly specialized dryolestoid from the Late Cretaceous of South America, Rougier et al. (2011) published a phylogeny of the Dryolestoidae including a broad sample of Laurasian taxa. This study is the most recent (and most comprehensive to date) cladistic analysis of relationships among Dryolestidae, highlighting the endemism that South American forms had evolved by the end of the Cretaceous. However, the contents and topology of both the Dryolestidae and Paurodontidae Marsh, 1887 resulting from their analysis are very different from traditional hypotheses (e.g., Prothero 1981; Martin 1999; Luo et al. 2002). For example, the Paurodontidae are restricted to just three of the sampled taxa, with *Henkelotherium* Krebs, 1991 (previously considered a paurodontid) placed instead at the base of the Dryolestidae. The relationships of characteristic dryolestid genera within the family also differ markedly from those proposed by Martin (1999), with *Laolestes* Simpson, 1927 sharing a closer relationship with *Amblotherium* instead of with *Dryolestes*. It should be noted that Bremer support is, however, very weak at all nodes in this region of their cladogram (Rougier et al. 2011: fig. S1). Given the somewhat unstable relationships within Laurasian Dryolestoidae and the proposed similarities between *Lakotalestes* and *Amblotherium*, more complete material from the earliest Cretaceous Lakota Formation could help provide additional resolution.

Stratigraphic and geographic range.—Lower Cretaceous (upper Berriasian–Valanginian), South Dakota, USA. Currently known only from the type locality and horizon.

cf. *Lakotalestes luoi* sp. nov.

Fig. 8B.

Material.—OMNH 62854, a partial right lower molar from OMNH V1254, Fuson Member, Lakota Formation (Lower Cretaceous: upper Valanginian–lower Barremian), Meade County, South Dakota, USA.

Description.—OMNH 62854 is a moderately to well-worn right lower molar lacking the talonid, which appears to have

been abraded off ($L = [0.69 \text{ mm}]$, $W = 0.84 \text{ mm}$). The roots are broken, but their bases show that the distal root was much smaller than the mesial root and was positioned lingually, under the distolingual base of the metaconid. This is a distinguishing feature of the Dryolestidae (Simpson 1927). The buccal side of the crown extends farther downward than the lingual side, reflecting a lower buccal than lingual alveolar border. This was described as a dryolestid apomorphy by Prothero (1981), though a similar condition presents in the Spalacotheriidae. Like other dryolestids, the trigonid is mesiodistally compressed compared to the condition in the Paurodontidae or stem Zatheria McKenna, 1975 (angle = 31° ; Fig. 8B₁). Each of the cusps shows apical wear, but it is clear that all were pointed and cusp-like; judged by what remains, they appear to have been gracile. Both the paracristid and protocristid are well developed and bear strap-like wear facets. Wear along the protocristid is especially strong, but because it is oblique to the occlusal plane this does not appear to have significantly affected the apex of the metaconid. The protoconid, which is also beveled on its mesial face (owing to wear on the paracristid), is most dramatically affected by apical wear, being only slightly taller than paraconid and metaconid. The metaconid has a broader base than the paraconid but the cusps are equal in height. The paraconid has a slight mesial tilt, but is best described as semi-erect rather than procumbent, best seen in lingual view (Fig. 8B₂).

Remarks.—OMNH 62854 cannot be directly compared with *Lakotalestes luoi*, which is based on an upper molar. It appears to have come from a slightly smaller individual than that represented by the holotype of the species (tooth lengths cannot be directly compared, as the talonid of OMNH 62854 is missing), but they are similar enough in size to have belonged to the same species. Though the two specimens are from different localities positioned at different horizons (and, presumably, differing somewhat in age), comparisons below suggest that OMNH 62854 is morphologically appropriate to have belonged to *Lakotalestes luoi* or a similar taxon. Taken together, the restricted stratigraphic interval represented by these two localities, the very small number of mammalian specimens recovered, and the favorable morphological comparisons between the upper and lower molars lead us to retain this tentative referral as a working hypothesis, at least until the record from the Lakota Formation improves. These comparisons follow the character polarities and tree presented by Martin (1999); numbers in parentheses refer to characters in his data matrix (Martin 1999: 83).

OMNH 62854 lacks apomorphies seen in the major clade of Dryolestidae identified by Martin (1999), that including the last common ancestor of *Dryolestes* and *Laolestes*, and all of its descendants. The paraconid is cusp-like, not shovel-like (9), as in *Dryolestes* and *Peraspalax* Owen, 1871; similarly, the metaconid is pointed and not mesiodistally elongate (11) as it is in *Phascolestes* Owen, 1871, *Guimarotodus* Martin, 1999, or *Laolestes*. Other apomorphies seen in one or more genera of this group are also lacking: extreme mesiodistal compression (20; *Phascolestes*), metaconid in-

flated and paraconid flexed (12, 16; *Guimarotodus*), and bifid metaconid (*Laolestes*).

Conversely, OMNH 62854 is similar to the clade (*Krebsotherium* (*Crusafontia* + *Amblotherium*)) in its pointed (not stocky) cusps (7). It lacks the flexed paraconid (16) seen in *Krebsotherium* (also seen in *Guimarotodus*, a presumed homoplasy). OMNH 62854 is similar to the clade (*Crusafontia* + *Amblotherium*) in having a semi-erect paraconid (Thomas Martin personal communication, 2011) and slender cusps, differing from *Crusafontia* in lacking a mesial cingulid. Significantly, the paraconid and metaconid of the Lakota specimen are of equal height (19), as is the case in *Amblotherium* spp. The identity of OMNH 62854 will remain unknown until and unless similar lower teeth are found in association with upper molars. However, as the upper molar OMNH 62673 is most comparable to those seen in species of *Amblotherium*, *Miccytyrans*, and *Kurtodon*, (which are suspected synonyms and which occupy the same position on the tree published by Martin 1999), OMNH 62854 is morphologically appropriate, at least in known respects, to belong to *Lakotalestes luoi*.

Superorder Zatheria McKenna, 1975

Remarks.—Kielan-Jaworowska et al. (2004) defined the Zatheria as a node-based taxon to include the last common ancestor of *Peramus* Owen, 1871 + Boreosphenida Luo, Cifelli, and Kielan-Jaworowska, 2001, plus all of its descendants (see Prothero 1981 for a character-based definition encompassing the same taxa). As pointed out by Martin (2002), this definition excludes taxa (e.g., *Amphitherium* Blainville, 1838; *Arguimus* Dashzeveg, 1979; *Nanolestes* Martin, 2002) generally accepted as stem-lineage(s) to the same monophyletic group. We follow Martin (2002) in recognizing the Zatheria as a stem-based taxon, including all mammals more closely related to the Tribosphenida McKenna, 1975 (= Boreosphenida, see Davis 2011b) than to the Dryolestoidae. We follow Lopatin and Averianov (2006b) and Davis (2011a) in referring to the single talonid cusp as a hypoconid rather than a hypoconulid (Kielan-Jaworowska et al. 2004) or simply “talonid cusp” (Sigogneau-Russell 2003).

Family, genus, and species indet.

Fig. 9A.

Material.—OMNH 67137, incomplete right lower molar from OMNH V1254, Fuson Member, Lakota Formation (Lower Cretaceous: upper Valanginian–lower Barremian), Meade County, South Dakota, USA.

Description.—OMNH 67137 is a very small (maximum length of preserved part <0.6 mm) lightly worn right lower molar missing the paraconid, most of the protoconid, and the apex of the hypoconid; the enamel is otherwise well preserved. The metaconid is erect and sharply pointed but mesiodistally broad-based, suggesting that the trigonid would have been relatively open lingually. The protocristid and what remains of the protoconid suggest that the metaconid would have

been positioned distal to that cusp, not transversely aligned with it (Fig. 9A₁). From the apex of the metaconid the distal metacristid forms a keel (worn almost flat) that descends the distal face of the metaconid, curving slightly buccally and distally as it approaches the talonid (Fig. 9A₃). Wear facet 1 (for the mesial face of the paracone on the opposing upper molar, numbering scheme follows that of Crompton 1971) is present as a continuous facet that occupies the entire distal face of the trigonid (as preserved), curving into the deepest recess of the ectoflexid, adjacent to the terminus of the distal metacristid. The talonid is low but mesiodistally elongate and tapers only slightly distally until the level of the hypoconid, where it is rounded in occlusal view. The ectoflexid is well marked and would have been prominent were the buccal face of the protoconid complete. A narrow notch separates the end of the distal metacristid from a small cusp, the “mesoconid” of Butler (1990) and Martin (2002), which is separated distally from the cristid obliqua by another, similarly narrow notch. The cristid obliqua ascends the talonid distobuccally, terminating at the hypoconid, which occupies the distobuccal corner of the tooth. The apex of the hypoconid is missing, but it does not appear to have been buccolingually expanded. No further talonid cusps or crests are present, nor is there any hint of a talonid basin. Wear facet 3 (for the distal face of the paracone on the opposing upper molar) appears on the mesial flank of the hypoconid, extending a short way mesiolingually into the ectoflexid and toward wear facet 1.

Remarks.—Incomplete as it is, OMNH 67137 preserves part of the trigonid and the talonid almost intact, which provide some basis for discussion of its affinities. The relatively open trigonid (as judged by the mesially extensive base of the metaconid) and, especially, features of the talonid preclude reference to the Dryolestoidae: the distal metacristid is well defined and leads to a prominent, distobuccally-oriented, ascending cristid obliqua; and the talonid is elongate, with a tall, buccally placed hypoconid (Fig. 9A). Each of these features is characteristic of the Zatheria sensu Martin (2002), to which we accordingly refer OMNH 67137. The Lakota specimen lacks an entocristid, incipient talonid basin, and entoconid; one or more of these derived characters are seen (sometimes variably and/or in subtle form) in *Palaeoxonodon* Freeman, 1979, *Peramus*, *Minimus* Sigogneau-Russell, 1999, *Magnimus* Sigogneau-Russell, 1999, and *Arguimus* (Sigogneau-Russell 1999, 2003; Martin 2002; Lopatin and Averianov 2006b; Davis 2012). Also worthy of note is the “mesoconid” present between distal metacristid and cristid obliqua on the talonid of OMNH 67137. According to Martin (2002), a similar cusp is present in *Nanolestes drescheriae* Martin, 2002, *Palaeoxonodon*, *Arguimus* and, variably, in *Peramus*. As Martin (2002) noted, the condition may prove to be a synapomorphy among certain Zatheria.

Of described basal Zatheria, OMNH 67137 is very close in overall size and appearance to lower molars of *Palaeoxonodon* from the Forest Marble (Bathonian) of Britain (Freeman 1979; Sigogneau-Russell 2003; placed within the Amphitheriidae by Davis 2011a); in fact, characters with

which to distinguish the two taxa are lacking (though they are separated by 25 Ma, and poor preservation of the Lakota specimen precludes comprehensive comparison). When compared with other stem zatherians, the talonid appears longer in OMNH 67137 (in reference to the metaconid) than in *Nanolestes*, and in this respect it also resembles *Amphitherium rixoni* Butler and Clemens, 2001, which is considerably larger. OMNH 67137 further differs from *Nanolestes* in that the metaconid is more distally placed (not transversely aligned with the protoconid) and erect (not distally curved).

It is likely that the stem zatherian from the Lakota Formation represents a new taxon. Given the incompleteness of the specimen, and the high degree of variability seen among basal Zatheria (e.g., Sigogneau-Russell 2003), taxonomic circumscription is best deferred until better material is available.

Subclass Tribosphenida McKenna, 1975

Remarks.—Luo et al. (2001) erected the Boreosphenida and Australosphenida for mammals with tribosphenic molars originating on northern and southern landmasses, respectively. Studies by Martin and Rauhut (2005), Rougier et al. (2007), and Davis (2011a) indicate that australosphenidans lack functionally tribosphenic molars. Boreosphenida is therefore a junior synonym of Tribosphenida McKenna, 1975.

Family, genus, and species indet.

Fig. 9B.

Material.—OMNH 64193, trigonid of left lower molar from OMNH V1254, Fuson Member, Lakota Formation (Lower Cretaceous: upper Valanginian–lower Barremian), Meade County, South Dakota, USA.

Description.—OMNH 64193 lacks the talonid but is otherwise well preserved ($L = [0.80 \text{ mm}]$); wear on the specimen is sufficient to show initial development of wear facets 1 and 2 (Crompton 1971) on the postvallid and prevallid surfaces, respectively, but not enough to have penetrated enamel on crests or cusp apices. The major cusps are tall, gracile, trenchant, and well individualized (Fig. 9B₂). Cusp positions in occlusal view appear to be unusual, though this cannot be adequately described because of lack of reference for orienting the specimen. If the protocristid is oriented transversely, the paraconid lies in a median position; if the paraconid and metaconid are aligned with respect to the tooth row, the metaconid occupies a remarkably distal position. Splitting the difference between these extremes, it would appear that both conditions probably pertain: the paraconid was probably not as lingually placed as the metaconid, and the latter cusp was probably situated well distal to the protoconid (Fig. 9B₁). The crown is dominated by the protoconid, which is about twice as tall as the other trigonid cusps when the specimen is viewed in lingual aspect. Both paraconid and protocristid are sharp and deeply notched. The paraconid and metaconid are equal in height, but the metaconid is slightly more robust. Cusp f is developed as a prominent knob that occupies much of the mesial face of the tooth at the base of the crown, below

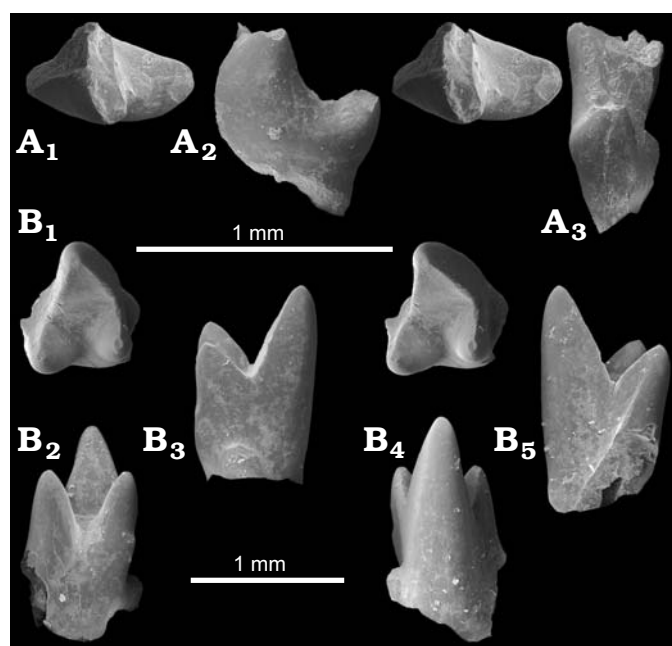


Fig. 9. Stem zatherian (A) and tribosphenidan (B) mammals from OMNH locality V1254, Lakota Formation (Lower Cretaceous: upper Valanginian–lower Barremian), South Dakota, USA. A. OMNH 67137, right lower molar in occlusal (A₁, stereopair), lingual (A₂), and distal (A₃) views. B. OMNH 64193, left lower molar (trigonid only) in occlusal (B₁, stereopair), lingual (B₂), mesial (B₃), buccal (B₄), and distal (B₅) views.

and slightly lingual to the notch in the paraconid (Fig. 9B₃). This cusp bears a distinct wear facet, most likely from the tip of the metacone on the occluding upper molar. Cusp e is best seen in lingual view, where it is shown as a faint bulge on the mesiolingual face of the paraconid, about half way between base and apex of that cusp, and well dorsal to cusp f. No other basal cuspules or remnants of cingulid are present. A faint ridge or keel lies along the mesiolingual face of the paraconid, extending downward from a point just dorsal to cusp e. The distal metacristid originates near the apex of the metaconid and descends distobuccally, becoming prominent (and flaring slightly) at the point where it meets the break in the specimen (Fig. 9B₅). This break appears to have followed the deepest part of the ectoflexid buccally.

Remarks.—OMNH 64193 does not compare closely to lower molars of spalacotheriid “symmetrodonts” (which have a basal cingulid and mesiolingual and distolingual cuspules, and lack a distal metacristid) or dryolestids (which are not as high crowned and have a paraconid that is procumbent and smaller relative to the metaconid, and in which the distal metacristid descends distally, not distobuccally). Judged by the size of the break, the talonid was substantially larger than that of a dryolestid or spalacotheriid.

OMNH 64193 compares more favorably to lower molars of stem Zatheria, with the following general differences: trigonid less open lingually, with bases of paraconid and metaconid more closely appressed; trigonid angle more acute (47°, most stem Zatheria range from 55–90°, though specimens from the Forest Marble variably have a more acute

trigonid, cf. Sigogneau-Russell 2003: table 1); and paraconid and metaconid are subequal (also seen in *Amphitherium*, see Mills 1964: pl. 2). Although referral to a stem zatherian cannot be definitively ruled out, these features tend to be more characteristic of the Tribosphenida, to which we accordingly refer the Lakota specimen. Additional support for tribosphenidan affinities is supplied by the position of cusp f on the mesial face of the trigonid, which can provide some indication of relative talonid development (as it functions in the interlocking mechanism between adjacent molars). In stem zatherians such as *Arguimus*, *Amphitherium*, and *Peramus*, cusp f is positioned buccal to the deepest point of the paracristid; this reflects the presence of only a single talonid cusp (hypoconid) or poor separation of the hypoconulid from the hypoconid (as in *Peramus*). In the basal tribosphenidan *Kielantherium* Dashzeveg, 1975, which possesses a basined but otherwise poorly-developed talonid, cusp f is positioned directly below the paracristid notch. Stem tribosphenidans with better-developed talonids (or evidence from upper molars suggesting the presence of a well-developed talonid), such as those from the Aptian–Albian Trinity Group of Texas and Oklahoma (e.g., *Pappotherium* Slaughter, 1965 and *Slaughteria* Butler, 1978), have cusp f positioned slightly lingual to the paracristid notch, a condition shared with OMNH 64193 (Fig. 9B₃).

In proportions and arrangement of the trigonid, OMNH 64193 closely resembles the basal eutherian *Montanalestes* Cifelli, 1999a from the Aptian–Albian of Montana, but differs in the retention of a distal metacristid. The balance of evidence supports referral of this specimen to an indeterminate tribosphenidan; beyond this, little can be said of the affinities of OMNH 64193, except that presence of a distal metacristid is a plesiomorphy seen in stem tribosphenidans such as *Kielantherium*, *Aegialodon* Kermack, Less, and Mussett, 1965, *Slaughteria*, and *Kermackia* Butler, 1978, as well as basal Metatheria (see Davis and Cifelli 2011).

Discussion

Age and “age” of the Lakota Formation.—Biostratigraphy based on ostracods and charophytes has proven to be a valuable tool to support and improve intraformational correlations in general and to establish age constraints to discriminate horizons within the Lakota Formation. The biostratigraphic framework for understanding the age of the Lakota Formation (late Berriasian–early Barremian based on data at hand; Sohn 1979; Sames et al. 2010; Sames 2011a, b; Fig. 2 herein) has improved in recent years, but obvious refinements are needed. Of particular interest, in the context of the Upper Jurassic–Lower Cretaceous “hiatus,” is the lower age constraint of the Lakota Formation. To date, no ostracods or charophytes are known from the lowest part, unit 1, of the Chilson Member. Hence, the lower age constraint for the unit as a whole remains poorly resolved. As well, given that most of the biostratigraphically informative ostracods and charophytes in

Chilson unit 2 derive from the lower part of the section (e.g., Martín-Closas et al. 2013; Sames et al. 2010; Sames 2011a, b), upper age constraints for the member remain to be firmly established. Further micropaleontological sampling of the Fuson Member in southern exposures of the Lakota Formation is also needed in order to provide context for correlating strata from elsewhere in the Black Hills.

Turning to vertebrates, Lucas (1993; see also Lucas et al. 2012) established the Buffalogapian land-vertebrate “age” on the basis of then-known fossils (principally dinosaurs) from the Lakota Formation, regarding the fauna as younger than the Comobluffian (from the Morrison Formation) and older than the Cashenranchian (from the Cloverly Formation). Correlation on the basis of ostracods and the character of the mammalian fauna uphold this view. Interestingly, the three Lakota dinosaurs identified to genus level are also known from the Early Cretaceous of Western Europe: *Polacanthus* (Barremian–Aptian; see Pereda-Suberbiola 1994; Blows 1998), *Iguanodon* (Valanginian–Aptian; see Blows 1998), and *Hypsilophodon* (Barremian of Britain, Barremian–Aptian of Spain; see Sanz et al. 1983, 1987; Blows 1998). Below we comment briefly on the Lakota mammals with respect to those known from the Early Cretaceous of Britain.

Whereas the general concept of a Buffalogapian land-vertebrate “age”, lying temporally between Comobluffian and Cashenranchian assemblages, remains valid (though we are skeptical as to its utility), it is clear that documenting stratigraphic position(s) of characteristic fossils will be critical to understanding vertebrate evolution during this time interval (at least 10 Ma, given current age constraints for the Lakota Formation). Within this context, we point out that the mammals of the Lakota Formation (discussed as an assemblage for general purposes herein) derive from two separate horizons with different estimated ages (late Berriasian–Valanginian and late Valanginian–early Barremian, respectively) and do not constitute a local fauna (see Tedford 1970).

Mammals of the Lakota Formation.—Though important specimens of mammaliaforms are now known from the Late Triassic–Early Jurassic of North America (Jenkins et al. 1983; Lucas and Hunt 1990; Montellano et al. 2008), the oldest well-represented mammalian assemblage on the continent is that from the Morrison Formation of the western USA. The mammalian fauna of the Morrison is of Late Jurassic (Kimmeridgian–Tithonian) age, and hence of particular interest in the present context. We base the following summary on the account of Kielan-Jaworowska et al. (2004). More than 20 genera of mammaliaforms have been recorded from the unit. Of these, basal Cladotheria (Dryolestidae and Paurodontidae) are most diverse and abundant, though “triconodonts” (“amphilestids” and “triconodontine” Triconodontidae) and “plagiulacidan” multituberculates (Allodontidae, Zofiabaataridae, and Glirodontidae) comprise significant elements of the assemblage. Other notable elements of the fauna include the mammaliaform *Docodon*, the highly-specialized basal mam-

mal *Fruitafossor*, and the obtuse-angled “symmetrodont” *Tinodon* (see also Rougier et al. 2003; Luo and Wible 2005).

Appreciable remains of mammals do not appear again in the North American fossil record until the latter part of the Early Cretaceous, some 35–40 Ma after deposition of the Morrison Formation. Individual specimens or assemblages have been reported from several units of Aptian–Albian age, including the Arundel Clay facies of the Patuxent Formation, Maryland (see citations in Cifelli et al. 2013), the Trinity Group, Texas and Oklahoma (Winkler et al. 1990; Davis and Cifelli 2011), and the Cloverly Formation, Wyoming and Montana (Jenkins and Schaff 1988; Cifelli et al. 1998; Cifelli 1999a). The upper part of the Cedar Mountain Formation, Utah, has yielded a slightly younger (Albian–Cenomanian) but reasonably diverse and well sampled mammalian fauna (see Kielan-Jaworowska et al. 2004 and references therein). Unsurprisingly, these late Early to early Late Cretaceous assemblages present some striking points of contrast with the mammalian fauna of the Morrison Formation. Notable by their absence are dryolestoids, so prevalent in the Morrison Formation; also lacking are docodonts. Multituberculata are diverse and abundant, and are dominated by cimolodontans, though “plagiaulacidans” apparently survived until the Cenomanian (Eaton and Cifelli 2001). Each assemblage mentioned includes one or several triconodontids belonging to the Alticonodontinae, which make their first North American appearance in the Aptian (Cifelli et al. 1999; phylogenetic analysis by Gaetano and Rougier 2011 suggests a Jurassic origin for the clade). Spalacotheriid “symmetrodonts” (Spalacolestinae) are also known from all of the better-sampled late Early Cretaceous assemblages of North America, being particularly diverse and abundant in the Albian–Cenomanian Mussentuchit Member of the Cedar Mountain Formation, Utah (Cifelli and Madsen 1999). Another noteworthy characteristic of late Early Cretaceous mammalian faunas of North America is the abundance and diversity of tribosphenic taxa. In addition to stem forms, both Metatheria (Deltatheroidea and Marsupialiformes) and Eutheria appear to be present (Richard L. Cifelli unpublished data; Cifelli 1999a; Davis and Cifelli 2011), though with one exception (Stagodontidae; see Cifelli 2004) families typical of the North American Late Cretaceous remain unidentified in this interval.

Though represented by fragmentary material, the fossil mammals from the Lakota Formation are noteworthy for a number of reasons: these are the first mammals described from the unit, which has otherwise yielded few vertebrate (mainly dinosaurian) remains (see summary by Lucas 1993); these are the first mammals described from the poorly-sampled earliest Cretaceous (pre-Aptian) of North America; and, perhaps most importantly, the fauna bridges the gap between the relatively well sampled Morrison Formation (Kimmeridgian–Tithonian) and the Albian–Cenomanian faunas of the Antlers, Cloverly, and Cedar Mountain formations. Of the comparatively small number of specimens (nine) from the Lakota Formation, eight taxa are represented (Table 1), and

each occupies a relevant place in the evolutionary history of mammals in North America.

Predictably, the mammalian fauna of the Lakota Formation includes a number of range extensions (Fig. 10). Among last occurrences, the “plagiaulacidan” multituberculate *Passumys angelli* gen. et sp. nov. represents a group (Alloodontoidea) otherwise known only from the Late Jurassic of North America and is most similar to *Glirodon*, from the Morrison Formation (Engelmann and Callison 1999). Likewise, at least one of the unidentified triconodontids is of “triconodontine” grade. Similar triconodontids occur in the Morrison Formation (Simpson 1929); geologically younger (Aptian–Cenomanian) North American members of the family all represent the monophyletic Alticonodontinae (e.g., Cifelli et al. 1999). Another last North American occurrence in the Lakota Formation is that of the Dryolestoidea (represented by *Lakotalestes luoi* gen. et sp. nov.)—a further similarity of the Lakota assemblage to that of the Morrison Formation.

A similar number of Lakota taxa (three) represent first occurrences of taxa previously documented from geologically younger (Aptian–Cenomanian) rocks in North America. The Plagiaulacoidea (a group best known from Eurasia, see Hahn and Hahn 2006), represented in the Lakota Formation by *Bolodon hydei* sp. nov., are also known from the Albian–Cenomanian Cedar Mountain Formation (*Janumys*; see Eaton and Cifelli 2001; Hahn and Hahn 2004). Both the Spalacotheriidae and Tribosphenida (represented in the Lakota assemblage by *Inferolestes rougieri* gen. et sp. nov. and an unidentified taxon, respectively) are reasonably diverse, abundant members of late Early Cretaceous North American faunas (e.g., Patterson 1956; Cifelli and Madsen 1999; Cifelli 1999a; Davis and Cifelli 2011).

The unidentified stem zatherian from the Lakota Formation is uninformative regarding the correlation of the unit, but deserves passing mention because it is the first mammal of this grade to be recorded from the fossil record of North America. Stem Zatheria are reasonably well represented in Middle Jurassic through Early Cretaceous faunas of Europe (Kielan-Jaworowska et al. 2004). In this context, it is somewhat surprising that they are not known from the Morrison Formation or elsewhere in the North American record. Intriguingly, the Lakota form shows close resemblance to British amphitheriids, which are structurally closest to paramurans (Davis 2011a).

Given their age, mammals of the Lakota Formation also invite comparison with those of the Early Cretaceous of Britain. Faunal similarity between the mammalian assemblages of the Morrison Formation (Kimmeridgian–Tithonian) and the slightly younger Purbeck Group (Berriasian) has long been noted, with some four genera in common (Simpson 1928, 1929; Ensom and Sigogneau-Russell 2000; Sigogneau-Russell and Kielan-Jaworowska 2002). The most significant differences between these assemblages lie in the composition of the multituberculates (Alloodontoidea, endemic to North America, are present in the Morrison, whereas the Purbeck includes Plagiaulacoidea and Paulchoffatoidea; Simpson 1928; Kielan-Ja-

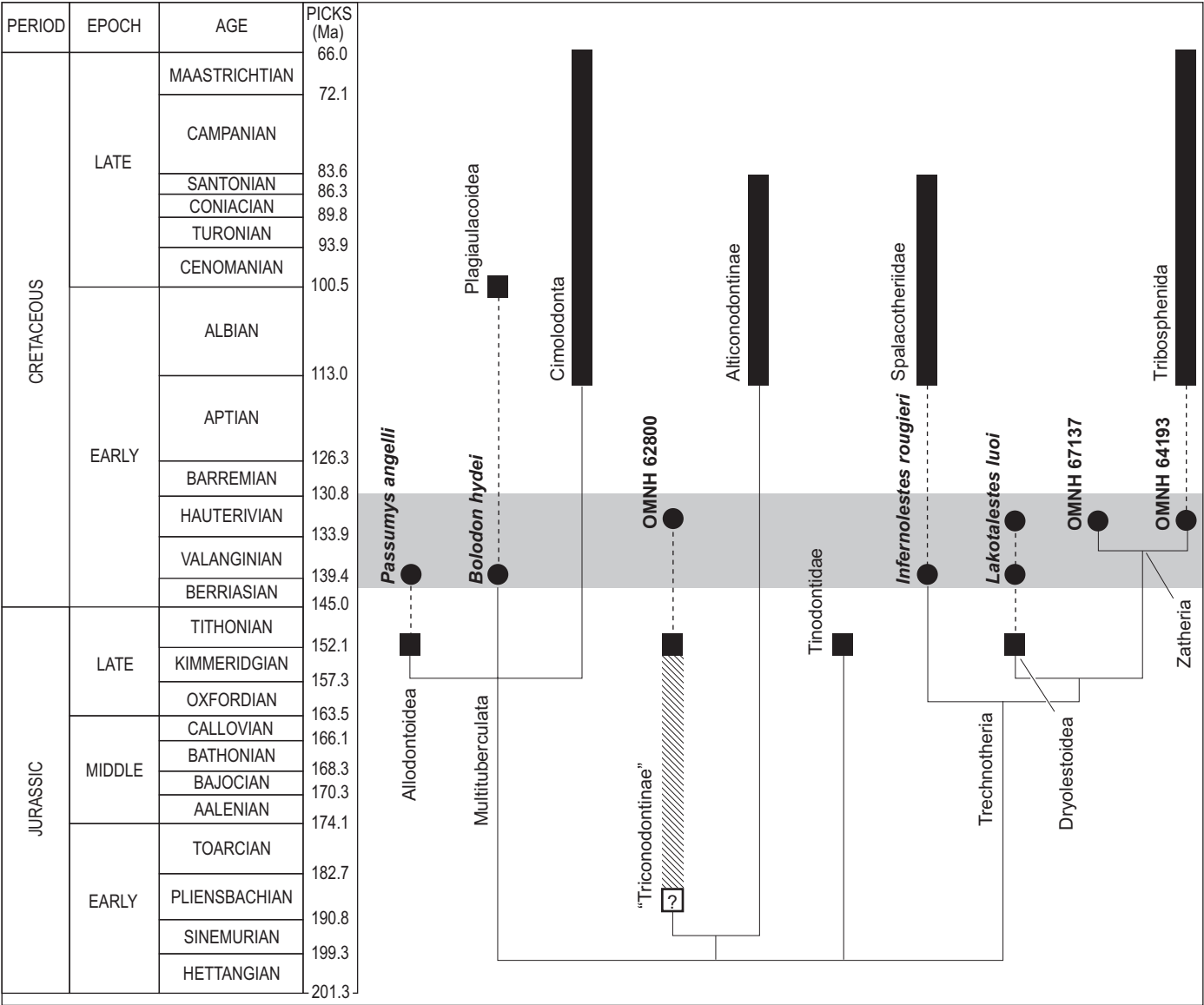


Fig. 10. Simplified cladogram showing known North American distribution of mammalian taxa during the Jurassic and Cretaceous. Grey bar indicates temporal range of deposits of the Lakota Formation (Lower Cretaceous: upper Berriasian–lower Barremian). Closed circles indicate mammalian fossils described in this study (temporal distributions given as mid-ranges for respective estimates). Dashed lines indicate stratigraphic range extensions of groups otherwise restricted to the Late Jurassic (Morrison Formation) or unrecorded until the Aptian–Cenomanian (Antlers, Arundel, Cloverly, and Cedar Mountain formations), highlighting the transitional composition of the Lakota assemblage. Cladogram modified from Luo (2007), geologic time scale modified from Gradstein et al. (2012).

worowska and Ensom 1992, 1994) and in the presence of Spalacotheriidae, stem Zatheria and Tribosphenida in the Purbeck (Ensom and Sigogneau-Russell 2000; Sigogneau-Russell et al. 2001; Gill 2004; Davis 2012). In this context, shared presence in the Lakota and Purbeck of Plagiaulacoidea (including a genus in common, *Bolodon*), Spalacotheriidae, Tribosphenida, and (perhaps) stem Zatheria appears to be significant, and suggests the possibility of Early Cretaceous immigration from Western Europe to North America. This possibility is supported by similarities in the dinosaur assemblages of the Lakota Formation (noted above) and the Wealden Supergroup (see also Kirkland et al. 1997), which ranges from upper Berriasian to lower Aptian (Allen and Wimbledon 1991). Mammals have

been recovered from several horizons in the Wealden of the UK and its presumed correlates in the Iberian Peninsula; most are of Valanginian or Barremian age (Kielan-Jaworowska et al. 2004; Sweetman and Hooker 2011). At the present level of taxonomic resolution and sampling, mammalian assemblages of the Wealden share the same points of contrast with that of the Morrison as do the Lakota and Purbeck faunas (presence of Plagiaulacoidea, Spalacotheriidae, Tribosphenida, and Zatheria), with one difference: Docodonts, present in the Morrison and Purbeck, are absent, as they are from the Lakota assemblage.

Taken as a whole, the mammalian fauna from the Lakota Formation has a foot in both the Late Jurassic (with simi-

larities to taxa from the Morrison Formation) and the late Early Cretaceous (with similarities to taxa from the Antlers, Cloverly, and Cedar Mountain formations; see Fig. 10). This is a transitional fauna in nearly every regard, and so far as the available data allow, it underscores a gradual taxonomic turnover at the beginning of the Cretaceous.

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