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A new taeniolabidoid multituberculate (Mammalia) from the middle Puercan of the Nacimiento Formation, New Mexico, and a revision of taeniolabidoid systematics and phylogeny

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Abstract

Multituberculates were amongst the most abundant and taxonomically diverse mammals of the late Mesozoic and the Paleocene, reaching their zenith in diversity and body size in the Paleocene. Taeniolabidoidea, the topic of this paper, includes the largest known multituberculates, which possess highly complex cheek teeth adapted for herbivory. A new specimen from the early Paleocene (middle Puercan; biochron Pu2) of the Nacimiento Formation, New Mexico represents a new large-bodied taeniolabidoid genus and species, *Kimbetopsalis simmonsae*. A phylogenetic analysis to examine the relationships within Taeniolabidoidea that includes new information from *Kimbetopsalis* **gen. et sp. nov. and gen. nov.** and from new specimens of *Catopsalis fissidens*, first described here, and data from all other described North American and Asian taeniolabidoids. This analysis indicates that *Catopsalis* is nonmonophyletic and justifies our transfer of the basal-most taeniolabidoid ‘*Catopsalis*’ *joyneri* to a new genus, *Valenopsalis*. *Kimbetopsalis* and *Taeniolabis* form a clade (Taeniolabididae), as do the Asian *Lambdopsalis*, *Sphenopsalis*, and possibly also *Prionessus* (Lambdopsalidae). Taeniolabidoids underwent a modest taxonomic radiation during the early Paleocene of North America and underwent a dramatic increase in body size, with *Taeniolabis taoensis* possibly exceeding 100 kg. Taeniolabidoids appear to have gone extinct in North America by the late Paleocene but the appearance of lambdopsalids in the late Paleocene of Asia suggests that they dispersed from North America in the early to middle Paleocene.

Keywords: body size, dispersal, ecological recovery, mammalian radiation, multituberculata, paleobiogeography, Paleocene, San Juan Basin, Taeniolabididae, Taeniolabidoidea.

Introduction

Multituberculates were a diverse group of mammals that thrived alongside dinosaurs during much of the Mesozoic, survived the end-Cretaceous extinction, radiated yet again in the post-extinction world of the Paleocene, and then rap-

idly dropped in diversity in the late Paleocene and early Eocene as more modern groups of mammals (particularly the anatomically and ecologically similar rodents) spread across the globe (Krause, 1986; Kielan-Jaworowska, Cifelli & Luo, 2004; Weil & Krause, 2008). Multituberculates reached their peak in species diversity, body size, and mor-

phological disparity in the early Paleocene, within a few million years of the non-avian dinosaur extinction (Weil & Krause, 2008; Wilson *et al.*, 2012). Some of the most distinctive multituberculates flourishing during this time were the taeniolabidoids. Taeniolabidoids attained the largest sizes of any multituberculates and were characterized by a short rostrum, reduced premolars, a pair of gliriform incisors separated from cheek teeth by a long diastema, and enormous molars with a high number of cusps, all of which permitted an unusual herbivorous diet. These taeniolabidoids – including such familiar taxa as *Taeniolabis* and *Catopsalis* – were amongst the most aberrant and specialized mammals of the early Paleocene, a time when terrestrial ecosystems were being dramatically reshaped and mammals were beginning their march to dominance.

The first taeniolabidoids were discovered during the geological surveys of western North America during the 1880s, around the same time that multituberculates were recognized as a distinct group of extinct mammals (Cope, 1884, 1888a; Marsh, 1889a, b). Taeniolabidoids are common components of Paleocene faunas of the western USA and are now also known from Asia. Some species are important index taxa in defining the mammalian biochronological timescale (Lofgren *et al.*, 2004; Ting *et al.*, 2011) and taeniolabidoids have played a key role in understanding patterns of extinction and survivorship, and changes in mammalian body size and dietary habits across the Cretaceous–Paleogene boundary (e.g. Archibald, 1983; Wilson *et al.*, 2012; Wilson, 2013, 2014).

Although taeniolabidoids have been known for some 130 years, their phylogenetic relationships are still poorly understood and their taxonomy is in need of revision. It is widely accepted that genera such as *Taeniolabis*, *Catopsalis*, and *Sphenopsalis* form an anatomically and paleobiologically distinctive taeniolabidoid clade (e.g. Rougier, Novacek & Dashzeveg, 1997; Kielan-Jaworowska *et al.*, 2004; Mao, Wang & Meng, 2015), but the number of valid species in this clade and their detailed ingroup relationships are the subject of debate. A pioneering phylogenetic analysis by Simmons & Miao (1986) found the characteristic North American genus *Catopsalis* to be a nonmonophyletic array of several diagnostic species, some constituting a paraphyletic grade of basal taeniolabidoids, and others forming a polytomy with *Taeniolabis* and a clade of Asian taxa. Over the following three decades, several new taeniolabidoid specimens have been discovered, which promise to provide insight into the evolution of large body size and high dental complexity in this clade (e.g. Simmons, 1987; Buckley, 1995; Lucas, Williamson & Middleton, 1997; Meng, Zhai & Wyss, 1998; Mao, Wang & Meng, 2015). These have yet to be synthesized into a comprehensive phylogenetic analysis and systematic revision of the group.

We here describe a peculiar new taeniolabidoid from the early Paleocene of the San Juan Basin of New Mex-

ico, USA. This is the first new taeniolabidoid taxon to be described in nearly 20 years, and the first to be described from New Mexico – one of the world's premier localities for early Paleocene mammal fossils – since 1884. We establish the validity of this species, compare it with other taeniolabidoids, and use this as a jumping-off point for a systematic revision of the group, based on a species-level phylogenetic analysis. We then use the results of this analysis to clarify the taxonomy of Taeniolabidoidea and ingroup clades, provide an updated list of all valid species, designate a new genus name for a problematic species of '*Catopsalis*' that is now strongly supported as a basal taeniolabidoid, and discuss evolutionary trends in diversification, body size, and biogeography across taeniolabidoid history.

Material and Methods

INSTITUTIONAL ABBREVIATIONS

AMNH, American Museum of Natural History, New York, USA; NMMNH, New Mexico Museum of Natural History and Science, Albuquerque, USA; SDSM, South Dakota School of Mines, Rapid City, South Dakota, USA; SPSM, St. Paul Science Museum, Minnesota, USA; UCM, University of Colorado, Boulder, USA; UM, University of Michigan, Ann Arbor, USA; UMVP, University of Minnesota Vertebrate Paleontology, Minneapolis, USA; USNM, United States National Museum, Washington D.C., USA; UW, University of Wyoming, Laramie, USA.

ANATOMICAL ABBREVIATIONS

I2, second upper incisor; L, length; M, upper molar; m, lower molar; P, upper premolar; W, width; cusp formula following the pattern established by Simpson (1929), counting the buccal row first and the lingual row last.

Systematic Paleontology

MAMMALIA LINNAEUS, 1758

MULTITUBERCULATA COPE, 1884

TAENIOLABIDOIDEA SLOAN & VAN VALEN, 1965

TAENIOLABIDIDAE GRANGER & SIMPSON, 1929

***KIMBETOPSALIS SIMMONSAE* GEN. ET SP. NOV.**

(FIGS 1, 2, TABLES 1 AND 2)

(<http://zoobank.org/urn:lsid:zoobank.org:pub:9E9F07C3-D042-4E8F-862A-279072E04035>)

Holotype

NMMNH P-69902 from locality L-9181.

Type locality and horizon

The specimen was discovered in the lower Paleocene part of the Nacimiento Formation of the San Juan Basin of

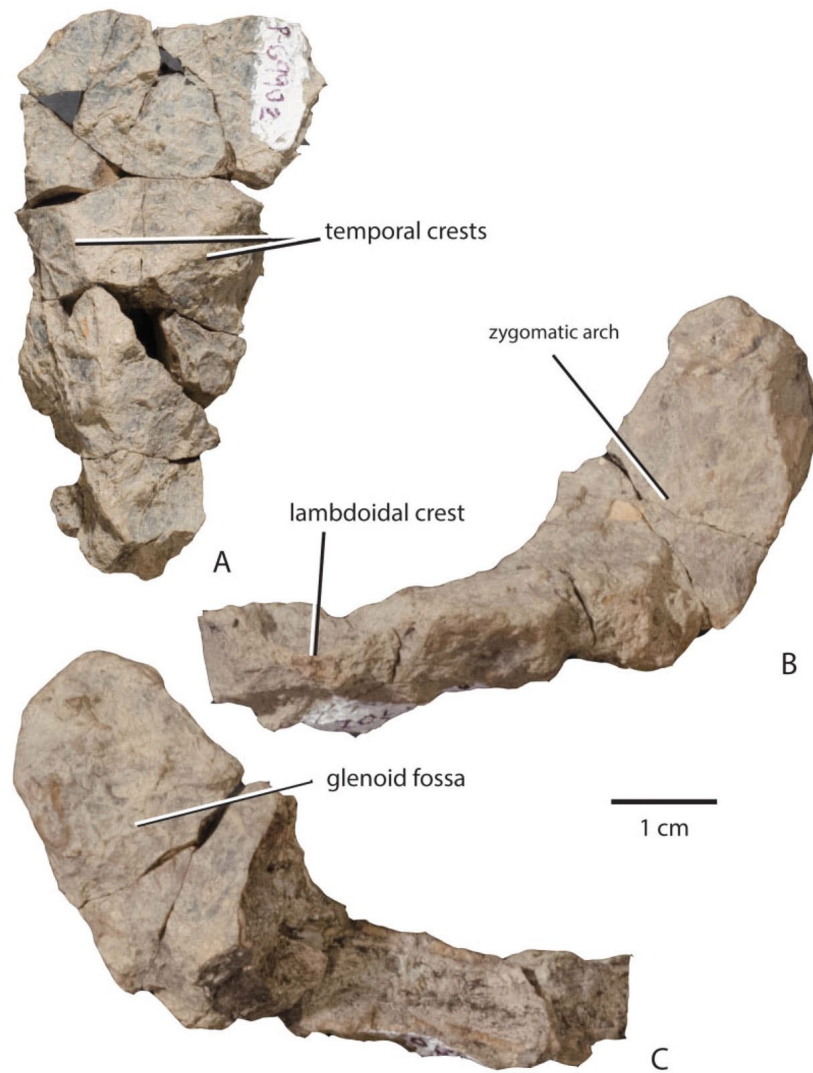


Figure 1. Holotype of *Kimbetopsalis simmonsae* gen. et sp. nov., NMMNH P-69902. A, dorsal view of partial skull roof; B–C, dorsal view of portion of braincase and base of right zygomatic arch in dorsal (B) and ventral (C) views.

northwestern New Mexico, in the west flank of Kimbeto Wash, at locality 11 of Williamson (1996: fig. 18). It is from Fossil Horizon A and within the *Hemithlaeus kowalevskianus* – *Taeniolabis taoensis* Biozone (H-T Zone) (Williamson, 1996). The vertebrate fauna from this horizon is considered part of the type faunas of the middle Puercan Interval Zone (Pu2) (Archibald *et al.*, 1987; Williamson, 1996; Lofgren *et al.*, 2004).

The west flank of Kimbeto Wash has yielded numerous taxa that are restricted to the H-T Zone, including *Hemithlaeus kowalevskianus* and *Conacodon entoconus*. These taxa are particularly abundant in H-T Zone faunas of the Nacimiento Formation, but are absent from the overlying Fossil Horizon B that yields the type faunas of the late Puercan Interval Zone (Pu3) (Williamson, 1996). Furthermore, no specimens of *T. taoensis* have been recovered from the west flank of Kimbeto Wash. This is im-

portant because the first occurrence of *Taeniolabis* defines the beginning of the Pu3 Interval Zone (Archibald *et al.*, 1987; Lofgren *et al.*, 2004). Although it does not in itself support a Pu2 age for the locality, the absence of *Taeniolabis* is further evidence that the west flank of Kimbeto Wash is not Pu3 in age (a time when other large taeniolabidids are known from the Nacimiento Formation). Specimen NMMNH P-69902 was found fragmented, but in close association, weathering from a silty mudstone in an area of low relief. There is no possibility that the specimen is float from a higher horizon and therefore we are confident that it is a member of the H-T Zone fauna, and thus is Pu2 in age.

Etymology

Kimbeto, for Kimbeto Wash; psalis, ‘cutting shears’ (Greek). Simmonsae, after Nancy Simmons, in recognition of her work on taeniolabidoid multituberculates.

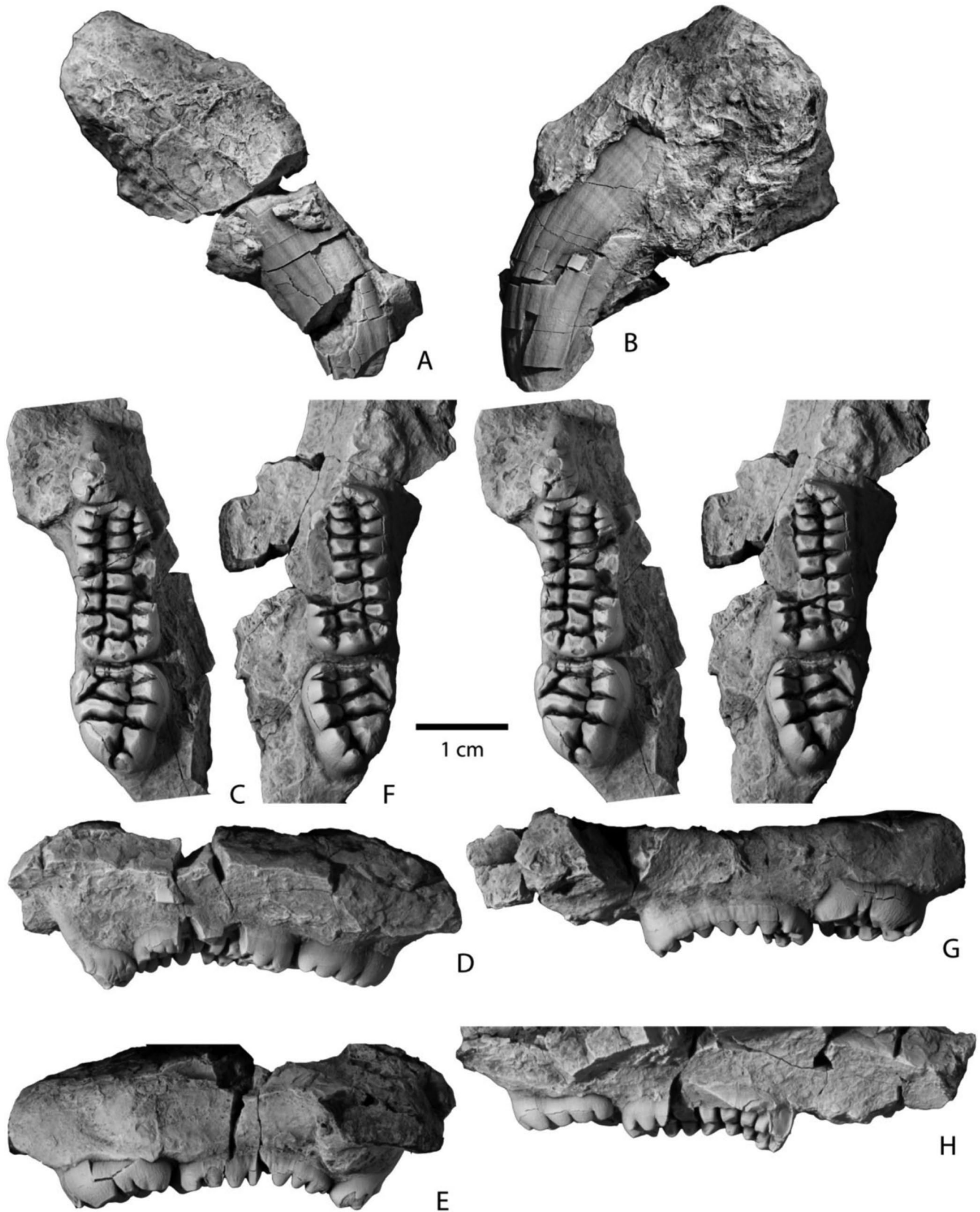


Figure 2. Holotype of *Kimbetopsalis simmonsae* gen. et sp. nov., NMMNH P-69902, A, right I2 in labial view; B, left pre-maxillary fragment with I2 and roots of I3 in labial view; C–E, right partial maxilla with P4–M2 in occlusal (C, stereopair), lingual (D), and buccal (E) views; F–H, left partial maxilla with partial M1–M2 in occlusal (F, stereopair), lingual (G), and buccal (H) views. I2, second upper incisor; M, upper molar; P, upper premolar.

Table 1. Measurements of the holotype of *Kimbetopsalis simmonsae* gen. et sp. nov., NMMNH P-69902. Measurements are in mm

Tooth	L	W	Cusp formula
I2		9.64*	
P4	8.6	5.16	
M1	18.23	9.69	8:8–9:9*
M2	12.37	10.69	1:4:5

I2, second upper incisor; L, length; M, upper molar; P, upper premolar; W, width.

*estimated.

Table 2. Measurements of *Catopsalis fissidens*. Measurements are in mm

Tooth	L	W	Cusp formula
I2			
NMMNH P-63938		5.36	
M1			
NMMNH P-63938	13.84	7.24	8:9:11*
M2			
NMMNH P-63938	7.86	9.26	2:3:4
I			
NMMNH P-62373		4.90	
NMMNH P-63938		4.44	
p4			
NMMNH P-62373	4.93*	2.21	
m1			
NMMNH P-62373	11.64	6.10	6:5
NMMNH P-63938	12.39	6.33	7:5
m2			
NMMNH P-62373	6.79	6.75	2:4
NMMNH P-63938	7.03	6.79	2:4

I2, second upper incisor; L, length; M, upper molar; m, lower molar; P, upper premolar; p, lower premolar; W, width.

*estimated.

Diagnosis

Taeniolabidid taeniolabidoid multituberculate that is smaller than *Taeniolabis* (4% smaller than *Taeniolabis lamberti*; ~21% smaller than *T. taoensis*), has fewer M1 cusps (eight cusps in the buccal and median rows of M1, compared with nine or more cusps in the buccal and medial rows in *Taeniolabis*; Simmons, 1987), and has a larger P4/M1 ratio (0.47, compared with 0.40 in *Taeniolabis*). It has a greater number of M2 cusps (1:4:5) than any species of taeniolabidoid other than *Taeniolabis* (outside of *Taeniolabis*, no taeniolabidoid has more than three cusps in the median cusp row of M2).

Possible additional specimens

Sloan (1981) referred an edentulous left dentary preserving two prominent alveoli from the Puercan of the San

Juan Basin (AMNH 3030) to *Catopsalis foliatus*. This specimen was originally referred by Cope (1888b) to the eucosmodontid multituberculate *Eucosmodon molestus*, an identification that Granger & Simpson (1929: 651) considered to be incorrect because it was much larger and more robust than the 'neotype' of *Eu. molestus*. McKenna (1960) also found the affinities of this specimen 'puzzling' because he considered that the two preserved alveoli would not have housed a large, elongate, double-rooted premolar, nor were they likely to have housed a small, single-rooted premolar and the anterior root of the m1. Sloan (1981) argued that the size and proportions of the ramus were consistent with the size and proportions of *Ca. foliatus*. However, Lucas *et al.* (1997) argued that the dentary was much larger than that of *Catopsalis fissidens*, which is significantly larger than *Ca. foliatus*, and with an incisor width of 8.3 mm, based on alveolar diameter, was within the size range of *T. taoensis*. An alternative interpretation is that AMNH 3030 is a mandibular ramus of *Ki. simmonsae*, which is expected to be smaller than *T. taoensis*, but larger than *Ca. fissidens*, the next largest taeniolabidoid that has been previously documented from the Nacimiento Formation. Unfortunately, the dentary and dentition is unknown for *Kimbetopsalis*, making direct comparison between *Kimbetopsalis* and AMNH 3030 currently impossible. We hope that additional discoveries will clarify the systematic position of AMNH 3030.

Sloan (1981) referred a left lower incisor from fossil horizon B of De-na-zin Wash (USNM 23273) to *Catopsalis utahensis* (here considered a junior synonym of *Ca. foliatus*; see below). He considered it much too large (maximum height = 8.0 mm; maximum width = 5.7 mm; ventral radius of curvature approximately 51 mm; Sloan, 1981) to belong to *Ca. foliatus*. It may be that this specimen belongs to *Ki. simmonsae*, a taxon unknown at the time of Sloan's description, but because it lacks longitudinal fluting it probably does not represent a lower incisor of that taxon.

ANATOMICAL DESCRIPTION

NMMNH P-69902 consists of associated cranial fragments and dentition with right I2, a partial left premaxilla preserving the I2 and roots of I3, and most of both maxillae with associated right P4–M2 and left M1–M2. The specimen is mostly encrusted with a concretionary covering, a preservation style common to fossils from this part of the Nacimiento Formation. However, the teeth are largely intact and unobscured. Reassembled parts of the skull are readily identified as a portion of the skull roof (Fig. 1A) and a portion of the zygomatic arch with the glenoid fossa (Fig. 1B, C).

Cranium

One preserved portion of the skull roof includes a nearly flat to slightly dorsally convex intraorbital area bordered

by temporal crests that converge posteriorly to the sagittal crest (Fig. 1A). The sides of the braincase lateral to the sagittal crest slope steeply laterally. No sutural contacts are visible. This skull roof portion closely resembles the interorbital region of the skull of *T. taoensis* (AMNH 16321) as illustrated in Broom (1914: fig. 6), Granger & Simpson (1929: fig. 5a), and Matthew (1937: fig. 72a).

An additional skull fragment (Fig. 1B, C) is interpreted to represent the posterolateral side of the braincase, preserving a portion of the right lambdoidal crest and the root of the right zygomatic arch. The glenoid fossa is preserved on the ventral surface of the fragment, but the surface is distorted and obscured by a concretionary crust.

The partial maxillae (Fig. 2C–H) preserve a portion of the vaulted palate and the roots of the zygomatic arches. The latter structures project laterally from the body of the maxilla, with the posterior margin of the arch bases positioned approximately between the P4 and M1 as in *T. taoensis*. Laterally directed zygomatic arches, which project approximately 90° transversely relative to the sagittal plane in dorsal view, are a synapomorphy of Taeniolabidoidea (e.g. Kielan-Jaworowska *et al.*, 2004). They act to demarcate the short and wide rostrum as a distinct region relative to the remainder of the skull.

Dentition

Incisors: Both left and right I2s are nearly complete, but are missing the tips and portions of the crowns (Fig. 2A, B). The roots appear to be intact, but are largely covered with a concretionary crust. In places, portions of the enamel are missing or crushed and fractured. The partial left premaxillary fragment is mostly obscured with concretion (Fig. 2B). However, a break in the specimen posterior to the I2 exposes the root of the I3 immediately posterior to the I2, indicating that the I3 is in the same position on the premaxilla as in other taeniolabidoids (e.g. Simmons & Miao, 1986; Simmons, 1993; Rougier *et al.*, 1997).

The incisors closely resemble those of *T. taoensis*; they are large, mesiodistally broad, curved, taper towards their apices, and bear pronounced longitudinal fluting and transverse growth bands. The longitudinal fluting tends to be regularly spaced mesiodistally across the labial enamel band and of uniform width. At least eight flutes are present near the base of the left I2. This fluting also occurs on both upper and lower incisors of *T. taoensis*. On upper incisors of *T. taoensis*, the flutes radiate basally and individual ‘flutes’ anastomose basally to create additional flutes. Flutes are truncated mesially and distally where they intersect the margins of the labial enamel band. Over ten flutes are present on I2s of *T. taoensis* (e.g. NMMNH P-2937, 12387). In both *T. taoensis* and *Kimbetopsalis* the fluting of the enamel band is

similar in size and spacing and also anastomoses basally. Although the upper incisors of *Kimbetopsalis* are very similar to those of *T. taoensis*, they differ from the fluting exhibited by *Ca. fissidens*, which outside of *T. taoensis* (incisors are unknown for *T. lamberti*) and *Kimbetopsalis*, has the most distinctive fluting amongst taeniolabidoids. In *Ca. fissidens* the individual flutes are narrower, fewer in number, more variable in size, less distinct, and do not anastomose. Some fluting is also evident in *Catopsalis alexanderi* (UCM 39553), but the I2 of this specimen possesses only three broad longitudinal ridges, which are separated by broad and shallow grooves. In addition, the entire enamel surface is also marked by fine irregular wrinkles that are orientated longitudinally. These are not present in *Kimbetopsalis*.

P4: An *in-situ* P4 is preserved on the right maxilla (Fig. 2C–E), and although the partial left maxilla (Fig. 2D–H) is missing P4 it preserves two corresponding alveoli of subequal size that are filled with matrix. These alveoli clearly show that the P4 has two roots; the mesial root projects mesiodorsally into the maxilla and the distal root appears to have been directed dorsally. The right P4 is pear-shaped in occlusal view, being mesiodistally elongate and expanded distally, and distinctly bulbous. Portions of the enamel surface are missing from the mesiolingual edge and the distobuccal face of the tooth. The right P4 bears a medial row of four cusps. The mesial-most, or first, cusp is about half the height of the other three cusps and rises from the steeply sloping mesial face of the tooth. The middle two cusps have worn apices, but it appears that the second of the row is the largest in diameter. The third cusp has the highest preserved height. Creases on the lingual and buccal faces of the tooth delimit each cusp. The distal face of P4 is broadly rounded and bears at least three basolingual cusps. A deep cleft separates the cusps area from the distal-most cusp of the medial row of cusps.

M1: Both the left and right M1s are present. They are both incomplete, but together they preserve most of the important anatomical features, and allow for an accurate determination of a complete cusp formula. The left M1 (Fig. 2F–H) is missing most of the lingual row of cusps but is otherwise well preserved. The right M1 (Fig. 2C–E) is more complete, missing a portion of one of the cusps of the buccal row, and several of the lingual row.

The M1 is approximately rectangular in occlusal view (Fig. 2C, F), with three rows of cusps extending mesiodistally down the entire length of the tooth, which is a synapomorphy of Taeniolabidoidea (e.g. Simmons & Miao, 1986; Kielan-Jaworowska *et al.*, 2004). The cusps are pyramidal in shape. Several of the cusps, especially

the two most distal cusps of the medial and lingual rows, exhibit weak crenulations. Although the lingual cusp row is incomplete on both specimens, the specimens together indicate that M1 had nine lingual cusps when complete. The medial row contains eight cusps, as does the buccal row. The resulting cusp formula is 8:8:9. The cusps of the lingual row decrease in size mesially and the mesial-most cusp is very small in comparison to the mesial-most cusp of the medial row. The mesial-most cusp of the buccal row is mesiodistally compressed. There are no accessory cuspules or basal cingula on any of the cusps of any of the rows. The buccal face of the tooth shows weak, transverse apicobasal wrinkling extending vertically, from the base of the crown towards the apex of each cusp.

M2: Both the left and right M2 are complete. They are approximately heart-shaped in occlusal view (Fig. 2C, F), with a concave mesial margin and a rounded distal margin, and they taper distally in buccolingual width. The most distinctive features of the M2 are its large, swollen, pyramidal cusps, which form three longitudinal rows as in the M1. The lingual row contains five cusps, but the distal-most cusp is small and might be considered a cuspule. The medial row consists of four cusps, the mesial-most of which is mesiodistally compressed. The buccal row consists of a single large cusp, located at the mesiobuccal corner of the tooth when seen in occlusal view. Several of the cusps have undulatory margins in occlusal view owing to weak folding of the enamel. The margins of the tooth also show transverse apicobasal wrinkling, particularly on the buccal side.

DISCUSSION

Comparisons with other taeniolabidoids

Kimbetopsalis simmonsae is clearly referable to Taeniolabidoidea by the possession of diagnostic characters of the clade not seen in other multituberculates, including transversely orientated zygomatic arches, a rectangular M1 with three longitudinal rows of cusps that extend along the entire length of the tooth, an M2 with four or more cusps in the lingual and medial rows, the very large size of I2 and M2, which are bigger in taeniolabidoids than in any other multituberculates, and small size of the P4 relative to the M1 (Table 3; e.g. Simmons, 1987; Kielan-Jaworowska *et al.*, 2004; Mao *et al.*, 2015).

Kimbetopsalis simmonsae is similar to species of *Taeniolabis* in many features. For example, it possesses some (but not all) features considered diagnostic for *Taeniolabis* by Simmons (1987), in her revision of *Taeniolabis* systematics. These include large I2 and M2 (which are larger in *Taeniolabis* and *Kimbetopsalis* compared with other

taeniolabidoids), nine or more cusps in the lingual row of M1, and four or more cusps in the lingual row of M2. However, *Ki. simmonsae* can be distinguished from both species of *Taeniolabis* [*T. taoensis* (Cope, 1882) and *T. lamberti* Simmons, 1987] by being smaller in size, based on M1 measurements. *Kimbetopsalis simmonsae* has an M1 length of 18.2 mm (Table 1), falling well outside of the range of M1 length (21.9–24.4 mm with a mean of 23.0 mm) reported by Simmons (1987: table 2) for *T. taoensis*. The M1 length of *Ki. simmonsae*, therefore, is 79% of the mean M1 length ($N = 22$) of *T. taoensis*. It is also smaller than, but closer in size to, the M1 referred by Simmons (1987) to *T. lamberti*, which is 18.9 mm in length (about 4% larger than in *Ki. simmonsae*). The M1 width of *Ki. simmonsae* (9.7 mm) is also smaller than in *T. taoensis* (10.8–12.1 mm range, 11.6 mm mean) and *T. lamberti* (10.0 mm) (Simmons, 1987).

Kimbetopsalis simmonsae can also be distinguished from *Taeniolabis* by its lower number of cusps in the buccal cusp row of M1, based on the diagnosis of Simmons (1987). The cusp number for the M1 of *Kimbetopsalis* is 8:8:9, lower than for *T. taoensis* and for *T. lamberti*. Simmons (1987) gave a range in cusp number for M1 of 8–11:8–10:7–11 for the genus *Taeniolabis* and 8–11:9–10:9–11 for the species *T. taoensis* (the upper range of *T. taoensis* is actually slightly higher, as AMNH 16313 has 12 lingual cusps). *Taeniolabis lamberti* has a cusp formula of 9:10:10 based on the single referred M1, UCMP 110452 (Simmons, 1987). However, the cusp formula of *Kimbetopsalis* is similar to that of some specimens referred to *Catopsalis*, including *Catopsalis calgariensis* (UW 6407), which has a cusp formula of 8:8:10 (see Middleton, 1982: plate 1, fig. 8) and *Ca. fissidens* (NMMNH P-63938), which has a cusp formula of 8:9:10? (Fig. 3).

The M1 cusp formula for *Kimbetopsalis* is the same as that of an isolated M1, UCMP 128280, from the Garbani Quarry, Montana, that Simmons (1987: fig. 6.1) referred to *Taeniolabis* sp. However, that specimen is notably different from *Kimbetopsalis* and all other M1 specimens referred to *Taeniolabis* in having a relatively short lingual cusp row. In UCMP 128280 the lingual cusp row extends anteriorly only as far as the sulcus between cusps 2 and 3 of the medial cusp row, whereas in the M1 of *Kimbetopsalis* and specimens referred to either *T. taoensis* or *T. lamberti*, it extends medially to a point lingual to the first cusp of the medial row (*Kimbetopsalis*), or at least as far as the sulcus between medial cusps 1 and 2 (*Taeniolabis*). UCMP 128280 is also larger than the M1 of *Kimbetopsalis* (M1L = 22.0; Simmons, 1987: table 4), and within the lower size range of *T. taoensis*. Simmons (1987) suggested that this one unusual specimen may be primitive compared with *T. taoensis* and *T. lamberti*. Regardless of its precise affinities, it is clear that this specimen does not belong to *Kimbetopsalis*.

Table 3. Compilation of dental measurements for taeniolabids and other taxa from a variety of sources: Archibald (1982), Buckley (1995), Clemens (1964), Fox (2005), Lucas *et al.* (1997), Mao *et al.* (2015), Matthew *et al.* (1928), Middleton (1982), Simmons & Miao (1986), Sloan & Van Valen (1965), Wilson (1987), and Chou & Qi (1978)

Taxa	p4 L	m1 L	m1 W	m1 cusp formula	m2 L	m2 W	m2 cusp formula	P4 L	P4 W	P4 cusp formula	M1 L	M1 W	M1 cusp formula	M2 L	M2 W	M2 cusp formula
<i>Microcosmodon conus</i>	1.6	3.0	1.1	7:4.5	1.3	1.2	3:2	1.7	0.7	3:4:0	2.5	1.3	7:7:5	1.4	1.3	1:3:4
<i>Essonodon browni</i>	4.2	7.1	1.1	3-4:7:6	2.5	3.6	3:2	3.3	2.1	1:5:0 $\frac{1}{2}$	7.5	3.9	8:7:7	2.7	2.8	0-R:2:3-4
<i>Cimexomys judithae</i>	3.2	2.0	3.8	6:4	1.2	1.1	3:2	2.2	0.6	3:5:0	2.3	1.1	5:6:1	1.3	1.3	1:3:3
<i>Cimolomys gracilis</i>	4.5	4.8	0.9	7-8:5-7	3.7	2.6	4-6:2-3	2.8	1.5	1-2:5-6:2-3	4.8	2.7	5-7:7-10:4-6	3.6	3.1	2-3:3-4:4-7
<i>Meniscoessus robustus</i>	4.0	9.4	2.1	5-6:4	7.3	4.7	4-5:2	4.1	2.8	1:4:1 $\frac{1}{2}$	9.1	5.2	5-6:7:6-7	6.3	6.0	3-5:3-4:4-5
<i>Bubodens magnus</i>	-	12.8	4.4	10:8	-	-	-	-	-	-	-	-	-	-	-	-
" <i>Catopsalis</i> " <i>joyneri</i>	3.5	6.4	3.3	5:4	5.5	-	3:2	3.2	2.3	1:5:1	8.1	4.4	8:7:8	5.2	-	1:3:3
<i>Catopsalis waddleae</i>	-	16.4	9.3	5:4	-	-	-	-	-	-	-	-	-	12.9	11.8	1:3:4
<i>Catopsalis foliatus</i>	4.07*	10.5	5.1*	6:4	6.7*	5.9	4:2	-	-	-	-	-	-	-	-	-
<i>Catopsalis fissidens</i>	4.8	12.6	6.4	5-7:4-6	7.5	7.1	4:2	-	-	-	14.9	7.3	8:9:11-12	8.2	8.4	1-2:3:4
<i>Catopsalis alexanderi</i>	4.3	8.7	4.8	5-9:4	6.5	5.0	3-4:2	4.3	3.3	0-1:4:1	10.3	5.6	7-8:7-8:9	6.5	5.9	1-2:3:3-4
<i>Taeniolabis taoensis</i>	6.6	19.8	10.4	7-8:6-7	14.1	11.5	4-6:4-6	7.1	-	0:4:1	23.0	11.6	8-11:9-10:9-12	14.4	12.0	1:4-5:4-6
<i>Taeniolabis lamberti</i>	5.7	16.0	8.0	8:6	15.4	10.7	6:4	5.8	3.9	0:4:1	18.9	10.0	9:10:10	15.7	13.5	2:4:7
<i>Kimbetopsalis simmonsae</i>	-	-	-	-	-	-	-	8.6	5.2	0:4:1*	18.2	9.7	8:8:9*	12.4	10.7	1:4:5
<i>Lambdopsalis bulla</i>	-	7.8	3.2	5:4	7.5	5.3	4:2	-	-	0:1:0	10.0	5.0	6-7:7-8:7	-	-	1:2:3
<i>Prionessus lucifer</i>	1.6	5.6*	2.4	5:4	3.1	2.9	3:2	-	-	0:1:0	5.6	3.3	7:6:5	3.7	3.5	1:3:3
<i>Sphenopsalis nobilis</i>	4.6	13.6	7.3	5:4	13.8	9.9	3:2	2.9	3.0*	-	16.4	8.3	7:7:8	13.3	12.2	1:2:4

*estimated; i2, second upper incisor; L, length; M, upper molar; m, lower molar; P, upper premolar; p, lower premolar; W, width.

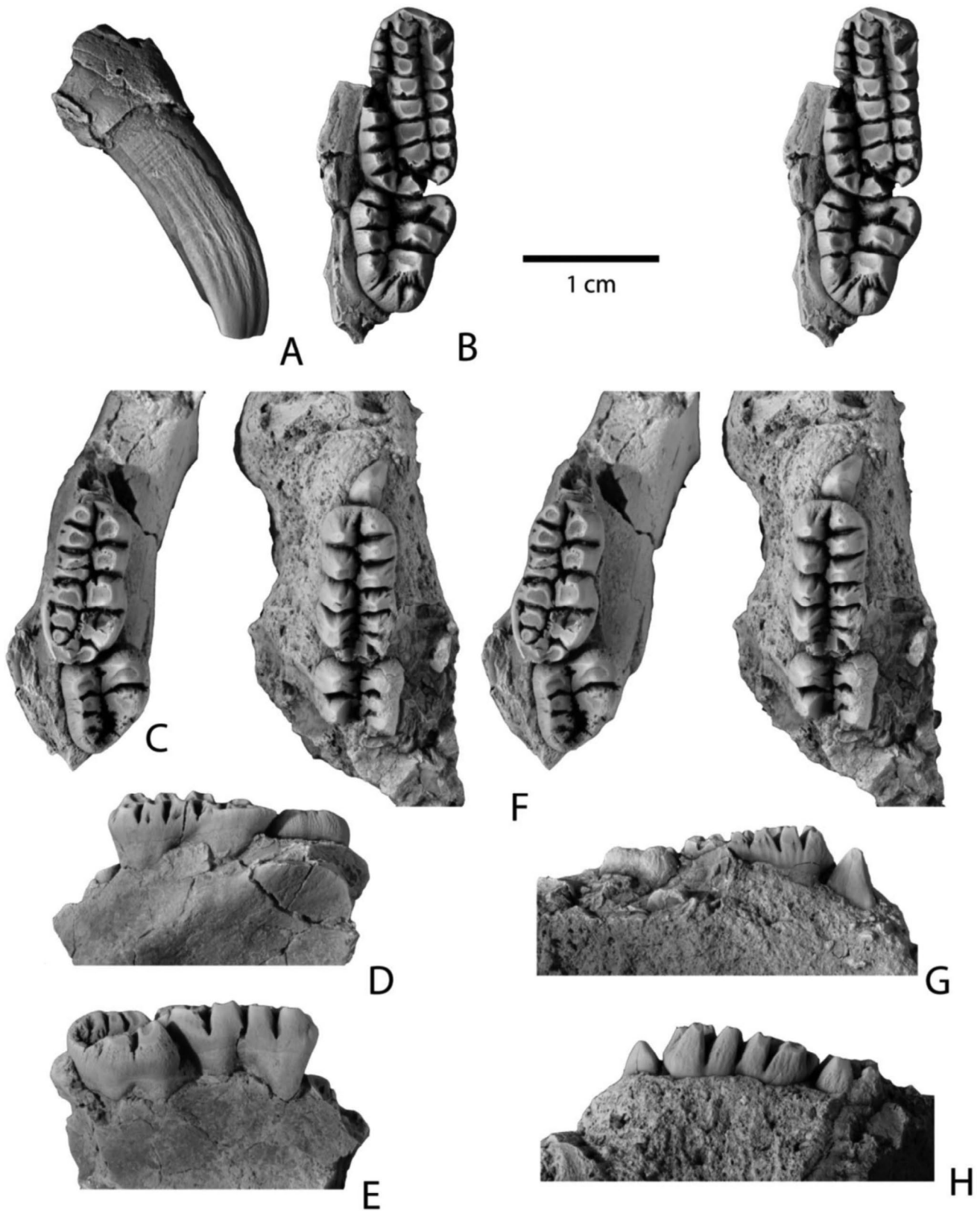


Figure 3. New specimens of *Catopsalis fissidens*. NMMNH P-63938. A, right partial premaxilla with I2 in labial view; B, left M1–M2 in occlusal view (stereopair), left partial dentary with roots of p4, m1–m2 in occlusal (C; stereopair), buccal (D), and lingual (E) views. NMMNH P-62373, right p4–m2 in occlusal (F; stereopair), buccal (G), and lingual (H) views. I2, second upper incisor; M, upper molar; m, lower molar; p, lower premolar.

The M2 of *Kimbetopsalis* is similar in size to that of *T. taoensis*, falling within the size range for length (12.37 mm, compared with 12.3–16.0 mm range of 11 teeth of *T. taoensis*: Simmons, 1987: table 2). The cusp formula of the *Kimbetopsalis* M2 also overlaps with that of *T. taoensis* (1:4–5:4–6; Simmons, 1987: table 1). However, the width of the *Kimbetopsalis* M2 (10.69 mm) is smaller than in *T. taoensis*, falling outside of the latter's size range (11.2–12.8 mm: Simmons, 1987: table 2). Compared with species of *Catopsalis*, the M2 of *Kimbetopsalis* is larger (about 20 per cent longer than the M2 of *Ca. calgariensis* and 50 per cent larger than that of *Ca. fissidens*) and has a higher cusp number than any known *Catopsalis* specimen.

Comparisons between the M2 morphology of *Kimbetopsalis* and *T. lamberti* are less straightforward, owing to uncertainty over whether some M2 specimens can be confidently referred to *T. lamberti*. Simmons (1987) refrained from referring an M2 to *T. lamberti*. However, she described an isolated M2, UCMP 128291, from the same locality as the holotype of *T. lamberti* (locality Garbani 13 of the Tullock Formation), but referred it to *Taeniolabis* sp. because of its large size, which was reported to be wider, with an estimated width of 11.1 mm, than any M2 referred to *T. taoensis*. However, she considered that it was possible that the tooth would prove to be referable to *T. lamberti* if discovery of more specimens indicated a larger range of variation in this species. The tooth differs from the M2 of *T. taoensis*, *Ki. simmonsae*, and all other taeniolabidoids in having a higher cusp formula of 2:4:7. A second distinctive specimen from the Tullock Formation (UMVP 1455) consists of a partial M2, also possessing two cusps in the buccal cusp row, supporting the idea that the Tullock taeniolabidoid has a distinctive M2 cusp formula. We suggest that it is most likely that there is only a single large taeniolabidoid present from the Garbani Quarry of the Tullock Formation, because in other faunas that contain taeniolabidoids, only a single large species is present. Therefore, we suggest that it is most parsimonious to consider that these specimens from Garbani 13 are all referable to a single taxon, *T. lamberti* (known from other definitive material from Garbani 13), rather than a different, but unknown coexisting species of *Taeniolabis*.

Tooth proportions also differ between *Kimbetopsalis* and *Taeniolabis*. The ratio of P4 length to M1 length (P4 L/M1 L) in *Kimbetopsalis* (0.47) is outside the upper range of this ratio in *Taeniolabis* (0.31–0.33; Simmons, 1987), but similar to the value found in '*Catopsalis*' *joyneri* and *Ca. alexanderi*. In addition, the ratio of M1 length to M2 length (M1 L/M2 L) in *Ki. simmonsae* (1.47) is below the range observed in *Taeniolabis* (1.59–1.79; Simmons, 1987), but similar to the values found in

'*Ca.*' *joyneri* (M1 L/M2 L = 1.49) and *Ca. fissidens* (1.50). Together, these ratios indicate that the M1 in *Kimbetopsalis* and *Catopsalis* is smaller relative to the other cheek teeth than in *Taeniolabis*. Large M1 size in *Taeniolabis*, therefore, is probably a derived feature amongst taeniolabidoids.

Differences in P4 morphology also distinguish *Kimbetopsalis* from *Taeniolabis*. Most notably, *Kimbetopsalis* has multiple distobuccal basal cusps on the P4, rather than the single basal cusp of *T. lamberti*. It also differs from the P4 of *Catopsalis*, where known, in which cusps tend to be arranged in two or more parallel cuspal rows ('*Ca.*' *joyneri*, *Ca. alexanderi*). The P4 is unknown for *Ca. foliatus* and *Ca. fissidens*. Only a partial P4 is known for *Ca. calgariensis* and this preserves only cusps of the medial cuspal row. It is not known if this taxon possessed distobuccal basal cusp(s).

One potential difference in P4 morphology used to differentiate taeniolabidoid taxa by previous authors does not hold up to scrutiny. *Kimbetopsalis* clearly possesses a double-rooted P4, as two alveoli for this tooth are present on the right maxilla. This differs from the supposed presence of a single-rooted P4 in some other taeniolabidoids, including *Taeniolabis* and *Catopsalis*. Simmons & Miao (1986) reported that the P4 of *Taeniolabis* is single-rooted and scored it as such in their phylogenetic data set. They also reported that both *Ca. alexanderi* and *Ca. calgariensis* possess a single-rooted P4. These character states have been perpetuated in subsequent phylogenetic analyses (e.g. Simmons, 1993; Rougier *et al.*, 1997; Weil, 1999). However, a review of the literature and collections demonstrates that neither *Taeniolabis* nor *Catopsalis* possess a single-rooted P4. This tooth is double-rooted in *Ca. alexanderi* (Middleton, 1982). *Catopsalis fissidens* is also double-rooted based on a new specimen, NMMNH P-63938, which includes a fragment of maxilla that contains the alveoli and broken roots of P4 (see below). Middleton (1982) reported that *Ca. calgariensis* is double-rooted based on an isolated P4 (UW 6387), although we have not been able to independently verify this. *Taeniolabis taoensis* is double-rooted based on several specimens, including AMNH 16313, NMMNH P-8621, 47470, and 47660; the latter three specimens each preserve two alveoli separated by a distinct septum for a double-rooted P4, identical to the condition in *Ki. simmonsae*. The condition in *T. lamberti* is unclear, as Simmons (1987) referred a single P4 to *T. lamberti* (UCMP 128281) and described it as not preserving a root. The only taeniolabidoids that can be confidently said to possess a single-rooted P4 appear to be the Asian lambdopsalid taxa *Sphenopsalis nobilis* and *Lambdopsalis bulla*. *Prionessus lucifer* includes specimens with both single-rooted and double-rooted P4s (Meng, Zhai & Wyss, 1998; Mao *et al.*, 2015).

PHYLOGENETIC ANALYSIS

The first study using modern phylogenetic methods for taeniolabidoidea was conducted by Simmons & Miao (1986). This pioneering study was amongst the first to use phylogenetic systematics to study extinct mammal phylogeny. They concluded that *Catopsalis*, as then conceived, was a paraphyletic taxon that gave rise to *Taeniolabis* and an Asian clade composed of *Lambdopsalis*, *Prionessus*, and *Sphenopsalis*. This study emerged as an important work on the phylogeny of Cretaceous and Paleocene mammals, and was held to have broader implications for understanding species turnover after the end-Cretaceous mass extinction. Archibald (1993), for example, included a slightly modified version of the Simmons & Miao (1986) cladogram to illustrate examples of ‘metaspecies’ and to show the impact of pseudoextinction on interpretations of early Paleocene species turnover.

Subsequently, very little work has been conducted on taeniolabidoid phylogeny and systematics, despite the importance of members of this group as Paleocene index taxa and their role as some of the first mammals to evolve mid-to-large body size after the end-Cretaceous extinction. Hypothetical inter-relationships of the Multituberculata, including a handful of taeniolabidids, were proposed by Kielan-Jaworowska & Hurum (2001: text-fig. 2) and reproduced in Kielan-Jaworowska *et al.* (2004: fig. 8.45), but these were not based on a numerical analysis. Some taeniolabidoidea were included in higher-level phylogenetic analyses of Multituberculata conducted by Simmons (1993), Rougier *et al.* (1997), Weil (1999), and Yuan *et al.* (2013). None of these analyses yielded well-resolved or strongly supported results. In the most recent higher-level analysis, Mao *et al.* (2015) included more taeniolabidoid taxa than previous studies, but scored *Taeniolabis* and ‘*Catopsalis*’ as single composite taxa, as the aim of their study was not to untangle the detailed inter-relationships of taeniolabidoidea but to test the monophyly of the group and place it on the larger multituberculate tree. The use of such composite taxa, although understandable in a higher-level analysis, has obscured the ingroup relations of taeniolabidoidea. Particularly troublesome is scoring ‘*Catopsalis*’ as a single composite, which in the study of Mao *et al.* (2015) was based on four species (‘*Ca.*’ *joyneri*, *Ca. foliatus*, *Ca. fissidens*, and *Ca. alexanderi*), because previous analyses have shown this genus to be non-monophyletic (Simmons & Miao, 1986).

We present a new phylogenetic analysis of Taeniolabidoidea, including all Asian and North American taxa referable to this clade. Several new taeniolabidoidea have been recognized and described since the Simmons & Miao (1986) analysis, including *T. lamberti*, *Catopsalis waddleeae*, and *Ki. simmonsae*. Additionally, new data are available for *Pr. lucifer* (Meng *et al.*, 1998), *S. nobilis* (Mao

et al., 2015), and *Ca. fissidens* (Lucas *et al.*, 1997, and described below). A wealth of new data is also now available on potential close outgroups of Taeniolabidoidea, including *Cimexomys*, *Meniscoessus*, and *Microcosmodon* (Montellano, Weil & Clemens, 2000; Fox, 2005).

Taxa not included in our analysis are three Asian taxa that Simmons & Miao (1986) included in Taeniolabidoidea [*Kamptobaatar*, *Djadochtatherium*, and *Catopsbaatar* (= ‘*Catopsalis*’) *catopsaloides* after Kielan-Jaworowska (1994)], which have subsequently been shown to be paraphyletic and remote from Taeniolabidoidea (*sensu stricto*; Simmons, 1993) and to be part of a monophyletic group of Asian taxa (Rougier *et al.*, 1997) that were relegated to the suborder Djadochtatheria by Kielan-Jaworowska & Hurum (1997). Hence, all remaining taeniolabidoidea are Paleocene in age, with the possible exception of *Bubodens magnus* (Wilson, 1987), a poorly known taxon, represented only by an isolated m1 from the Upper Cretaceous Fox Hills Formation of South Dakota. *Bubodens* was tentatively referred to Taeniolabidoidea (= Taeniolabidoidea in our usage) by Kielan-Jaworowska *et al.* (2004; see also Weil & Krause, 2008).

We used the results of our analysis to revise the systematics of taeniolabidoidea, erect a new genus-level taxon (whose distinctiveness follows from the phylogenetic analysis), and comment on the evolutionary history of the group.

TAXON SAMPLING FOR PHYLOGENETIC ANALYSIS

‘*Catopsalis*’ *joyneri* Sloan & Van Valen, 1965: ‘*Catopsalis*’ *joyneri* was illustrated and briefly described by Sloan & Van Valen (1965) from the Bug Creek Anthills locality of eastern Montana. Sloan & Van Valen (1965) considered this site to be Cretaceous in age, but it has since been shown to be a mixed assemblage of earliest Paleocene and reworked Cretaceous fossils (Lofgren, 1995). The ‘*Catopsalis*’ specimens are now considered to be early Paleocene (early Puercan; Pu1) in age (Lofgren *et al.*, 2004; Wilson, 2013) [note that Wilson (2014) listed only *Catopsalis foliatus* in Pu1 faunas of Garfield County, which is a mistake (G. P. Wilson, pers. comm., 2014)]. Scoring of this taxon was based on descriptions and illustrations in Sloan & Van Valen (1965), Archibald (1982), Lofgren (1995), and Fox (2005).

Catopsalis alexanderi Middleton, 1982: Middleton (1982) described numerous specimens of *Ca. alexanderi* from the early Paleocene (Pu1) of the Denver Basin. He distinguished *Ca. alexanderi* from ‘*Ca.*’ *joyneri* and *Ca. foliatus* by its intermediate size. Specimens from the early Paleocene (Pu1) of the Tullock or Hell Creek formations were tentatively referred to *Ca. cf. Ca. foliatus* by Archibald

(1982), but were subsequently referred to *Ca. alexanderi* (Middleton, 1982). Sloan (1981) referred several specimens from the early Puercan Mantua Quarry of the Fort Union Formation in northern Wyoming to *Ca. foliatus* and these were also subsequently referred by Middleton to *Ca. alexanderi*. We based our scoring of this taxon on descriptions and illustrations in Middleton (1982) and on casts of UCM 14550 (left P4), 16647 (right M1), 16648 (right M2), 16649 (left m1), and 16650 (left m2), 34146 (right M1), 34186 (left partial dentary with p4–m1), 34979 (right partial dentary with I, p4–m2; the holotype of *Ca. alexanderi*), 39553 (left I2, right I2–3, left and right P4–M2), YPM PU 18196, (I2), 14550 (left P4), 16647 (right M1), 16648 (right M2), 16649 (left m1), 16650 (left m2).

Catopsalis waddleae Buckley, 1995: Buckley (1995) described three isolated teeth, one fragmentary, from the Simpson Quarry of Puercan age, Bear Formation, Crazy Mountain Basin of Montana, as a new taxon, *Ca. waddleae*. Our scorings are based on descriptions and illustrations from Buckley (1995) and casts of UM 90242 (right m1, not left m1 as reported by Buckley, 1995; the holotype of *Ca. waddleae*), 90212 (partial right m1), and 90215 (left M2).

Catopsalis foliatus Cope, 1882: The precise provenance of the lectotype of *Ca. foliatus*, AMNH 3035, a partial dentary preserving p4–m2, remains uncertain. It is probably Puercan or Torrejonian in age (see Lucas *et al.*, 1997). Lucas *et al.* (1997) suggested that a second specimen, AMNH 16325, a partial skeleton not preserving a dentition (see Granger & Simpson, 1929), may be referable to this taxon.

We consider another species of *Catopsalis*, *Catopsalis johnstoni* Fox, 1989, to be synonymous with *Ca. foliatus*. *Catopsalis johnstoni* was based on three isolated teeth from the lower Paleocene Porcupine Hills Formation of southern Alberta: a left I2, a lower incisor, and a left m1. Lucas *et al.* (1997) tentatively synonymized *Ca. johnstoni* with *Ca. foliatus*, outlining that Fox (1989) had stated only that *Ca. johnstoni* was intermediate in size (m1 L = 9.7; W = 4.65; Johnston & Fox, 1984: table 18) between ‘*Ca.*’ *joyneri* or *Ca. alexanderi* and *Ca. calgariensis*, and therefore did not distinguish the species from *Ca. foliatus* or *Ca. fissidens*. Johnston & Fox (1984) described this taxon (*Catopsalis* n. sp.) as having a higher m1 cusp formula (7:4) than ‘*Ca.*’ *joyneri*, *Ca. foliatus*, or *Ca. alexanderi*. However, we found that the type of *Ca. foliatus* (m1 L = 10.3; W = 5.15) has an m1 cusp formula of 6:4 (not 5:4 as reported by Johnston & Fox, 1984: p. 209), with a small cusp on the distal end of the buccal cusp row. A similar small sixth cusp is present on at least some specimens referred to *Ca. alexanderi*, but the distinction of this cusp can be

erased with wear (Middleton, 1982) and so the m1 cusp formula is probably variable (4–5:4). Lucas *et al.* (1997) also found the m1 cusp formula of *Ca. fissidens* to be variable (5–7:4–6; Lucas *et al.*, 1997) based on a small sample ($N = 8$) from the San Juan Basin. Two new m1s of *Ca. fissidens* (described below) fall within this range of cusp formula, with formulas of 6–7:5.

Johnston & Fox (1984) and Fox (1989, 1990) considered specimens referred to *Ca. johnstoni* from the Long Fall horizon (the Wounded Knee Local Fauna; Fox, 1989) of the Ravenscrag Formation of southcentral Saskatchewan to be latest Cretaceous in age, based partly on the presence of typical latest Cretaceous dinosaur teeth and mammalian taxa (*Alphadon* sp. and *Pedionmys elegans*) characteristic of the Lancian Land Mammal Age (Johnston & Fox, 1984; Cifelli *et al.*, 2004). Other workers considered the Wounded Knee Local Fauna to be early Paleocene in age (Lerbekmo, 1985; Sloan, 1987; Archibald & Lofgren, 1990; Cifelli *et al.*, 2004; Lofgren *et al.*, 2004). We consider it possible that the Wounded Knee Local Fauna represents a time-averaged assemblage (Rogers, 1993) that is a mix of latest Cretaceous and early Paleocene faunas, similar to the Bug Creek Anthills in Montana. The fossils are from the Medicine Hat Brick and Tile Quarry and the deposits that yielded the fossils have since been removed by mining operations.

We scored this taxon based on casts of AMNH 3035, the lectotype of *Ca. foliatus*.

Catopsalis fissidens Cope 1884: The lectotype of *Ca. fissidens*, AMNH 3044, a partial dentary with m1–m2 from the Chico Springs locale (Williamson & Lucas, 1997) of Gallegos Canyon, Nacimiento Formation, San Juan Basin, New Mexico, remained the only known specimen of this taxon for many decades. Several additional specimens were referred to *Ca. fissidens* by Lucas *et al.* (1997). Lucas *et al.* (1997) concluded that *Ca. utahensis* Gazin, 1939, described from specimens from the Dragon local fauna of central Utah, is a junior synonym of *Ca. fissidens*, a conclusion that we follow here.

Two new specimens of *Ca. fissidens* from the Chico Springs locale (see Williamson & Lucas, 1997), which we describe and figure here for the first time, represent topotypic specimens of this species (Fig. 3). The first of these specimens is NMMNH P-63938, which includes a fragment of the right premaxilla with the complete and little-worn right I2 (Fig. 3A); the partial left premaxilla containing the root and crown base of the left I2; left? maxilla fragment containing the roots of P4; left maxilla fragment with M1–2 (Fig. 3B); left partial dentary with base of i, roots of p4, and m1–2; and right partial dentary with base of i, alveoli for p4, and m1–m2 (Fig. 3C–E). This represents the most complete specimen of *Ca. fissidens* currently known.

The second specimen, NMMNH P-62373, consists of a concreted left partial dentary with *i*, roots of p4, alveoli for m1, and fragments of the left m1 and m2; and a concreted right partial dentary with the base and fragments of the first lower incisor and p4–m2 (Fig. 3F–H). This specimen includes the first complete p4 for *Ca. fissidens*. Although both specimens are at least partially concreted, the teeth are mostly in good condition and unobscured. Specimens of *Ca. fissidens* from the San Juan Basin are rare and the new specimens provide important new morphological information for this taxon. Therefore, they warrant a brief description here.

The complete I2 of NMMNH P-63938 (Fig. 3A) is curved, with the enamel restricted to the labial surface. The tip is worn to a chisel point. The enamel of the labial surface bears longitudinal fluting, with five prominent parallel ridges extending nearly the entire length of the tooth. Growth bands are present and most prominent near the base of the enamel.

The maxilla of NMMNH P-63938 contains two roots of P4. The mesial and distal roots are subequal in transverse diameter, but the anterior root is nearly circular in cross-section and the distal root is mesiodistally compressed to give an ovoid cross-section.

The M1 of NMMNH P-63938 (Fig. 3B) is nearly complete, but missing a portion of the lingual cusp row, a small portion of the buccal tooth row near the anterior end of the tooth, and a small fragment at the distal margin of the tooth at the distal end of the medial cusp row. The M1 is nearly rectangular in occlusal view. The cusps of the lingual row decrease in size anteriorly and reach nearly to the mesial margin of the tooth, terminating lingual to the midpoint of the second cusp of the medial row. We estimate that three cusps are missing from the lingual tooth row and the apex of one cusp is missing from the buccal tooth row, giving a reconstructed cusp formula of 8:9:11, which is somewhat different from the cusp formula in the single previously reported well-preserved M1 of this taxon (NMMNH P-8608; Lucas *et al.*, 1997: fig. 2.11–12), which has a cusp formula of 8:9:12. Similar variability in cusp number is found in other taeniolabidoids such as *Ca. alexanderi* (Middleton, 1982) and *Ta. taoensis* (Simmons, 1987).

The M2 of NMMNH P-63938 (Fig. 3B) is notable in possessing two cusps in the buccal cusp row: a mesial mesiodistally compressed cusp and a larger distal cusp. The cusps are conjoined near their bases. There are three cusps in the medial row, and four in the lingual row. Three relatively large accessory cusps are present on the distal margin of the tooth, the largest of which is situated distal to the distal-most cusp of the medial cusp row. Lucas *et al.* (1997) briefly described, but did not illustrate, the M2 of *Ca. fissidens* based on three specimens, all of which

have a cusp formula of 1:3:4. The new specimen NMMNH P-63938 shows that *Ca. fissidens* has a M2 cusp formula with a variable number of cusps in the buccal tooth row (one or two), similar to what is found in *Ca. alexanderi* (Middleton, 1982).

Both the left and right lower first incisors of NMMNH P-63938 are incomplete, but the portions preserved show a relatively narrow labial band of enamel that is rugose with longitudinally aligned, irregular wrinkles, rather than the strong fluting preserved on the I2 of the same specimen, or on the upper and lower incisors of *T. taoensis*. The left lower first incisor of NMMNH P-62373 is nearly complete, missing only the tip, and only the enamel on the labial face of the tooth is unobscured by concretion. It possesses a smoother enamel surface, with a more muted corrugated texture than does NMMNH P-63938, but there are two relatively distinct longitudinal ridges, one near the lingual margin of the labial face and one at about the midpoint of the labial surface, separated by a shallow furrow. Two similar, but less distinct, flutes occupy the distal half of the labial surface.

The p4 of NMMNH P-62373 is well preserved, but the base is partially obscured by concretion (Fig. 3F–H). It is nearly triangular in profile, but canted distally, with a single cusp at the apex, unlike the p4 of '*Ca.*' *joyneri*, which bears two to three rows of multiple cusps, or *Ca. alexanderi*, and *Taeniolabis*, which have multiple cusps in one row. The p4 is unknown for *Ca. calgariensis* and *Ca. waddeae*. *Prionessus* and *Sphenopsalis* have smaller, transversely compressed crowns that are not canted distally. The p4 of the holotype and only known specimen of *Ca. foliatus* is too poorly preserved to discern whether or not multiple cusps are present. The p4 of NMMNH P-62373 also differs from the p4 of '*Ca.*' *joyneri*, *Ca. alexanderi*, and *Taeniolabis* in lacking a distinct basal cusp or cingulid at the distobuccal margin of the tooth, but there is a swelling in the same area of the tooth.

The m1 of both NMMNH P-63938 (Fig. 3C–E) and 62373 (Fig. 3F–H) resemble those previously described for *Ca. fissidens* by Lucas *et al.* (1997). The m1 of NMMNH P-62373 (Fig. 3F–H) shows only a small amount of wear. The distobuccal margin of the right m1 is damaged, but the corresponding portion is preserved on a fragment of the left m1. The m1 is rugose with apicobasally aligned wrinkles. The cusps are pyramidal in shape. A distobuccal cingulid is present and connects the distal-most three cusps on the buccal cusp row. The cusps of the lingual row are generally larger, but the dorsal-most cusp is small. No accessory cusps are present, unlike some other specimens referred to this taxon (Lucas *et al.*, 1997). The m1 cusp formula for this tooth is 6:5. The m1 of NMMNH P-63938 (Fig. 3C, D) is more heavily worn than in NMMNH P-62373 and the enamel surface is smoother, with less

pronounced apicobasal wrinkling. A basal cingulid is present at the mesial margin of the tooth before the first cusp of the lingual cusp row and the distobuccal cingulid is better-developed and connects the last four cusps of the buccal cusp row. It has a cusp formula of 7:5.

The m2 of both NMMNH P-62373 and 63938 are similar to those previously described for *Ca. fissidens* by Lucas *et al.* (1997). They have a cusp formula of 2:4. The cusps of the buccal tooth row become progressively more mesio-distally compressed and crenulated from front to back. A distal cuspidate cingulum is situated at the distal margin of the tooth connecting the lingual margin of the lingual cusp row with a ridge descending from the apex of the distal cusp of the buccal cusp row. A similar morphology is present in the type of *Ca. foliatus* and *Ca. calgariensis*, but the m2 of both specimens are heavily worn. However, this is different than in '*Ca. joyneri* and *Ca. alexanderi*' in which the cusps of the buccal cusp row are subequal in size and fewer in number.

Catopsalis calgariensis Russell, 1926: The holotype of *Ca. calgariensis* was collected from the Porcupine Hills Formation of Alberta (Russell, 1926; Fox, 1990; Scott, Spivak & Sweet, 2013) and Middleton (1982) referred additional specimens to this taxon, all consisting of isolated teeth, from the Shotgun fauna (Twin Buttes) of the Fort Union Formation of Wyoming (UW localities V-600014 and V-60016; region 'VIII G' of Lofgren *et al.*, 2004, regarded by them to be Ti1 in age). *Catopsalis calgariensis* has also been reported from the Torrejonian/Tiffanian 'Overlap Zone' of the Hanna Basin, southern Wyoming (Higgins, 2003). *Catopsalis calgariensis* occurs in To3 to Ti1 age faunas and is the youngest reported species of *Catopsalis* (which has a generic range of Pu1 through to Ti4, according to Lofgren *et al.*, 2004, although the report from Ti4 appears to be erroneous). Our scorings for this taxon are based on specimens described and illustrated by Russell (1926), which are from the Porcupine Hills Formation of Alberta. We also utilized the additional teeth referred to *Ca. calgariensis* by Middleton (1982) from the Shotgun Member of the Fort Union Formation of Wyoming. We also examined casts of specimens AMNH 11324 (right m2; plastotype of *Ca. calgariensis*), UW 6387 (partial right P4), 6388 (left m2), 6407 (right M1), 14058 (right M2), 14063 (I2), and 14068 (I2), and NMMNH C-62711 (right M1–2; right m1, left m2).

Taeniolabis taoensis Cope, 1882: *Taeniolabis taoensis* is known from numerous specimens including partial skulls, dentaries, and teeth from the late Puercan (Pu3) of the Nacimiento Formation. We based our scorings of *T. taoensis* on descriptions and illustrations in Granger & Simpson (1929), Matthew (1937), and Simmons (1987)

as well as on personal examination of numerous specimens housed at the NMMNH (see above) and casts of AMNH 725 (left partial m1–m2; holotype of *T. taoensis*), 16313 (partial I2, left P4–partial M1, M2, right M1–2), and 27745 (right M1).

Taeniolabis lamberti Simmons, 1987: *Taeniolabis lamberti* is known from several specimens, including the holotype, a partial lower jaw preserving p4–m2, and two isolated teeth from the Garbani Quarry, Tullock Formation of eastern Montana (see Clemens, 2013 for a recent discussion of the geological setting of the Garbani Quarry). This taxon was scored based on descriptions and illustrations in Simmons (1987). We used the isolated M2 (UCMP 128291) from Garbani Quarry that Simmons (1987) referred to *Taeniolabis* sp. to score this tooth position for *T. lamberti*.

Lambdopsalis bulla Chou & Qi, 1978: *Lambdopsalis bulla* is represented by numerous specimens including skulls and dentaries from the Gashatan Asian Land Mammal Age (ALMA; Ting, 1998), from the upper Paleocene Naran Bulak Formation of China (Meng *et al.*, 2005; Van Itterbeeck *et al.*, 2007). We scored *L. bulla* based on descriptions and illustrations in Chow & Qi (1978), Simmons & Miao (1986), Miao (1988), and Van Itterbeeck *et al.* (2007), and on casts (NMMNH C-1035: left M1–2, right p4–m2) of unnumbered specimens.

Sphenopsalis nobilis Matthew, Granger & Simpson, 1928: *Sphenopsalis nobilis* is represented by a few isolated teeth and tooth fragments from the Gashato Formation of the Gashatan ALMA, Mongolia, that were described by Matthew *et al.* (1928) and Granger & Simpson (1929), and from additional material, including some postcranial bones, from the upper Paleocene Nomogen Formation, Erlian Basin, Inner Mongolia, China, described and illustrated by Mao *et al.* (2015). We based our scoring for this taxon on descriptions and illustrations in Matthew *et al.* (1928), Granger & Simpson (1929), Simmons & Miao (1986), and Mao *et al.* (2015). We also examined casts of AMNH 21713 (partial left m2), 21715 (partial left m1), 21719 (partial left m1), and 21736 (left M2).

Prionessus lucifer Matthew & Granger, 1925: *Prionessus lucifer* is known with certainty only from a few specimens of the Gashatan ALMA, from the upper Paleocene Nomogen and Bayan Ulan formations and the Naran and Zhigden members of the Naran Bulak Formation of Mongolia (Meng *et al.*, 2005; Van Itterbeeck *et al.*, 2007). Descriptions and illustrations in Matthew *et al.* (1928), Granger & Simpson (1929), Simmons & Miao (1986), and Meng *et al.* (1998) formed the basis of our scorings for this taxon. We also examined casts of AMNH 21710 (right partial

dentary with partial m1, m2), 21717 (left alveolus for P4, left and right M1–M2), 21724 (partial left M1, right M2), and 21731 (left partial dentary with p4–m2).

Bubodens magnus Wilson, 1987: *Bubodens magnus* is represented only by a single isolated m1, SDSM 13033, from the Lancian North American Land Mammal Age (NALMA), Fox Hills Formation of South Dakota, which was named and described by Wilson (1987). We used this paper to score this taxon.

OUTGROUP TAXA

The choice of an outgroup taxon for a taeniolabidoid ingroup analysis is difficult. Ideally, the closest relatives of Taeniolabidoidea, as found in higher-level multituberculate phylogenetic analyses, could be chosen. It is not clear, however, what these closest relatives may be. In their higher-level phylogenies, Simmons (1993) and Rougier *et al.* (1997) found *Meniscoessus* as the closest sister to Taeniolabidae (*sensu* Simmons, 1993). Weil (1999) found little resolution amongst higher-level multituberculate relationships, but recovered *Essonodon browni*, followed by *Meniscoessus robustus*, and then followed by a clade composed of *Meniscoessus major* and *Cimolomys gracilis*, as the progressive sister taxa to Taeniolabidae (= Taeniolabidoidea in our usage). However, she included only three taeniolabidoid taxa in her analysis: *Ca. joyneri*, *Ca. alexanderi*, and *T. taoensis*. Weil (1999) concluded that based on her analyses there was support for a paraphyletic Cimolomyidae that gave rise to Taeniolabidae. Yuan *et al.* (2013) and Mao *et al.* (2015) also found low resolution in their strict consensus trees and neither analysis included *Essonodon* or *Cimolomys*, taxa that have been found to be close to Taeniolabidoidea (*sensu* Simmons, 1993) in previous studies.

Owing to the uncertainty regarding the closest relatives of Taeniolabidoidea, we experimented with different outgroups: *Microcosmodon conus*, *Men. robustus*, *Cimo. gracilis*, *Cimexomys judithae*, and *Es. browni*. As only a single outgroup can be employed in the phylogenetic program that we used (TNT), we ran multiple analyses in which each of these taxa was considered the outgroup. Each of these outgroups requires further discussion.

Microcosmodon conus Jepsen, 1930: *Microcosmodon conus* is from the Tiffanian NALMA of the Silver Coulee beds of the Bighorn Basin, Wyoming (Jepsen, 1930; Krishtalka, Black & Riedel, 1975; Rose, 1981; Wilf *et al.*, 1998; Secord, 2008), and the Ravenscrag Formation of Saskatchewan (Krause, 1977; Fox, 1990). Descriptions and illustrations used to score this taxon are from Jepsen (1930), Weil (1998), Fox (2005), and Secord (2008). *Meniscoessus* robus-

tus Marsh, 1889a: *Meniscoessus robustus* is from the latest Cretaceous of Alberta, Saskatchewan, Montana, Wyoming, the Dakotas, and Colorado (Kielan-Jaworowska *et al.*, 2004; Wilson, Dechesne & Anderson, 2010). Descriptions and illustrations used to score *Men. robustus* are from Archibald (1982). We also examined casts AMNH 57400 (left partial dentary with p4–m1 and lower incisor fragments), 57961 (left m2), 57469 (left P4), 57422 (right M1), and 57445 (right M2), and UCMP 48109 (left M1), 51999 (left m1), and 48154 (left m2). Although Weil (1999) argued that *Men. robustus* may be derived relative to other members of its genus, and therefore not a good exemplar species to use as an outgroup for a taeniolabidoid phylogenetic analysis, we used this species because it is substantially more complete than other species of *Meniscoessus*, and is the only member of this genus that can be scored for cranial characters.

Cimolomys gracilis Marsh, 1889a: *Cimolomys gracilis* is from the Lancian NALMA, late Maastrichtian of Alberta, Saskatchewan, Montana, South Dakota, and Wyoming. Descriptions and illustrations used to score *Cimo. gracilis* are from Archibald (1982) and Clemens (1964).

Cimexomys judithae Sahni, 1972: *Cimexomys judithae* is reported from the late Campanian, Late Cretaceous of Wyoming, Montana, and New Mexico (Kielan-Jaworowska *et al.*, 2004). We based our scoring of *Cime. judithae* on descriptions and illustrations from Montellano (1992) and Montellano *et al.* (2000), and of casts AMNH 77100 (right p4; holotype of *Cime. judithae*).

Essonodon browni Simpson, 1927: *Essonodon browni* is a latest Cretaceous taxon reported from the Lance Formation of Wyoming (Clemens, 1964), the Hell Creek Formation of eastern Montana (Archibald, 1982), and the Naashoibito Member of north-western New Mexico (Lehman, 1984). The scoring of this taxon is based on the descriptions and illustrations in Archibald (1982) and Lehman (1984). Archibald (1982: 85) suggested that P4s tentatively referred to *Men. robustus* of 'atypical morphology' might pertain to *Es. browni*. These teeth possess four medial cusps and lack a mesioexternal cusp and distal basal cusps. They are used to score *Es. browni* for characters of the P4. We also examined specimens NMMNH P- 32570 (left M2), 32771 (right? m1), 32773 (left m2), and cast AMNH 14410 (m2; holotype of *Es. browni*).

CHARACTER DATA SET

We scored the ingroup and outgroup taxa for 42 characters of the dentition and cranium. This data set was compiled by combining characters from previous anatomical

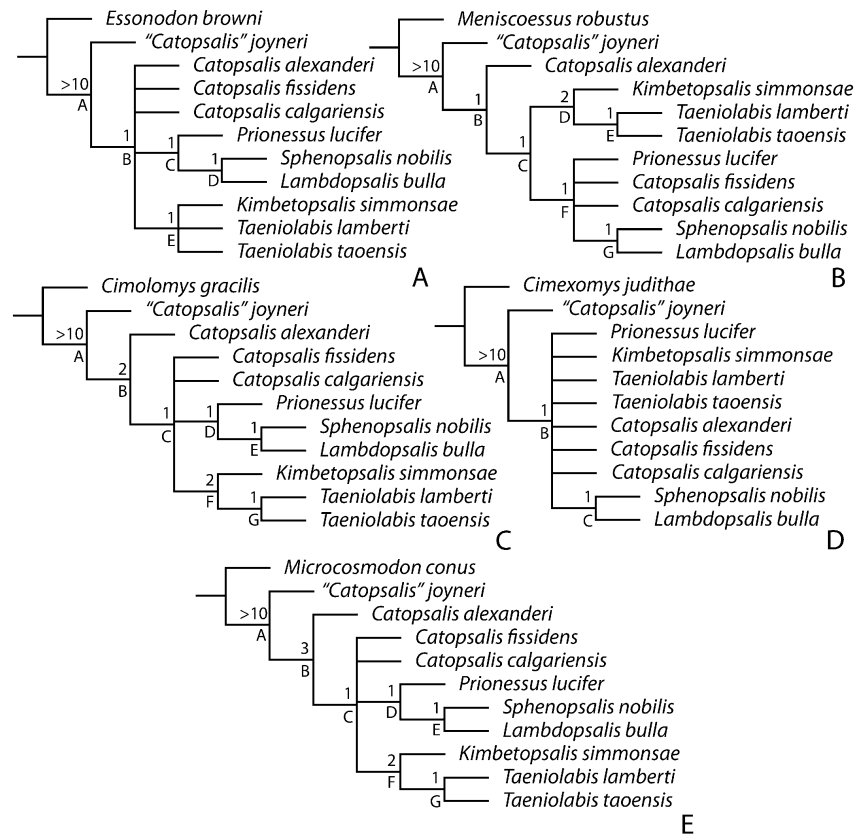


Figure 4. Cladograms resulting from phylogenetic analyses. Data matrix for each analysis includes 11 taxa and 46 characters. Letters refer to nodes (see Appendix S3 for list of common synapomorphies for each node). Numbers above each node are Bremer support values. A, *Essonodon browni* as outgroup, 51 steps, nine trees, consistency index (CI) = 0.647, retention index (RI) = 0.600; B, *Meniscoessus robustus* as outgroup, 62 steps, two trees, CI = 0.677, RI = 0.615; C, *Cimolomys gracilis* as outgroup, 56 steps; two trees; CI = 0.661; RI = 0.604; D, *Cimexomys judithae* as outgroup, 64 steps; 25 trees; CI = 0.703; RI = 0.620; E, *Microcosmodon conus* as outgroup, 60 steps; two trees; CI = 0.733; RI = 0.673.

descriptions and phylogenetic analyses (Archibald, 1982; Simmons & Miao, 1986; Simmons, 1993; Rougier *et al.*, 1997; Weil, 1999; Kielan-Jaworowska & Hurum, 2001) with novel characters revealed during our comparative study of taeniolabidoids, which are used here for the first time. Published source data sets were scrutinized so that characters were not duplicated in our data set, and all characters were written in a standardized language. The character list is presented in Appendix S1, with previous usage of the characters cited. Character scores for the taxa are presented in Appendix S2.

ANALYTICAL PROTOCOLS

We analyzed our data set in TNT v. 1.1 (Goloboff *et al.*, 2008). We first analyzed the data set (Appendix S2) under the 'New Technology' search option, using sectorial search, ratchet, drift, and tree fuse options with default settings. The minimum length tree was found in ten replicates, a procedure that aims to sample a large swathe

of tree space by jumping between as many tree islands as possible. The recovered trees were then analyzed under traditional tree bisection reconnection branch swapping, which more meticulously explores each tree island. This analytical procedure was conducted five separate times, as a different analysis was run using each of the five outgroups (see above).

Results

Strict consensus trees for each of the five analyses with a different outgroup are shown in Figure 4. Reconstructions of taeniolabidoid cheek teeth are shown next to the most resolved consensus tree (with *Cimo. gracilis* or *Men. robustus* as outgroups) in Figure 5. Excluded a posteriori from these trees were three fragmentary taxa that act as wildcards and decrease resolution (*Ca. foliatus*, *Ca. waddeae*, and *Bubodens*). The topologies of these trees range from nearly completely resolved (with *Cimo. gracilis*, *Men.*

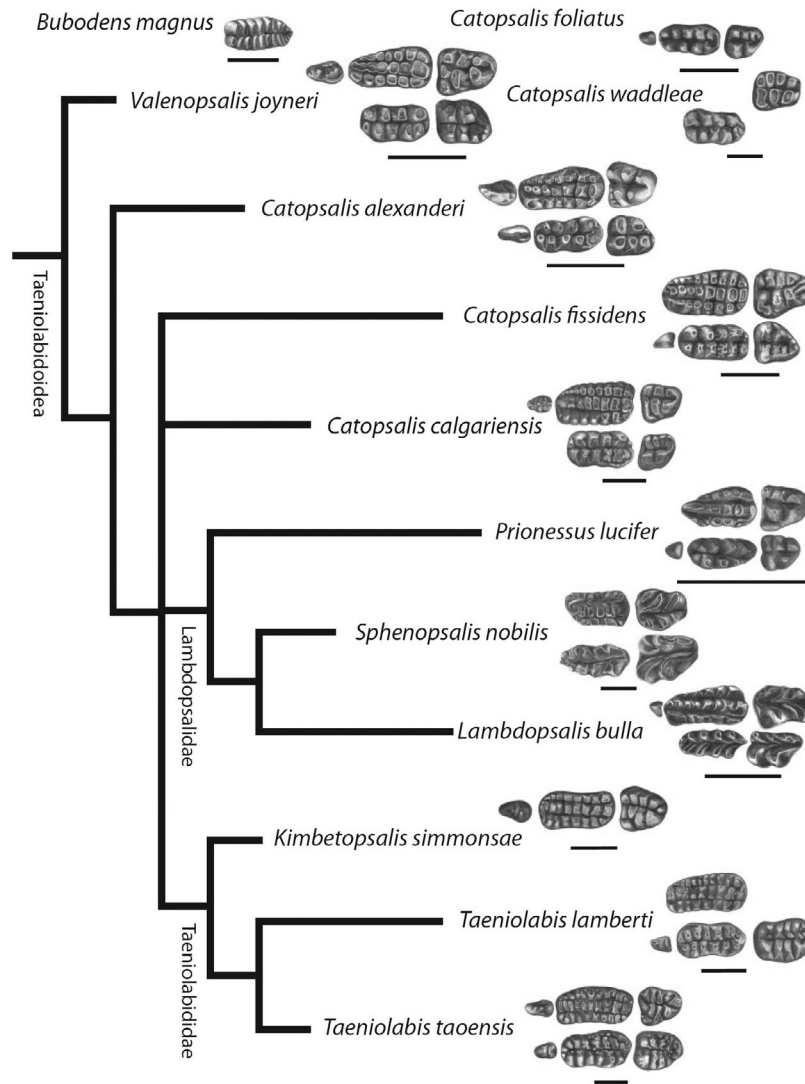


Figure 5. Reconstructions of taeniolabidoid cheek-teeth next to the most-resolved consensus tree from our phylogenetic analysis illustrating major trends in the dental evolution of Taeniolabidoidea. The teeth of *Bubodens magnus*, *Catopsalis waddleae*, and *Catopsalis foliatus* are also shown, although they were not included in the phylogenetic analysis. Their placement on the figure is arbitrary. Right P4–M2 and left p4–m2 are shown, where possible. Mesial is to the left. Cheek teeth are drawn to approximately the same m1 or M1 length. Scale bars = 1 cm. M, upper molar; m, lower molar; P, upper premolar; p, lower premolar.

robustus, and *Mi. conus* as outgroups) to very poorly resolved (with *Cime. judithae* as outgroup). Despite the variable amount of resolution using different outgroups, most of the strict consensus trees agree in three major respects.

First, *Kimbetopsalis* forms a clade of derived taeniolabidoids with *T. lamberti* and *T. taoensis*. This is seen in four of the five consensus trees (all except the tree with *Cime. judithae* as the outgroup). Of these four trees, the two *Taeniolabis* species are sister taxa in all except for the analysis with *Essonodon* as an outgroup, in which the two *Taeniolabis* species and *Kimbetopsalis* form a polytomy. In all four trees the derived *Kimbetopsalis*–*Taeniolabis* clade is supported by some of the highest Bremer support

values on the tree (Bremer value of 2 except for the tree with *Essonodon* as the outgroup). This provides firm evidence that *Kimbetopsalis* is more closely related to *Taeniolabis* than to the various species of *Catopsalis*, despite some shared similarities with the latter (see above). It also demonstrates that *Kimbetopsalis* is something of a phylogenetic intermediate between the species of *Catopsalis* and the highly derived *Taeniolabis*.

Second, in none of the strict consensus topologies do all *Catopsalis* species comprise their own clade exclusive of all other taeniolabidoids. In the four analyses with the greatest resolution (using *Es. browni*, *Men. robustus*, *Cimo. gracilis*, and *Mi. conus* as outgroups), *Ca. alexan-*

deri, *Ca. fissidens*, and *Ca. calgariensis* are more closely related to the clade of *Taeniolabis* + *Kimbetopsalis* (taeniolabidids, see below) and/or lambdopsalids (*Prionessus* and *Sphenopsalis* + *Lambdopsalis*) than is '*Ca.*' *joyneri*, which is consistently recovered as the basal-most taeniolabidoid. Furthermore, in three of these trees '*Ca.*' *joyneri* and *Ca. alexanderi* comprise a series of successive outgroups on the line toward a clade of *Ca. fissidens*, *Ca. calgariensis*, and the derived taeniolabidoids. These results support the idea, first proposed by Simmons & Miao (1986), that *Catopsalis* is a paraphyletic array of species rather than a single monophyletic taxon. Depending upon which outgroup is used and how polytomies are resolved, the degree of paraphyly ranges from moderate to total (i.e. a stepwise array of taxa on the line to the derived taeniolabidoids).

Third, in all of the strict consensus topologies *L. bulla* and *S. nobilis* form a sister-taxon pair. In three of the trees, *Pr. lucifer* is the outgroup to this pair, with these three Asian taxa forming their own clade. This agrees with the results of Mao *et al.* (2015), which recovered *Lambdopsalis* and *Sphenopsalis* in their own subgroup, and goes a step beyond that analysis in finding moderately strong support for *Prionessus* as a member of this group. Mao *et al.* (2015) considered *Prionessus* as *incertae sedis* (not easily assigned to any particular taeniolabidoid subgroup), both based on the results of their phylogenetic analysis and their intuition that its molar morphology is 'primitive' and more similar to that of Late Cretaceous multituberculates than other taeniolabidoids.

Systematic revision of Taeniolabidoidea

Our phylogenetic analysis prompts a systematic revision of Taeniolabidoidea. This includes a clarified usage of the names Taeniolabidoidea and Taeniolabididae (which have been used variably in the literature), new phylogenetic definitions for important clades, and the designation of a new genus name for '*Ca.*' *joyneri*.

Phylogenetic definitions delineate clades based on ancestry instead of possession of 'key' characters of the anatomy or a simple list of a priori included species (e.g. de Queiroz & Gauthier, 1990; de Queiroz & Gauthier, 1992; Sereno, 2005). Such genealogically based definitions are held to be more stable, clear, and objective than other approaches (de Queiroz & Gauthier, 1990, 1992), and they have been employed commonly by mammalian paleontologists Rowe, 1987; Rowe, 1988; Novacek *et al.*, 1997; Luo, Kielan-Jaworowska & Cifelli, 2002; Sereno, 2006; Williamson *et al.* 2012). However, to our knowledge, such definitions have yet to be applied to taeniolabidoids or ingroup clades.

We here define Taeniolabidoidea as the most inclusive clade containing *T. taoensis* Cope, 1882, but not *Es.*

browni Simpson, 1927, *Men. robustus* Marsh, 1889a, *Cimo. gracilis* Marsh, 1889a, *Cime. judithae* Sahni, 1972, *Catopsbaatar catopsaloides* (Kielan-Jaworowska, 1974); *Eu. molestus* Cope, 1886; *Mesodma formosa* Marsh, 1889b; *Ptilodus montanus* Douglass, 1908; *Krauseia clemensi* (Sloan, 1981), *Mi. conus* Jepsen, 1930, *Buginbaatar transaltaiensis* Kielan-Jaworowska & Sochava, 1969, *Kogaionon ungureanui* Rădulescu & Samson (1996), or *Boffius splendidus* Vianey-Liaud, 1979.

Given that a clade of taeniolabidoids including *Kimbetopsalis* and the *Taeniolabis* species is recovered in all of our phylogenetic analyses, and is supported by relatively high Bremer values, we feel that this important group of derived, fairly large-bodied taeniolabidoids should have a clear name. The commonly used Taeniolabididae is well suited for such a group. We here define Taeniolabididae to be the most inclusive clade containing *T. taoensis* (Cope, 1882), but not *L. bulla* Chow & Qi, 1978.

We also recovered a clade of taeniolabidoids that includes *Lambdopsalis* and *Sphenopsalis*, and possibly *Prionessus*. Lambdopsalidae, a family-level taxon erected by Chow & Qi (1978) and resurrected by Mao *et al.* (2015), is a well-suited name for this group. We here define Lambdopsalidae to be the most inclusive clade containing *L. bulla* Chow & Qi, 1978, and not *T. taoensis* (Cope, 1882).

Our phylogenetic results strongly support the hypothesis that the various named species of *Catopsalis* do not form a single monophyletic group, but rather a paraphyletic array. Therefore, if one considers a genus to be a clade, as is standard practice in modern vertebrate paleontology, then the genus name *Catopsalis* should not be applied to all of the species that currently bear this name. The most extreme taxonomic revision could give a new genus name to all *Catopsalis* species except for the type species. However, because the degree of paraphyly of *Catopsalis* differs depending upon the outgroup chosen and the resolution of polytomies, we feel that this is too extreme of a step to take at this point in time, while the evidence is still equivocal. With that said, our analyses strongly support the hypothesis that one species of *Catopsalis*, '*Ca.*' *joyneri*, is a basal-most taeniolabidoid that does not closely group with other *Catopsalis* species (at least some of which do belong to a restricted subclade of multiple *Catopsalis* species in some of our most parsimonious topologies). For this reason, we here erect a new genus name for '*Ca.*' *joyneri*.

VALENOPSALIS GEN. NOV.

Etymology: Named after the late Leigh Van Valen, one of the 20th century's great mammalian paleontologists, who studied Cretaceous–Paleogene multituberculates (includ-

ing '*Ca. joyneri*') and was a colorful inspiration to T. E. W. (who fondly remembers Leigh's visit to the NMMNH collections when he was a graduate student) and S. L. B. (when he was an undergraduate student in Chicago).

Type species: *Catopsalis joyneri* Sloan & Van Valen, 1965.

Included species: Type species only.

Diagnosis: As for the type species.

Distribution

Early Puercan (Pu1) of eastern Montana.

VALENOPSALIS JOYNERI (SLOAN & VAN VALEN, 1965)

Holotype: UMVP 1494, a right maxilla with M1, roots of P4.

Type locality and horizon: Bug Creek Anthills and Bug Creek West, Montana, USA.

Diagnosis: Differs from all other taeniolabidoidea in having a p4 with two roots that are subequal in size, p4 length relatively greater compared with m1 length ($p4L/m1L > 0.4$), P3 present, the M1 internal cusp row length being between 50 and 80% of the length of the tooth, and the molar crown not being ornamented.

THE EVOLUTION AND BIOGEOGRAPHY OF TAENIOLABIDOIDEA

Multituberculates were amongst the most abundant and taxonomically diverse groups of mammals throughout the Cretaceous (Kielan-Jaworowska *et al.*, 2004). They originated by the earliest part of the Late Jurassic (*c.* 160 Mya, Yuan *et al.*, 2013) and experienced a rapid increase in taxonomic diversity, dental complexity and disparity, and maximum body size beginning about 20 000 000 years before the end of the Cretaceous, coincident with the ecological rise of angiosperms (Wilson *et al.*, 2012).

Amongst the latest Cretaceous multituberculates is a poorly known taxon from western North America, *Bub. magnus* Wilson, 1987, represented by a single isolated m1. *Bubodens* was amongst the largest mammals of the day: it attained a body size of about 5 kg, based on estimates derived from tooth size (Table 4; see Legendre, 1986; Wilson *et al.*, 2012). Additionally, it had bulbous cusps that show apical cusp wear, similar to that of taeniolabidoidea (Kielan-Jaworowska *et al.*, 2004; Mao *et al.*, 2015). It may represent the oldest, and only, Cretaceous

example of Taeniolabidoidea. This remains to be adequately tested by a higher-level multituberculate phylogenetic analysis that includes an array of taeniolabidoidea and other multituberculates.

Multituberculates and other mammals with relatively large body size and more specialist diets (such as strict carnivory and herbivory) were decimated at the end-Cretaceous mass extinction, approximately 66 Mya (Wilson, 2013, 2014). Following the mass extinction, multituberculates underwent an additional burst in taxonomic and morphological diversification and the earliest undisputed taeniolabidoidea are present in earliest Paleocene assemblages of western North America (Fig. 6). These taxa – *Valenopsalis joyneri* and *Ca. alexanderi* – exhibit the hallmark dental adaptations found in other taeniolabidoidea, including large, chisel-shaped incisors with enamel restricted to the labial surface, a large diastema separating incisors from cheek teeth, relatively reduced P4s, large molars with long rows of many cusps, and large body size. At an estimated size of about 2 kg, both exceed the size of any known Mesozoic multituberculate with the exception of *Bub. magnus* (Table 4; Wilson *et al.*, 2012). It may be noteworthy that the earliest Paleocene taeniolabidoidea are smaller than *Bubodens* (Fig. 6), a probable latest Cretaceous ancestor or close relative, as this would fit with the general pattern of body size selectivity across the Cretaceous–Paleogene boundary (Wilson, 2013, 2014).

Although Clemens (2010) recognized *Bubodens* to be a Cretaceous member of Taeniolabidoidea, he considered *V. joyneri* and *Ca. alexanderi* to be immigrant taxa, presumably because he did not consider *Bubodens* to be directly ancestral to these taxa. We are unable to corroborate or refute this based on our phylogenetic analysis. However, we agree with his conclusion that there is no compelling evidence that taeniolabidoidea originated in the Cretaceous of Asia and dispersed into North America near the beginning of the Paleocene. We currently consider the origins and ancestral geographical range of taeniolabidoidea to be uncertain.

Within a geologically brief time, during the first 2,000,000 years of the Paleocene, even larger taeniolabidoidea appear in the North American fossil record (Fig. 6). These taxa include *Ca. waddleae*, *Ki. simmonsae*, and species of *Taeniolabis*, all of which exceeded 10 kg in body size. The largest and most aberrant of these, *T. taoensis*, may have reached masses of 100 kg (Wilson *et al.*, 2012), exceeding the size of the extant beaver (*Castor canadensis*) (Weil & Krause, 2008). *Taeniolabis taoensis* is the largest multituberculate that has yet been found and may represent something of a maximum size bound for this long-lived and ecologically diverse group of mammals. Trends in body size evolution are not currently clear, owing to uncertainties in the phylogenetic relationships of taeniolabidoidea, but it is possible that there was a general trend of

Table 4. Mass estimates for taeniolabidoids and the outgroup taxa used in the phylogenetic analyses. For taxa for which m1s are not known, m1 area [length (L) × width] was predicted using a regression formula derived from the m1 vs. M1 area for other taeniolabidoids. Mass estimates were estimated using Wilson *et al.*'s (2012) formula from skull L, from m1 area using Legendre's (1986) formula for all mammals and also for only rodents, and Wilson *et al.*'s (2012) formula from skull L–m1

Taxon	M1 area (mm ²)	Skull length (mm)	Mass estimates (kg)			
			From skull length	From m1 area – Legendre (1986, all mammals)	From m1 area – Legendre (1986, rodents)	From skull L–m1 – Wilson <i>et al.</i> (2012)
<i>Microcosmodon conus</i>	3.11			0.05	0.07	0.05
<i>Essonodon browni</i>	27.27			2.56	3.02	1.18
<i>Cimexomys judithae</i>	1.73			0.02	0.02	0.02
<i>Cimolomys gracilis</i>	10.08			0.42	0.52	0.28
<i>Meniscoessus robustus</i>	41.36	69.0	1.208	5.49	6.31	2.15
<i>Bubodens magnus</i>	76.80			17.01	18.82	5.25
<i>Valenopsalis joyneri</i>	21.45			1.65	1.98	0.83
<i>Catopsalis waddleae</i>	152.52			59.57	63.27	14.13
<i>Catopsalis foliatus</i>	53.55			8.80	9.95	3.12
<i>Catopsalis fissidens</i>	80.64			18.59	20.52	5.63
<i>Catopsalis alexanderi</i>	41.76			5.59	6.41	2.18
<i>Catopsalis calgariensis</i>	139.73			50.76	54.2	12.45
<i>Kimbetopsalis simmonsae</i>	126.16			42.12	45.25	10.74
<i>Taeniolabis taoensis</i>	205.92	160.0	22.697	103.09	107.55	21.79
<i>Taeniolabis lamberti</i>	128.00			43.29	46.42	10.97
<i>Lambdopsalis bulla</i>	24.96	60.8	0.776	2.18	2.58	1.04
<i>Prionessus lucifer</i>	13.44			0.70	0.87	0.42
<i>Sphenopsalis nobilis</i>	99.28			27.19	29.63	7.60

M, upper molar; m, lower molar.

size increase after the end-Cretaceous extinction, or alternatively that different taeniolabidoids may have evolved large size independently of each other (Fig. 6).

North American taeniolabidoids underwent a modest taxonomic diversification early in the Paleocene. At least seven species are present in the Western Interior of North America within the first *c.* 1 500 000 years of the beginning of the epoch. A single taeniolabidid is present in numerous early Paleocene North American faunas, but only one fauna contains more than one taxon: the middle or late Puercan of the San Juan Basin of New Mexico. This fauna contains the very rare (represented by only a single specimen) *Ca. foliatus*, which either co-occurs with the equally rare middle Puercan *Kimbetopsalis*, or with the relatively more abundant late Puercan *T. taoensis*. Whereas some taxa are very rare and represented by at most only a few specimens, all from a single fauna (e.g. *Ca. foliatus*, *Ca. waddleae*, *Kimbetopsalis*, *T. lamberti*), several taxa are represented by numerous specimens and from multiple faunas from relatively widely separated locales (e.g. *Ca. alexanderi*, *Ca. fissidens*, *Ca. calgariensis*, *T. taoensis*). Taeniolabidoids survived into the later part

of the early Paleocene (*Ca. fissidens*) and the early part of the late Paleocene (*Ca. calgariensis*) before apparently going extinct in western North America. *Catopsalis calgariensis* had a body mass exceeding 10 kg, suggesting that taeniolabidoids remained fairly large in North America before disappearing.

One subgroup of taeniolabidoids, Lambdopsalidae, is a uniquely Asian clade that represents the last surviving radiation of Taeniolabidoidea. This clade includes *Lambdopsalis* and *Sphenopsalis* at a minimum, and probably also *Prionessus*. Long the subject of debate, they appear to co-occur and are now each represented by several specimens from multiple localities in the late Paleocene, *c.* 57 Mya (see Mao *et al.*, 2015). The appearance of taeniolabidoids in the late Paleocene of Asia, without any obvious close Asian relatives, strongly indicates that taeniolabidoids dispersed into Asia from North America, probably at some point during the early–middle Paleocene. Several clades of therian mammals occurred in the Paleocene of both Asia and North America (e.g. Dinocerata, Carpolestidae, Carnivoramorpha, Arctostylopidae, Mesonychia, Tillodontia, Pantodonta), indicating that one or more disper-

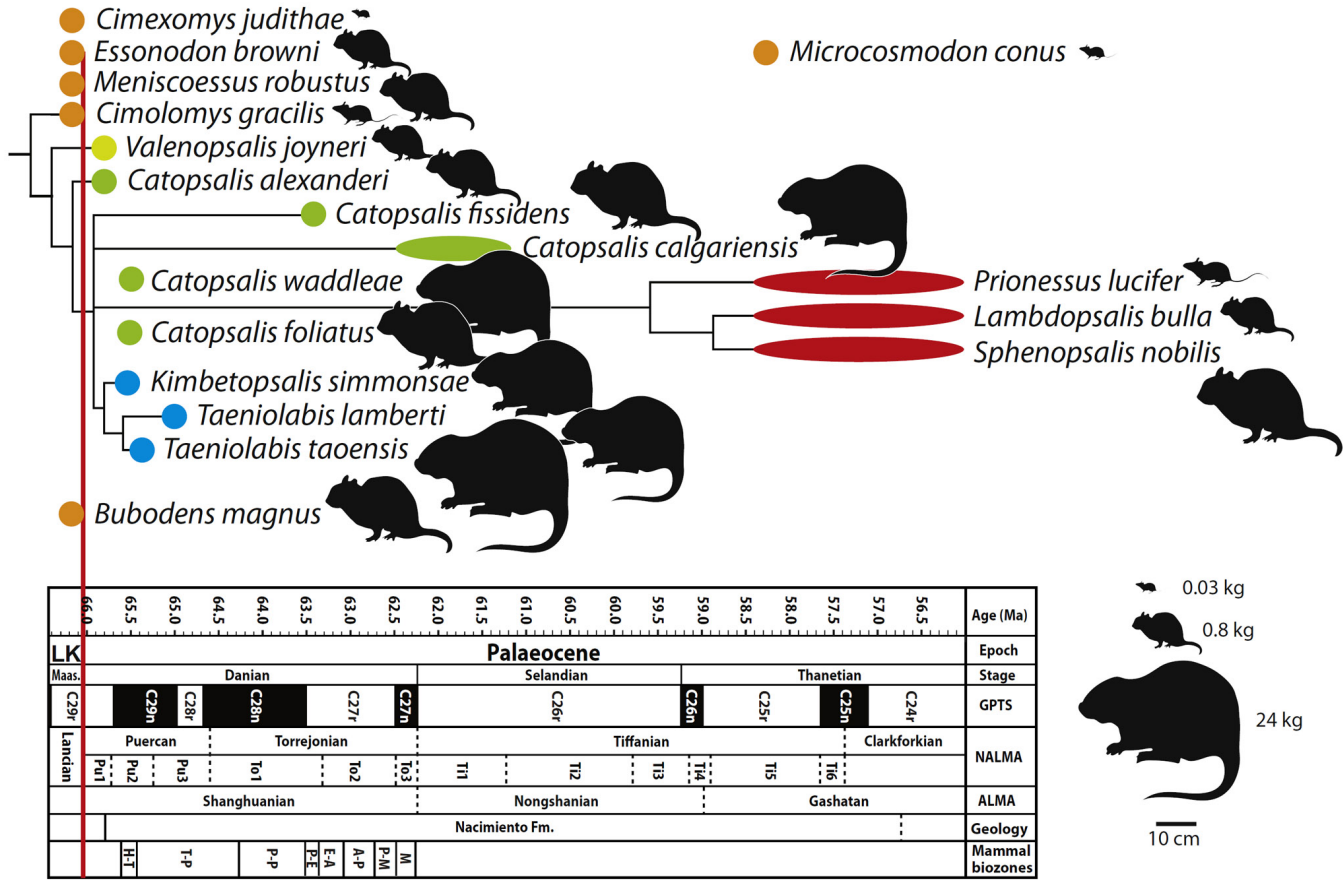


Figure 6. Time-calibrated phylogeny based on the most-resolved consensus tree from our phylogenetic analyses. Each taxon is accompanied by a silhouette that illustrates the relative sizes resulting from our mass estimates (Table 4; skull length – m1 estimate). The area of the silhouette is proportionate to the mass [$\ln(\text{area}) = 0.6667 \cdot \ln(\text{volume}) + 0.231$]. The time scale follows Ogg (2012). The placement of the Puercan faunas of the Nacimiento Formation is after Williamson *et al.* (2014). Asian Paleocene mammal biochronology is after Ting *et al.* (2011). Fm., Formation.

sive episodes occurred between the two continents, but the number and timing of such episodes is not well resolved. The lambdopsalids were, on the whole, smaller than most Paleocene North American taeniolabidoidea in body size (Table 4). This could represent a phylogenetic reduction in size that characterizes the Asian clade. As the last-surviving North American taeniolabidoidea were quite large, and because phylogenetic relationships are still fairly uncertain, it is not clear that the small size of the late-surviving Asian taxa is the culmination of any long-term trend in body size reduction in Taeniolabidoidea.

THE PALAEOBIOLOGY OF TAENIOLABIDOIDEA

Taeniolabidoidea had an unusual diet amongst multituberculates, as indicated by their dental morphology. The dentition and dentaries of multituberculates superficially resemble those of rodents, but modern rodents are an imprecise functional analogue for Cretaceous–Paleocene

multituberculates (Jenkins & Krause, 1983; Wilson *et al.*, 2012). Unlike rodents, or any extant mammals, multituberculates chewed with a palinal (front-to-back) chewing motion. Taeniolabidoidea probably evolved from a multituberculate with large, laterally compressed and blade-like P4s, which were probably used to chew in a two-phase, slicing–crushing masticatory cycle (Krause, 1982). Most multituberculates that possessed these dental adaptations were probably omnivorous (Weil & Krause, 2008; Wilson *et al.*, 2012). Taeniolabidoidea, however, differ from this ancestral pattern in having greatly reduced P4s relative to molar size, which is related to the reduction or elimination of the slicing–crushing chewing phase and an increased emphasis on the grinding phase of the mastication cycle. The small P4s are seen in all taeniolabidoidea, regardless of stratigraphical age or body size, and is a diagnostic feature of the group. Therefore, a grinding-focused chewing stroke evolved early in the history of the group and set taeniolabidoidea apart from most other multituberculates.

Additional evidence for the aberrant diets of taeniolabidoids comes from their distinctive molar morphology. All taeniolabidoids have complex molars with three rows of prominent cusps, which is another diagnostic feature of the group. The molars of early taeniolabidoids are large, with many cusps. These cusps are bulbous and in some taxa (e.g. *Taeniolabis*), highly crenulated. This results in high orientation patch count values, a measure of dental complexity, which reaches its peak amongst multituberculates in *T. taoensis* (Wilson *et al.*, 2012). These adaptations are related to herbivory, as described by Wilson *et al.* (2012). This shift to herbivory in taeniolabidoids is also accompanied by an increase in body size, as is the case in many terrestrial tetrapods. Senescent *T. taoensis* specimens exhibit extreme molar and incisor wear (Granger & Simpson, 1929), and tooth wear may have been a factor in an individual's longevity.

The large incisors of taeniolabidoids are gliriform, with an enamel band that provides a sharp, chisel-like cutting apex, and were probably used for snipping vegetation. In some taeniolabidoids (e.g. *Ca. fissidens*, *Ki. simmonsae*, *T. taoensis*), the incisors bear longitudinal striations that probably strengthened the tooth against compressive forces applied to their tips.

There is some evidence that the Asian lambdopsalids may have diverged from their North American relatives and developed a somewhat different diet. *Sphenopsalis* and *Lambdopsalis* have uniquely high-crowned molars with crescentic cusps (Mao *et al.*, 2015). The high, narrow, and sharp, v-shaped cusp crests form opposing, triangular-shaped cutting blades that would have formed an effective shearing mechanism. This probably indicates a more folivorous diet than in other taeniolabidoids, particularly the North American *Taeniolabis*-like taxa.

Little is known about the locomotor habits of taeniolabidoids, because substantial postcrania are known for only two taxa: the lambdopsalids *Sphenopsalis* (Mao *et al.*, 2015) and probably *Lambdopsalis* (Kielan-Jaworowska & Qi, 1990; Mao *et al.*, 2015). Amongst these specimens are partial humeri, which are very robust, suggesting that these taxa were fossorial (Miao, 1988; Kielan-Jaworowska & Qi, 1990; Mao *et al.*, 2015).

Conclusions

The recovery of a new genus and species of large taeniolabidoid multituberculate, *Ki. simmonsae*, from the early Paleocene (middle Puercan; Pu2) of the Nacimiento Formation prompted a revision of Taeniolabidoidea and an evaluation of their phylogeny and evolution. Our phylogenetic analysis of Taeniolabidoidea included all Asian and North American species referable to this clade. Owing to

uncertainties over the choice of an appropriate outgroup we ran analyses using five different outgroups and found that trees were highly resolved using three (*Cimo. gracilis*, *Men. robustus*, and *Mi. conus*) of the five outgroups. In the highly resolved trees, species of the largest-bodied North American forms, *Kimbetopsalis* and *Taeniolabis*, consistently form a monophyletic clade as do species of the Asian *Lambdopsalis*, *Sphenopsalis*, and *Prionessus*. We here define *Kimbetopsalis* and *Taeniolabis* as the basis of Taeniolabidoidea and *Lambdopsalis* and *Sphenopsalis* as the basis of Lambdopsalidae.

This study underscores the extreme rapidity of development of large body size and the increase in dental complexity within taeniolabidoids within the first 800 Kyr of the end-Cretaceous mass extinction (Wilson *et al.*, 2012; Williamson *et al.*, 2014). Taeniolabidoids evolved extremely unusual and highly specialized, large, chisel-shaped incisors and massive, multicusped cheek teeth for grinding vegetation and attained large body masses, exceeding 20 kg. The shifts to larger body sizes and increased cusp complexity strongly suggest a shift toward herbivory, and possibly folivory.

Bubodens magnus, the largest multituberculate and largest mammal of the latest Cretaceous, probably represents the sole Cretaceous representative of Taeniolabidoidea. Taeniolabidoids of the earliest Paleocene faunas of North America include *V. joyneri*, which our phylogenetic analyses found to be the basalmost taeniolabidoid. We find that *Kimbetopsalis simmonsae* is the basal-most member of Taeniolabidoidea and it provides a plausible progenitor for *T. taoensis*, which first appeared in the San Juan Basin within the next 200 Kyr.

Although taeniolabidoids disappeared from North America several million years before the end of the Paleocene, they dispersed to Asia where they underwent a subsequent modest radiation towards the end of the Paleocene, becoming extinct near the Paleocene–Eocene boundary.

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SUPPORTING INFORMATION

Appendix S1. Character list.

Appendix S2. Character data matrix (text file).

Appendix S3. Common synapomorphies for each of the phylogenetic analyses.

Appendix 1. Character list.

Characters

1. Enamel microstructure: prismless (0); small prismatic (1); intermediate (2); gigantoprismatic (3); Ordered. Modified from Simmons (1993) ch. 1, Rougier *et al.* (1997) ch. 1, Kielan-Jaworowska & Hurum (2001) ch. 1, Weil (1998) ch. 1, and Mao *et al.* (2015) ch. 77.
2. Incisor enamel surface texture: rugose with irregular wrinkles (0); longitudinal ridges, fluted (1).
3. i2 enamel: uniform thickness (0); thicker labially than lingually (1); restricted to labial surface (2). Ordered. From Weil (1998) ch 2, Weil (1999) ch. 16, similar to Kielan-Jaworowska & Hurum (2001) ch. 20, modified from Simmons (1993) ch. 3, Rougier *et al.* (1997) ch. 3.
4. p3: present (0); absent (1). Modified from Simmons & Miao (1986), Rougier *et al.* (1998) ch. 7, Weil (1999) ch. 5, Kielan-Jaworowska & Hurum (2001) ch. 24, and Mao *et al.* (2015) ch. 35.
5. Roots of p4: subequal in size (0); anterior root larger than posterior root (1). Modified from Weil (1998) ch. 8, Weil (1999) ch. 12.
6. p4 shape in profile view: parabolic (0); triangular (1). Modified from Simmons & Miao (1986), Rougier *et al.* (1998) ch. 11, Weil (1999) ch. 8, Kielan-Jaworowska & Hurum (2001) ch. 27, and Mao *et al.* (2015) ch. 42.
7. p4 laterally-compressed and blade-like: yes (0); no (1). From Luo *et al.* (2002) ch. 160 and Mao *et al.* (2015) ch. 41.
8. p4 posterobuccal basal cusp or ridge: present (0); absent (1).

9. p4 number of cusps in median cuspal row: > 1 (0); 1 (1).
10. m1 cusp formula: $\leq 4:3$ (0); $\geq 4:3$ and $< 5:4$ (1); $\geq 5:4$ and $< 7:6$ (2); $\geq 7:6$ (3) . Ordered.
Modified from Simmons & Miao (1986), similar to Kielan-Jaworowska & Hurum (2001) ch. 36.
11. Posterobuccal cingulid on m1: absent (0); present (1).
12. m2 cusp formula: $\geq 3:2$ and $< 4:4$ (0); $\geq 4:4$ (1). Modified from Simmons & Miao (1986).
Similar to Kielan-Jaworowska & Hurum (2001) ch. 37.
13. p4L/m1L: < 0.30 (0); ≥ 0.30 and < 0.40 (1); ≥ 0.40 and < 0.45 (2); ≥ 0.45 and < 0.65 (3);
> 0.65 (4). Ordered. Modified from Weil (1998) ch. 31, Weil (1999) ch. 34, Kielan-Jaworowska & Hurum (2001) ch. 31, and Mao *et al.* (2015) ch. 48.
14. Molar crown ornamentation: smooth (0); grooved or ridged (1). Modified from Weil (1999) ch. 33, Kielan-Jaworowska & Hurum (2001) ch. 39, Mao *et al.* (2015) ch. 76.
15. I2 enamel: uniform thickness (0); thicker labially than lingually (1); restricted to labial surface (2). Ordered. Weil (1999) ch. 16, similar to Kielan-Jaworowska & Hurum (2001) ch. 20, modified from Rougier *et al.* (1997) ch. 20.
16. I2 morphology: peg-like or single-cusped (0); two-cusped or more (1). From Rougier *et al.* (1998) ch. 19, Kielan-Jaworowska & Hurum (2001) ch. 3, Mao *et al.* (2015) ch. 19.
17. I2 cusp count: 4 (0); 3 or less (1). From Simmons (1993) ch. 19, Rougier *et al.* (1997) ch. 19, Weil (1999) ch. 15, Kielan-Jaworowska & Hurum (2001) ch. 3.
18. Diastema between I2 and I3: absent (0); present (1). Modified from Yuan *et al.* (2013) ch. 18 and Mao *et al.* (2015) ch. 18.

19. I3 morphology: single-cusped or peg-like (0); 2 cusps or more (1). Modified from Rougier *et al.* (1998) ch. 21, Kielan-Jaworowska & Hurum (2001) ch. 4, and Mao *et al.* (2015) ch. 20.
20. I3 placement: marginal (0); near sagittal midline (1). Modified from Simmons & Miao (1986), Rougier *et al.* (1997) ch. 22, Weil (1999) ch. 17.
21. P1: present (0); absent (1). From Simmons & Miao (1986). Kielan-Jaworowska & Hurum (2001) used a single character (ch. 6) that scored the number of premolars present (5, 4, 3, 2 or 1). Weil (1999) combined presence/absence of P1-P3 (chs. 19-21) with cusp counts.
22. P2: present (0); absent (1).
23. P3: present (0); absent (1).
24. p4L/P4L: ≤ 1.1 (0); > 1.1 and ≤ 1.8 (1); > 1.8 (2). Ordered. From Weil (1999) ch. 36.
25. P4: single rooted (0); double rooted (1). Rougier *et al.* (Rougier *et al.*, 1997) ch. 37, Simmons & Miao, (1986), Simmons (1993) ch. 37, Weil (1999) ch. 23.
26. P4 cusp formula: 0-5:1-4:0-5 (0); 0-5:5-10:0-5 (1); 5-7:5-8:2-5 (2). Ordered. From Kielan-Jaworowska & Hurum (2001) ch. 18.
27. M1 cusp formula: $> 5:5:0$ and $< 5:5:4$ (0); $\geq 5:5:4$ and $< 6:6:5$ (1); $\geq 6:6:5$ and $< 9:8:9$ (2); $> 9:8:9$ (3). Ordered. Modified from Simmons & Miao (1986), see Kielan-Jaworowska & Hurum (2001) ch. 10.
28. M1 length of internal cusp row compared to total M1 length: internal row absent (0); $< 50\%$ length of tooth (1); $\geq 50\%$ and $< 80\%$ length of tooth (2); $\geq 80\%$ length of tooth (3). Ordered. Weil (1999) ch. 26, may be approximately the same as Kielan-Jaworowska &

- Hurum (2001) ch. 11. “M1 posterolingual wing to M1 length, wing absent (0); below 0.2 (1); between 0.2 and 0.3 (2); above 0.3 (3).”
29. M1 length: < 5.5 mm (0); ≥ 5.5 mm and < 9.5 mm (2); ≥ 9.5 and < 13.5 (3); ≥ 13.5 mm and < 17.5 mm (3); ≥ 17.5 mm (4). Ordered. Modified from Simmons & Miao (1986), Weil (1999) ch. 24.
30. M1/m1 multiple accessory roots: absent (0); present (1). Weil (1999) ch. 29.
31. P4L/M1L: < 0.5 (0); P4L/M1L ≥ 0.5 (1). Ordered. Modified from Simmons and Miao (1986), Weil (1999) ch. 34. Weil (1999) used different divisions; 1, 1.75 for p4/m1 and 1.75, 0.8 for P4/M1. Similar to Kielan-Jaworowska & Hurum (2001) ch.8 and Mao *et al.* (2015) ch. 29.
32. P4W/M1W: > 0.9 (0); ≤ 0.9 and > 0.6 (1); ≤ 0.6 and > 0.45 (2); ≤ 0.45 and > 0.2 (3). Ordered. Modified from Kielan-Jaworowska & Hurum (2001) ch. 19 and Mao *et al.* (2015) ch. 32.
33. M2 cusp formula: 1-4:2-3:3-4 (0); 1-2:4:5-7 (1).
34. M1L/M2L: ≤ 1.5 (0); > 1.5 and ≤ 2.25 (1); > 2.25 and ≤ 2.5 (2); > 2.5 (3). Ordered. From Weil (1999) ch. 35; similar to character from Simmons & Miao (1986).
35. Cusp shape: conical or quadrangular (0); crescentic (1). Modified from Simmons & Miao (1986), Kielan-Jaworowska & Hurum (2001), ch. 38.
36. Premaxilla with facial process: height > anteroposterior length (0); height \leq length (1). From Simmons (1993) ch. 42, Rougier *et al.* (1997) ch. 42.
37. Infraorbital foramen: double (0), single (1). From Kielan-Jaworowska & Hurum (2001) ch. 16 and Mao *et al.* (2015) ch. 80; modified from Simmons (1993) ch. 43 and Rougier *et al.* (1997) ch. 43.

38. Palatal vacuities absent (0), single (1), double (2). Ordered. From Simmons (1993) ch. 58, Rougier *et al.* (1997) ch. 58, Kielan-Jaworowska & Hurum (2001) ch. 17, Mao *et al.* (2015) ch. 81.
39. Ridge between the palate and lateral walls of premaxilla: absent (0), present (1). From Kielan-Jaworowska & Hurum (2001) ch. 40 and Mao *et al.* (2015) ch. 82.
40. Shape of the snout in dorsal view: incurved in front of the zygomatic arches with anterior part directed posterolaterally (0); incurved with anterior part of zygomatic arches directed transversely (1); trapezoid, not incurved in front of the zygomatic arches (2). From Kielan-Jaworowska & Hurum (2001) ch. 41, similar to Simmons (1993) ch. 48 and Rougier *et al.* (1997) ch. 48.
41. Number of pairs of vascular foramina on nasal: 1 (0); 2 (1); more than 2 (2). Ordered. From Kielan-Jaworowska & Hurum (2001) ch. 42 and Mao *et al.* (2015) ch. 84.
42. Infraorbital foramen position: dorsal to P1 (0), dorsal to P2 (1), dorsal to P3 or P4 (2). Ordered. Modified from Simmons (1993) ch. 45, Rougier *et al.* (1997) ch. 45, from Kielan-Jaworowska & Hurum (2001) ch. 43, Mao *et al.* (2015) ch. 85.
43. Base of zygomatic arch as marked by posterior edge: dorsal to P4 or more anterior (0); dorsal or posterior to P5/M1 or P4/M1 embrasure (1). Modified from Simmons (1993) ch. 49 and Rougier *et al.* (1997) ch. 49, from Kielan-Jaworowska & Hurum (2001) ch. 44 and Mao *et al.* (2015) ch. 86.
44. Incisive foramen: situated within premaxilla (0); limited posteriorly by maxilla (1). From Kielan-Jaworowska & Hurum (2001) ch. 52 and Mao *et al.* (2015) ch. 95; similar to Simmon (1993) ch. 57 and Rougier *et al.* (1997) ch. 57.

45. Posterior border of palate: medial or posterior to posterior edge of M2 (0); medial to middle of M2 (1); medial to M1-M2 embrasure (2). Ordered. Modified from Simmons (1993) ch. 59, Rougier *et al.* (1997) ch. 59.
46. Coronoid process: parallel to the rest of the outer wall of the dentary (0); flared laterally (1). From Kielan-Jaworowska & Hurum (2001) ch. 58.

xread

46 18

Bubodens_magnus ?????????30??1??
Meniscoessus_robustus 30101001020141?1011110011013110200010100?210??
Microcosmodon_conus 202000002004111111000010220112010?1100?20??
Essonodon_browni 3????????3?0?????????????0?10231102031????????????
Cimolomys_gracilis 30?00000030131?????????11113011?01[0 1]????????????
Cimexomys_judithae 300010?1020140??????00011112001201011?1?220??
Catopsalis_waddleae ?????????20??0?????????????????1??0????????????
Catopsalis_joyneri ?02?01?002003021??????0010221102010????????????
Catopsalis_calgariensis ?02?11???210102?1?????????02341??010????????????
Catopsalis_foliatus ?????11?1120010????????????????????????????????
Catopsalis_fissidens ?12111?11210112??1?????????2331??010????????????
Catopsalis_alexanderi ?02111?0?210?121?100??010232?02000????????????
Taeniolabis_taoensis 312111?003110121010011101033410211001001?21?00
Taeniolabis_lamberti ???1?1?0030101??????????00334?03??0????????????
Kimbetopsalis_simmonsae ?1?????????????12?????0??1?10234?03100?????1??1??
Lambdopsalis_bulla 3021-1?1120100201000111?00232?0310111000121121
Sphenopsalis_nobilis ?021-1?????00020?00011110?233?03001??01??11??
Prionessus_lucifer ??21-1?1120000????????????[0 1]?231?03010??01????1???

;

cnames

{0 Enamel_microstructure: prismless. small_prismatic. "intermediate. gigantoprismatic.;
{1 Incisor_enamel_surface_texture: rugose_with_irregular_wrinkles. longitudinal_ridges,_fluted.;
{2 i2_enamel_uniform_thickness. thicker_labially_than_lingually. restricted_to_labial_surface.;
{3 p3: present. absent.;
{4 Roots_of_p4_subequal_in_size. anterior_root_larger_than_posterior_root.;
{5 p4_shape_in_profile_view: parabolic. triangular.;
{6 p4_laterally-compressed_and_blade-like: yes. no.;
{7 p4_posterobuccal_basal_cusp_or_ridge: present. absent.;
{8 p4_number_of_cusps_in_median_cusp_row: >_1. 1.;
{9 m1_cusp_formula: "?<_4:3. "?>_or_= 4:3_and <_5:4. "?>_or_= 5:4_and <_7:6. "?>_or_= 7:6.;
{10 Posterobuccal_cingulid_on_m1 absent. present.;

{11 m2_cusp_formula: "?>_or_ = 3:2_and_ < 4:4. "?>_or_ = 4:4.;

{12 p4L/m1L: <_0.30. "?>_or_ = 0.30_and_ < 0.40. "?>_or_ = 0.40_and_ < 0.45._
"?>_or_ = 0.45_and_ < 0.65._ >_or_ = 0.65.;

{13 Molar_crown_ornamentation: smooth. grooved_or_ridged.;

{14 I2_enamel: uniform_thickness. thicker_labially_than_lingually_or_medially.
restricted_to_labial_surface.;

{15 I2_morphology: Peg-like_or_single_cusp. Two-cusped_or_more.;

{16 I2_cusp_count: 4. 3_or_less.;

{17 Diastema_between_I2_and_I3: absent. present.;

{18 I3_morphology: Single-cusped_or_peg-like. 2_cusps_or_more.;

{19 I3_placement: marginal. near_sagittal_midline.;

{20 P1: present. absent.;

{21 P2: present. absent.;

{22 P3: present. absent.;

{23 p4L/P4L: <_or_ = 1.1. >_1.1_and_ <_or_ = 1.8. >_1.8.;

{24 P4: single_rooted. double_rooted.;

{25 P4_cusp_formula: 0-5:1-4:0-5. 0-5:5-10:0-5. 5-7:5-8:2-5.;

{26 M1_cusp_formula: >_5:5:0_and_ <_5:5:4. >_or_ = 5:5:4_and_ <_6:6:5. >_or_ = 6:6:5_and_ <_9:8:9.
>_9:8:9.;

{27 M1_length_of_internal_cusp_row_compared_to_total_M1_length: _internal_row_absent.
<_50%_length_of_tooth. >_or_ = 50%_and_ <_80%_length_of_tooth. >_or_ = 80%_length_of_tooth.;

{28 M1_Length: <_5.5_mm. >_or_ = 5.5_mm_and_ <_9.5_mm. >_or_ = 9.5_mm_and_ <_13.5_mm.
>_or_ = 13.5_mm_and_ <_17.5_mm. >_or_ = 17.5_mm.;

{29 M1/m1_multiple_accessory_roots: absent. present.;

{30 P4L/M1L: <_0.5. >_or_ = 0.5.;

{31 P4W/M1W: >_0.9. <_or_ = 0.9_and_ >_0.6. <_or_ = 0.6_and_ >_0.45. <_or_ = 0.45_and_ >_0.2.;

{32 M2_cusp_formula: 1-4:2-3:3-4. 1:4:5.;

{33 M1L/M2L: <_or_ = 1.50. "?>_1.5_and_ <_or_ = 2.25. >_2.25_and_ <_or_ = 2.5. "?>_2.5.;

{34 Cusp_shape: conical_or_quadrangular. crescentic.;

{35 Premaxilla_with_facial_process_height_>_anteroposterior_length. height_>_or_ = length.;

{36 Infraorbital_foramen: double. single.;

{37 Palatal_vacuties: absent. single. double.;

{38 Ridge_between_the_palate_and_lateral_walls_of_premaxilla: absent. present.;

```
{39 Shape_of_the_snout_in_dorsal_view:  
incurved_in_front_of_the_zygomatic_arches_with_anterior_part_directed_posterolaterally.  
incurved_with_anterior_part_of_zygomatic_arches_directed_transversely.  
trapezoid,_not_incurved_in_front_of_the_zygomatic_arches.;  
{40 Number_of_pairs_of_vascular_foramina_on_nasal: 1. 2. >_2.;  
{41 Infraorbital_foramen_position: dorsal_to_P1. dorsal_to_P2. dorsal_to_P3_or_P4.;  
{42 Base_of_zygomatic_arch_as_marked_by_posterior_edge:_ dorsal_to_P4_or_more_anterior.  
dorsal_or_posterior_to_P5/M1_or_P4/M1_embrasure.;  
{43 Incisive_foramen: situated_within_premaxilla. limited_posteriorly_by_maxilla.;  
{44 Posterior_border_of_palate medial_or_posterior_to_posterior_edge_of_M2.  
medial_to_middle_of_M2. medial_to_M1-M2_embrasure.;  
{45 Coronoid_process:_ parallel_to_the_rest_of_the_outer_wall_of_the_dentary. flared_laterally.;  
;
```

```
ccode + 0 2 9 12 14 23 25.28 30 31 33 37 40 41 *;
```

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proc /;  
comments 0  
;
```

Appendix S3. Common synapomorphies for each of the phylogenetic analyses.

Appendix 2. Common synapomorphies.

Essonodon browni as Outgroup.

Synapomorphies common to 9 trees

(Node numbers refer to nodes in consensus, Fig. 3A)

Node A:

All trees:

No synapomorphies

Node B:

Some trees:

Char. 22: 0 → 1

Char. 28: 1 → 2

Node C:

All trees:

Char. 12: 1 → 0

Some trees:

Char. 7: 0 → 1

Char. 10: 1 → 0

Char. 31: 2 → 3

Node D:

All trees:

Char. 33: 1 → 0

Char. 34: 0 → 1

Node 5 :

All trees:

Char. 32: 0 → 1

Some trees:

Char. 1: 0 → 1

Char. 9: 2 → 3

Char. 11: 0 → 1

Char. 12: 1 → 0

Char. 28: 3 → 4

Appendix 3. *Meniscoessus robustus* as Outgroup.

Synapomorphies common to 5 trees

(Node numbers refer to nodes in consensus, Fig. 3B)

Node A:

All trees:

No synapomorphies

Node B:

All trees:

Char. 28: 1 → 2

Some trees:

Char. 10: 0 → 1

Node C:

All trees:

Char. 31: 2 → 3

Some trees:

Char. 28: 2 → 3

Node D:

All trees:

Char. 28: 23 → 4

Char. 32: 0 → 1

Char. 39: 0 → 1

Some trees:

Char. 1: 0 → 1

Node E:

All trees:

Char. 26: 2 → 3

Node F:

All trees:

Char. 7: 0 → 1

Char. 8: 0 → 1

Some trees:

Char. 13: 1 → 0

Char. 16: 0 → 1

Node G:

All trees:

Char. 34: 0 → 1

Some trees:

Char. 17: 1 → 0

Char. 33: 1 → 0

Appendix 4. *Cimolomys gracilis* as Outgroup.

Synapomorphies common to 2 trees

(Node numbers refer to nodes in consensus, Fig. 3C)

Node A:

All trees:

No synapomorphies

Node B:

All trees:

Char. 26: 2 → 3

Node C:

All trees:

Char. 4: 0 → 1

Char. 10: 0 → 1

Char. 28: 1 → 2

Node D:

All trees:

Char. 33: 1 → 0

Char. 34: 0 → 1

Node E:

All trees:

Char. 32: 0 → 1

Some trees:

Char. 1: 0 → 1

Char. 28: 3 → 4

Node F:

All trees:

Char. 31: 2 → 3

Some trees:

Char. 28: 2 → 3

Node G:

All trees:

Char. 10: 1 → 0

Char. 12: 1 → 0

Some trees:

Char. 13: 1 → 0

Appendix 5. *Cimexomys judithae* as Outgroup.
Synapomorphies common to 25 trees
(Node numbers refer to nodes in consensus, Fig. 3D)

Node A:

All trees:

No synapomorphies

Node B:

All trees:

Char. 27: 2 → 3

Some trees:

Char. 8: 0 → 1

Char. 10: 0 → 1

Char. 12: 3 → 01

Char. 13: 0 → 01

Char. 22: 0 → 1

Char. 28: 1 → 23

Char. 31: 2 → 3

Node C:

All trees:

Char. 34: 0 → 1

Some trees:

Char. 15: 1 → 0

Char. 17: 1 → 0

Char. 24: 1 → 0

Char. 33: 1 → 0

Appendix 6. *Microcosmodon* as Outgroup.

Synapomorphies common to 2 trees

(Node numbers refer to nodes in consensus, Fig. 3E)

Node A:

All trees:

No synapomorphies

Node B:

All trees:

Char. 4: 0 → 1

Char. 10: 0 → 1

Char. 27: 2 → 3

Char. 28: 1 → 2

Node C:

All trees:

Char. 31: 2 → 3

Some trees:

Char. 28: 2 → 3

Node D:

All trees:

Char. 10: 1 → 0

Char. 12: 1 → 0

Some trees:

Char. 13: 1 → 0

Node E:

All trees:

Char. 33: 1 → 0

Char. 34: 0 → 1

Node F:

All trees:

Char. 32: 0 → 1

Some trees:

Char. 1: 0 → 1

Char. 28: 3 → 4

Char. 39: 0 → 1

Node G:

All trees:

Char. 26: 2 → 3