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Northernmost record of the Metatheria: a new Late Cretaceous pediomyid from the North Slope of Alaska

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The northernmost record of Metatheria, *Unnuakomys hutchisoni* gen. et sp. nov., is described from the Pediomys Point locality in Upper Cretaceous (lower Maastrichtian) strata of the Prince Creek Formation cropping out along the Colville River on the North Slope of Alaska, USA (70°N). Based on over 60 specimens (including tooth-bearing dentaries and a maxillary fragment), the new taxon is unusual in having two well-developed stylar cusps in the C position flanking the deepest part of the ectoflexus. To examine the relationship between *U. hutchisoni* and other metatherians, *U. hutchisoni* was scored into the taxon character matrix of other studies. Our results corroborate prior studies that suggest the new Alaskan pediomyid. However, in contrast to other studies, we do not recover a sister-group relationship between *U. hutchisoni* and *Pediomys elegans*. Rather, our study suggests that *U. hutchisoni* is more closely allied with Aquilan species *Iqualadelphis lactea* and ?*Aquiladelphis laurae*. Teeth of *U. hutchisoni* greatly outnumber those recovered from other mammals at Pediomys Point, like Late Cretaceous localities in the Western Interior where metatherians are among the most abundant mammalian fossils. However, what differs between Late Cretaceous mid-latitude localities and the assemblage from the North Slope of Alaska is metatherian richness. Whereas other studies have reported up to a dozen species of metatherians from Late Cretaceous mid-latitude North American assemblages, to date all the metatherian teeth collected from Pediomys Point appear to belong to just *U. hutchisoni*. A sampling bias may play a role in this pattern. This can be tested through additional collection from the Prince Creek Formation. However, the abundance of *U. hutchisoni* at Pediomys Point implies that this tiny metatherian thrived in an environment well above the Arctic Circle whose climatic extremes may have acted as a biogeographical filter to other metatherians. As the first mammal to be described from the Prince Creek Formation, *U. hutchisoni* provides support for the existence of a northern high-latitude early Maastrichtian faunal province identified by others on the basis of its distinctive dinosaurian fauna – the Paaŋaqtat Province.

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Keywords: Metatheria; Arctic; Pediomyidae; Alaska; Prince Creek Formation; Cretaceous

Introduction

The Metatheria (marsupials and their closest fossil relatives) includes over 330 living species, most of which live in the Southern Hemisphere (Armati *et al.* 2006; Williamson *et al.* 2014). However, the origin and early diversification of the clade, which trace back to the Mesozoic, appear to have occurred in the Northern Hemisphere (Bennett *et al.* 2018). *Sinodelphys szalayi* from the Early Cretaceous Jehol biota of Asia has been regarded as the oldest known, undoubted metatherian (Luo *et al.* 2003, 2011; Williamson *et al.* 2012). Discovery of *Ambolestes zhoui* added to the therian diversity of this biota (Bi *et al.* 2018). Their phylogenetic analysis of the therians in the Jehol biota placed *S. szalayi* within the Eutheria. If confirmed, the oldest current records of metatherians are a deltatheridian, a poorly documented marsupialiform, and a possible metatherian from the Albian Cloverly Formation in North America (Cifelli & Davis 2015). By the end of the Cretaceous, metatherians had dispersed across Europe, Asia and North America and outnumbered, and were more diverse than, their eutherian contemporaries (Williamson *et al.* 2014). The majority of Late Cretaceous metatherian species are represented almost exclusively by isolated teeth and jaws collected by

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*Corresponding author. Email: Jaelyn.Eberle@Colorado.edu screen-washing sediments from fossil localities in western North America.

Here, we describe the northernmost record of Metatheria – a new genus and species from Upper Cretaceous (lower Maastrichtian) strata in the Prince Creek Formation on the North Slope of Alaska (70° N). Since the first reported discovery of dinosaurs from the North Slope (Clemens & Allison 1985; Brouwers *et al.* 1987; Davies 1987), the number of studies describing the dinosaurian remains from the Prince Creek Formation has greatly increased (e.g. Gangloff *et al.* 2005; Fiorillo *et al.* 2009; Gangloff & Fiorillo 2010; Brown & Druckenmiller 2011; Fiorillo & Tykoski 2012, 2014; Watanabe *et al.* 2013). Noting that none of the species of dinosaurs known from the Prince Creek Formation can be definitively referred to species found in more southerly latitudes, Erickson & Druckenmiller (2011) (and see Mori *et al.* 2015) suggested the presence of a distinct, early Maastrichtian polar faunal province provisionally termed the Paaŋaqtat Province. By contrast, with the exception of brief notes indicating the presence of at least four kinds of fossil mammals in the Prince Creek Formation (Clemens 1991; Clemens & Nelms 1993), no mammals have been formally described from the unit.

In 1989, a joint team from the University of California Museum of Paleontology and University of Alaska Fairbanks collected the first mammalian fossils from the Prince Creek Formation. These are represented by isolated teeth discovered in screen-washed sediments from a locality known as Pediomys Point. More recent field collections by teams from the University of Alaska Fairbanks and the Perot Museum of Nature and Science have considerably augmented the number of specimens from Pediomys Point. These include multiple dentaries, a maxillary fragment, and dozens of isolated molars, premolars and incisors. Although fossils of multituberculates and eutherians (to be described elsewhere) have also been recovered from Pediomys Point, teeth of the new metatherian outnumber the teeth collectively belonging to those taxa by over 2:1.

The Prince Creek Formation metatherian was previously referred to Pediomyidae (Clemens & Nelms 1993; Davis 2007), a well-supported clade of Late Cretaceous metatherians. The oldest records of Pediomyidae *sensu* Williamson *et al.* (2012, 2014) are from upper Santonian rocks of the upper Milk River Formation in southern Alberta and stratigraphically correlative rocks of the Eagle Formation in northern Montana, and from middle or upper Santonian deposits of the John Henry Member of the Straight Cliffs Formation in southern Utah (Eaton & Cifelli 2013; Williamson *et al.* 2014; Davis *et al.* 2016). Pediomyids are abundantly represented in more recent Cretaceous mammalian faunas in northern North America (Williamson *et al.* 2012, 2014). Here, we describe the Prince Creek Formation pediomyid and place the new taxon in phylogenetic context.

History of collecting

In 1961, Robert L. Liscomb, a Shell Oil Company geologist, collected several large isolated bones on a beach along the Colville River upstream from Ocean Point (Fig. 1). The remains, initially believed to be from Pleistocene mammals, were curated into the Shell Oil Company palaeontological collections. Nearly two decades later, these fossils were recognized as belonging to the Dinosauria (see Davies 1987). News of the discovery of dinosaurs at a high northern palaeolatitude generated considerable scientific and public interest. In 1984, US Geological Survey field parties relocated the site, now known as the Liscomb Bonebed. The following year, a field party from the University of California Museum of Paleontology and the University of Alaska Museum in Fairbanks made exploratory excavations at the Liscomb Bonebed and in surrounding fossiliferous deposits. This cooperative research resumed in the summer of 1987 and continued through to 1990. Gangloff (2012) and Fiorillo (2018) present detailed accounts of the early phases of field research and study of the dinosaurs found on the North Slope.

The Pediomys Point locality was discovered in 1988. Andrea Krumhardt, from the University of Alaska Museum, and J. Howard Hutchison and Mark Goodwin, from the University of California Museum of Paleontology, prospected outcrops along the Colville River from Umiat downstream to the area of the Liscomb Bonebed. About 8 km upstream from the bonebed, Hutchison discovered a series of fossiliferous channel deposits exposed in a steep riverbank. A small sample of these deposits was collected and shipped to the University of California Museum of Paleontology for screen-washing and recovery of the vertebrate fossils.

In 1989, a much larger sample of fossiliferous sediments from the Pediomys Point locality was collected and screen-washed on site. In addition to mammalian fossils, primarily isolated teeth, tooth and/or skeletal fossils representing one or more taxa of hadrosaurid, thescelosaurid, and avian and non-avian theropod dinosaurs were recovered as well as fragmentary material of osteichthyans (Clemens & Nelms 1993).

The concentration of small vertebrate fossils at Pediomys Point provided an opportunity to more

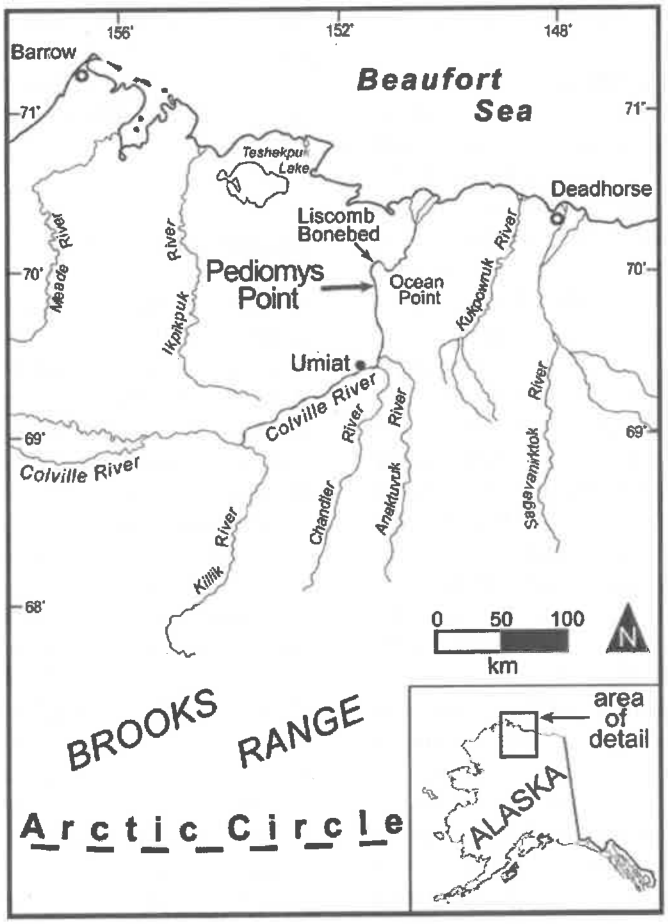

Figure 1. Study area map in northern Alaska, USA showing the location of the Pediomys Point and Liscomb Bonebed localities along the Colville River.

completely assess the composition of a Late Cretaceous, probably 'Edmontonian', terrestrial fauna on the North Slope. Field parties from the University of Alaska Museum collected at the site in 1993 and 2009. In 2006 and 2007 field parties from the Perot Museum of Nature and Science collected samples from Pediomys Point. Groups from both museums worked at Pediomys Point in 2012 and 2014. The collections of pediomyid material from all of these field projects have been combined and serve as the basis for the following report.

Geological setting

The Prince Creek Formation (formerly referred to as the Kogosukruk Tongue of the PCF; Gryc *et al.* 1951; Mull *et al.* 2003) crops out discontinuously along a 110 km segment of the Colville River, between Umiat and Ocean Point, on the North Slope of Alaska (Fig. 2). The Prince Creek Formation represents a tidally influenced continental succession deposited on a low-gradient, Arctic coastal/alluvial plain that accumulated sediments eroded from the geologically young Brooks Range (Mull *et al.* 2003; Flaig *et al.* 2011). The unit is characterized by sandstones, siltstones, organic-rich mudstones, coals, palaeosols and bentonites, deposited in fluvial channels, crevasse-splay complexes and floodplains (Phillips 2003; Flaig *et al.* 2011, 2013). Due to a slight structural dip, the unit becomes progressively younger downriver (to the north).

The Prince Creek Formation ranges from Late Cretaceous (Campanian) to Palaeogene in age (Mull *et al.* 2003). Analyses of palynomorphs (Brouwers *et al.* 1987; Frederiksen 1991; Frederiksen & McIntyre 2000; Flores *et al.* 2007), ostracods (Brouwers & DeDecker 1993) and arenaceous foraminiferans (Brouwers *et al.* 1987) from the upper, vertebrate-bearing portion of the unit near Ocean Point indicate a temporal range from as old as late Campanian to as young as late Maastrichtian, with the majority indicating an early Maastrichtian age.

Palynomorphs from the Kikak-Tegoseak Bonebed (approximately 40 km upriver of Pediomys Point) indicate an earliest Maastrichtian biostratigraphical age (Fiorillo *et al.* 2010). K/Ar and $^{40}Ar/^{39}Ar$ dates from near the Liscomb Bonebed, a hadrosaurid dinosaur-dominated bonebed along the lower Colville River, indicate an age of 68–71 Ma, with a weighted mean of 69 Ma (Conrad *et al.* 1992). Recent $^{40}Ar/^{39}Ar$ analysis of a tuff from this same interval, which is approximately seven km downriver from Pediomys Point, produced an age of 69.2 ± 0.5 Ma (Flaig *et al.* 2014), correlative with the early Maastrichtian. However, slumping and vegetation cover prevents an exact correlation of Pediomys Point with the Liscomb Bonebed. These radioisotopic age determinations suggest the fossil vertebrate-bearing part of the Prince Creek Formation falls within the 'Edmontonian', a poorly defined temporal interval between the Judithian (79–74 Ma) and Lancian (*c.* 67.5–66 Ma) North American Land Mammal Ages (Cifelli *et al.* 2004). In their study of mammalian biochronology of the latest Cretaceous, Cifelli *et al.* (2004) favoured the possibility that future discoveries would facilitate diagnosis of an Edmontonian Land Mammal Age. By contrast, Hunter *et al.* (2010) concluded that the 'Edmontonian' is best seen as a transitional interval between the Judithian and Lancian Land Mammal Ages and is not a distinct unit. The occurrence of a new metatherian in Alaska during this interval adds to the gamma diversity of 'Edmontonian' mammalian faunas but not to increased biochronological resolution.

The Pediomys Point locality is currently located at 70°N, but in the Late Cretaceous, this area may have been as much as 15° latitude farther north, with estimates of palaeolatitude for northern Alaska at 80°–85°N in the Maastrichtian (Witte *et al.* 1987; Besse & Courtillot 1991; Spicer & Herman 2010; Herman *et al.* 2016). Given the high latitude setting, Alaskan Maastrichtian mammalian faunas would have experienced up to ~120 days of winter darkness with ~15 days of spring and autumn twilight (Herman *et al.* 2016). Palaeobotanical proxies of Late Cretaceous Arctic palaeoclimate in northern Alaska indicate a mean annual temperature (MAT) of $6.3 \pm 2.2\,^{\circ}C$ during the early Maastrichtian (70 Ma) (Spicer & Herman 2010).

Pediomys Point is a deposit containing microvertebrate remains that varies from approximately 2 to 15 cm in thickness and hosts disarticulated vertebrate remains ranging in size from small mammal and dinosaur teeth (~0.5 mm maximum dimension) and up to 10 cm long appendicular and axial skeletal elements. The horizon is located at the base of a large channel fill that fines upward from medium- to fine-grained, trough cross-bedded sandstone to inclined heterolithic stratified (HIS) very fine sandstones and siltstones with 1–3 cm thick bedsets (Fig. 2). Ripple cross-lamination is common in the HIS, with fine carbonaceous drapes typically mantling ripple crests. The deposit is lithologically distinctive compared to over- and underlying beds, and consists of interbedded sand and silt (HIS) with iron oxide or siderite nodules up to 0.5 cm in diameter, clay rip-up clasts and an abundance of organic fragments, particularly coalified logs and wood fragments. Jarosite mottles and concretions are common near organic-rich lenses. The fossil-bearing bed is interpreted to be a time-averaged lag deposit that incorporated reworked organic remains, including mammal teeth, from the surrounding fluvial environments.

Material and methods

The holotype and hypodigm were collected by screen-washing and sorting sedimentary matrix from the Pediomys Point locality (Fig. 1) by field parties from the University of California Museum of Paleontology, Perot Museum of Nature and Science, and University of Alaska Museum over multiple field seasons ranging from 1988 to 2014. The holotype and multiple other specimens are housed at the Perot Museum of Nature and Science in Dallas, Texas, while most of the hypodigm is housed at the University of Alaska Museum in Fairbanks. Detailed locality data are on file at the three institutions.

Although recent studies seem to agree that the therian ancestor of eutherians and metatherians had seven or eight postcanine teeth, including four or five premolars and three molars (O'Leary *et al.* 2013; Williamson *et al.* 2014 and references therein), tooth homologies between metatherians and eutherians are controversial. O'Leary *et al.* (2013) hypothesized that metatherians lost the permanent ultimate premolar (P5/p5) and retained the deciduous ultimate premolars DP5/dp5, although they have traditionally been identified as M1/m1 in metatherian dentitions (e.g. Clemens 1966), given their position and morphology. O'Leary *et al.* (2013) further postulated that both metatherians and eutherians lost P3/p3 during evolution, and consequently the metatherian premolar/molar formula in their opinion contains: P1/p1, P2/p2, P4/p4, DP5/dp5, M1/m1, M2/m2, and M3/m3. Williamson *et al.* (2014) accepted these homologies and identified the first tooth in the metatherian molar series as DP5/dp5, rather than M1/m1 as described in older literature. We do not disagree with the model proposed by O'Leary and colleagues (2013), nor does the new Alaskan pediomyid

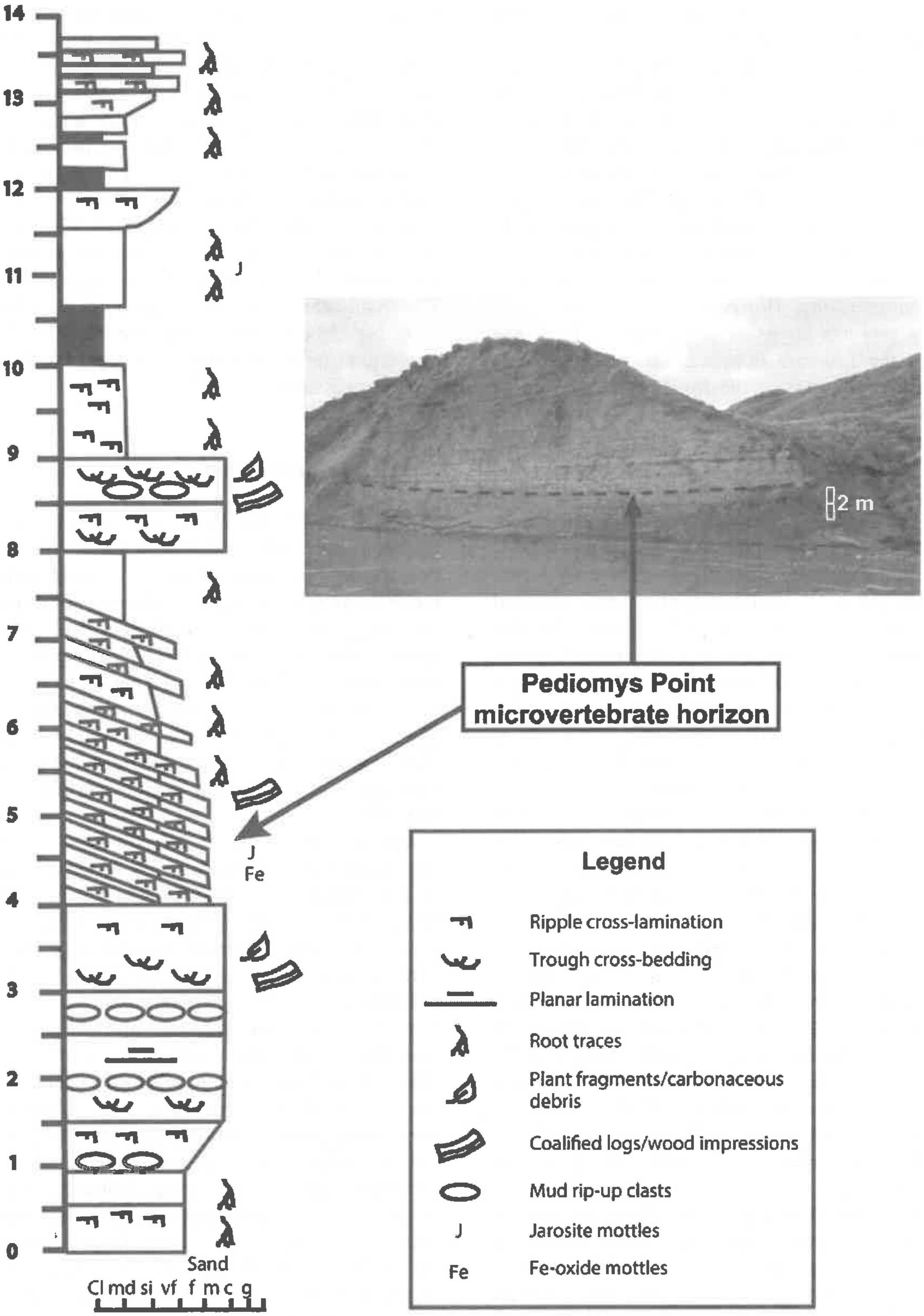

Figure 2. Image and measured stratigraphical section through the Pediomys Point locality showing the position of the microvertebrate horizon from which the fossils of *Unnuakomys hutchisoni* were recovered.

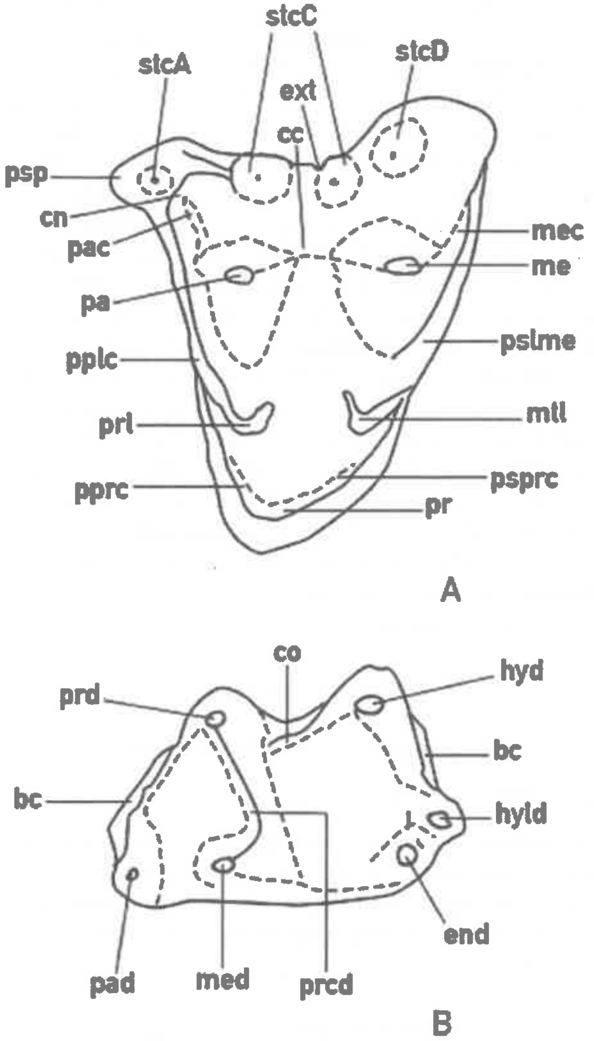

Figure 3. Diagrams of occlusal views of: **A,** an upper molar; and **B,** a lower molar of the Prince Creek Formation pediomyid illustrating dental nomenclature used here. **Abbreviations: bc**, basal cingulid; **cc**, centrocrista; **cn**, carnassial notch; **co**, cristid obliqua; **end**, entoconid; **ext**, ectoflexus; **hyd**, hypoconid; **hyld**, hypoconulid; **me**, metacone; **mec**, postmetacrista; **med**, metaconid; **mtl**, metaconule; **pa**, paracone; **pac**, preparacrista; **pad**, paraconid; **pplc**, preparaconule crista; **pprc**, preprotocrista; **pr**, protocone; **prcd**, protocristid; **prd**, protoconid; **prl**, paraconule; **psmle**, postmetaconule crista; **psp**, parastylar process; **psprc**, postprotocrista; **stc**, stylar cusp.

suggest an alternative hypothesis for tooth homologies than that presented by these authors. Nevertheless, to facilitate comparison with the vast majority of metatherian taxa described in the literature, we use the traditional metatherian tooth designations of P1/p1–P3/p3 and M1/m1–M4/m4 in our description of the new Alaskan metatherian.

The dental nomenclature used here is illustrated in Figure 3. It has long been recognized (e.g. Bensley 1906; Simpson 1936) that the size and number of stylar cusps on their upper molars varies within extant and extinct species of metatherians. The alphabetical designations of the stylar cusps used here are based entirely on their positions relative to the paracone, metacone and ectoflexus (see Clemens 1966). A stylar cusp in the B position can be an exception. The stylocone and paracone linked by a crest, the preparacrista, have been interpreted as forming one of the primary shearing blades on the precursors of the tribosphenic upper molar (Patterson 1956). On tribosphenic molars of therians with this functional unit the stylar cusp in the B position – buccal to the paracone – is hypothesized to be homologous with the stylocone. The stylocone and the preparacrista were greatly reduced if not lost in pediomyids, an autapomorphy of the family.

On M1 through M4 of the new Alaskan metatherian, two cusps are present around the ectoflexus in the stylar cusp C position, the anterior cusp usually distobuccal to the paracone and the posterior cusp located mesiobuccal to the metacone. In his extensive study of the pediomyids, Davis (2007, p. 218) noted, "… the term 'stylar cusp in the C position' will be used instead of 'stylar cusp C' to denote topographic position and not necessarily homology". Significant advances have been made in understanding the developmental patterning of mammalian molariform teeth (e.g. Polly & Mock 2018). In a pioneering study on the development of marsupial molars, specifically those of *Monodelphis*, by Moustakas *et al.* (2011), the heritability of patterns of development of metatherian stylar cusps was not addressed. Given the documented variability in size and number of stylar cusps as well as the lack of developmental or other supporting data, we do not speculate on the possible homologies of the two cusps in the C position on molars of the new Alaskan metatherian with single cusps in this area on the molars of other metatherians. For brevity, the two cusps in the C position on molars of the new Alaskan metatherian are designated the anterior and posterior cusp C. In our phylogenetic analysis we note the absence or number of stylar cusps in the C position and consider the consistent presence of two stylar cusps C on all of its molars as an autapomorphy of the new Alaskan metatherian. Similarly, stylar cusps are designated A and D solely on the basis of their positions on the stylar shelf. Otherwise, dental nomenclature follows Lillegraven (1969) and Davis (2007). Dental measurements were obtained using an

Ehrenreich Photo Optical Shopscope^{TM}, and measurement protocol follows Clemens (1966). Taxonomy follows Williamson *et al.* (2012, 2014).

Moving on from the work of Williamson *et al.* (2012, 2014), here the phylogenetic analysis was conducted using TNT version 1.5 (Goloboff & Catalano 2016). Detailed methods are provided prior to the presentation of the phylogenetic analysis. The character matrix was inputed and organized in Mesquite version 3.51 (Maddison & Maddison 2018).

Micro-CT images of specimens were done on a Zeiss Xradia Versa XRM-520^{TM} X-ray microscope in the CU Biomechanics and Biomimetics Laboratory, and 3D reconstructions were generated from micro-CT images using Dragonfly Pro software (Object Research Systems, ORS, Inc.) and conventional thresholding methods. Scanning electron microscope (SEM) images were completed in the Nano Characterization Facility (NCF). Both laboratories are in the Engineering School at the University of Colorado at Boulder.

Institutional abbreviations

DMNH, Dallas Museum of Natural History (= Perot Museum of Nature and Science), Dallas, Texas, USA; **UAMES**, University of Alaska Museum, Fairbanks, Alaska, USA; **UALVP**, University of Alberta Laboratory of Vertebrate Palaeontology; **UCMP**, University of California Museum of Paleontology, Berkeley, California, USA.

Anatomical abbreviations and measurements

L, left tooth; **R**, right tooth; **P/p**, upper/lower premolar; **M/m**, upper/lower molar; **Wtri**, width of trigonid; **Wtal**, width of talonid.

Systematic palaeontology

Metatheria Huxley, 1880
'Didelphimorphia' Gill, 1872
Pediomyoidea Simpson, 1927
Pediomyidae Simpson, 1927

Remarks. The Pediomyidae, named by Simpson (1927), is composed of a diverse group of small- to medium-sized, opossum-like marsupials that lived in North America during the Late Cretaceous (Aquilan through Lancian NALMA; Kielan-Jaworowska *et al.* 2004; Davis 2007; Williamson *et al.* 2012, 2014; Davis *et al.* 2016). Davis (2007) presented a thorough historical review of the use of suprageneric nomina based on *Pediomys*. Whereas Davis defined the clade based on a list of included genera, specifically *Pediomys*, *Leptalestes* and *Protolambda* (=*Aletridelphys*), more recently Williamson *et al.* (2012, 2014) used a phylogenetic definition (stem-based) in which the Pediomyidae is the most inclusive clade that contains *Pediomys elegans*, but not *Peradectes elegans*, *Herpetotherium fugax*, *Didelphis virginiana* or *Didelphodon vorax*. In contrast to Davis's (2007) phylogeny, the phylogenetic analysis of Williamson *et al.* (2012, 2014) found the Aquilan taxa *Iqualadelphis* and *Aquiladelphis* to be members of Pediomyidae, in addition to *Pediomys*, *Leptalestes* and *Protolambda*. We follow the interpretation of Williamson *et al.* (2012, 2014). Below, we describe a new genus and species of pediomyid from the Late Cretaceous (early Maastrichtian) of the North Slope of Alaska. Although initially tentatively identified as a species of *Pediomys* (Clemens 1991), our analysis of the new Alaskan metatherian shows it to be sufficiently different in size and morphology from *P. elegans* and other pediomyid genera to warrant its placement in a new genus.

Genus ***Unnuakomys*** gen. nov.

Type species. *Unnuakomys hutchisoni* sp. nov.

Diagnosis. As for the type species.

Derivation of name. 'Unnuak' (pronounced Oo-noo-ok), Iñupiaq word for night, in reference to the several months of night or darkness the Prince Creek fauna endured during the long polar winters, and 'mys', Greek for mouse.

Unnuakomys hutchisoni sp. nov.

(Figs 4, 5A–C, E, F, 6)

Diagnosis. Pediomyid metatherian whose molars are two-thirds to three-quarters the size of *Pediomys elegans*; upper molars with transverse width greater than anteroposterior length, twinned anterior and posterior stylar cusps in the C position flanking the deepest part of the ectoflexus, straight centrocrista, small para- and metaconules, metacone somewhat taller than paracone on M2 and M3, and carnassial notch on M3 (variably on M2) separating the labial end of the preparacrista from stylar cusp A; p2 and p3 uninflated and smaller than m1; on m1–m3, talonid slightly wider than trigonid, metaconid taller than paraconid, entoconid larger than hypoconulid, and cristid obliqua contacts the posterior trigonid wall labial to protocristid notch, at the midline of the protoconid. Differs from other pediomyids in smaller size and the occurrence of well-developed anterior and posterior stylar cusps in the C position flanking the deepest part of the

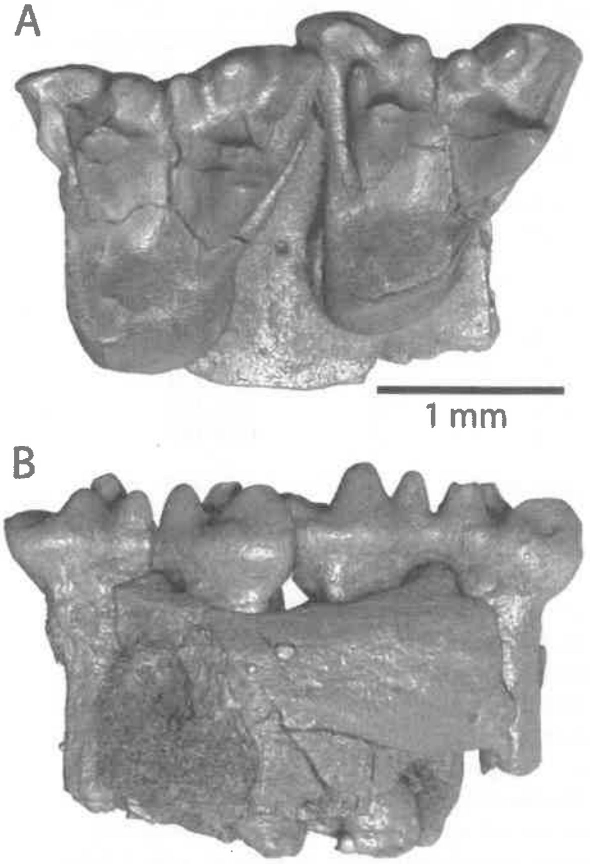

Figure 4. *Unnuakomys hutchisoni* from Pediomys Point locality. Micro-CT scans of DMNH 21353 (holotype), left maxillary fragment with M2–M3, in **A**, occlusal; and **B**, labial views. Scale bar equals 1 mm.

ectoflexus. M2 and M3 differ from M2s and M3s of *Pediomys*, *Protolambda*, and *Leptalestes* in having a more labial parastylar process and stylar cusp A, better developed anterior stylar shelf and preparacrista, carnassial notch on M3 (variably on M2), and a better developed ectoflexus. Further differs from *Pediomys* and *Protolambda* in having small conules. Lower molars differ from *Pediomys* in that cristid obliqua contacts the trigonid more lingually. Differs from *Iqualadelphis lactea* in lacking stylar cusp B, presence of two stylar cusps in the C position, and paraconule and metaconule are approximately equidistant between the protocone and the paracone and metacone, respectively.

Derivation of name. Latinization of 'Hutchison', in honour of J. Howard Hutchison, long-time Arctic palaeontologist, colleague and friend, who discovered the Pediomys Point locality.

Holotype. DMNH 21353, a left maxillary fragment containing M2 and M3 (Figs 4, 5A).

Hypodigm. UAMES 34430, RM1; UAMES 34471, LM1; UAM 34450, nearly complete LM1; UAMES 34474, M1 labial fragment; UAMES 34435, RM2; UAMES 34458, RM2; UAMES 34469, RM2; UAMES 34472, LM2; UAMES 34422, LM2; UAMES 34473, LM2; DMNH 21362, RM3; UAMES 34409, RM3; UAMES 34428, RM3; UAMES 34452, LM3; UAMES 34427, RM3; UAMES 34434, LM3; UAMES 34454, LM3; UAMES 34498, LM3; UAMES 34470, LM4; UAMES 34457, LM4; UAMES 34421, LM4; UAMES 35312, incomplete RMX; UAMES 35327, left dentary with p2, incomplete p3, and m1–m3; DMNH 21349, left dentary fragment with p2–p3; UAMES 34488, left dentary fragment with p2; UAMES 34486, Lp3; UAMES 35326, Lp3; UAMES 34449, Rm1; UAMES 34432, Rm1; UAMES 35310, Rm1; UAMES 34420, Rm1; UAMES 34449, Rm1; UAMES 34405, Rm2/m3; UAMES 34406, Rm2/m3; UAMES 34424, Lm2/m3; UAMES 34455, Lm2/m3; UAMES 34502, Rm2/m3; UAMES 34509, Rm2/m3; UAMES 34510, Rm2/m3; UAMES 34462, Lm2/m3; UAMES 34463, Rm2/m3; UAMES 34465, Rm2/m3; UAMES 34468, Rm2/m3; UAMES 34440, Rm2/m3; UAMES 34499, Rm2/m3; UAMES 35308, Lm2/m3; UAMES 34415, Rm2/m3; UAMES 34466, Rm2/m3; UAMES 34467, Lm2/m3; UAMES 34410, Rm2/m3; UAMES 35313, Lm2/m3; UAMES 35317, Lm4?; UAMES 35320, Lm4?; UAMES 34423, Rm4; UAMES 34453, Rm4; UAMES 34508, Rm4; UAMES 35314, Lmx trigonid; UAMES 35315, Rmx talonid; UAMES 35323, Rmx talonid.

Type locality. Pediomys Point locality, Prince Creek Formation, Colville River, northern Alaska, USA (Upper Cretaceous, lower Maastrichtian). Exact locality information is on record with the Bureau of Land Management Arctic Field Office in Fairbanks, Alaska, the University of Alaska Museum, the University of California Museum of Paleontology, and the Perot Museum of Nature and Science.

Occurrence. Known only from Upper Cretaceous (lower Maastrichtian) strata of the Prince Creek Formation.

Description

The holotype, DMNH 21353, is an incomplete maxilla containing M2–M3 (Figs 4, 5A). The hypodigm includes dentaries with premolars and molars, as well as a large number of isolated lower premolars and upper and lower molars. Molars of *Unnuakomys hutchisoni* are two-thirds to three-quarters the size of molars of *Pediomys elegans* (dental measurements are found in Tables 1–3).

Table 1. Dental measurements (in mm) of upper molars of *Unnuakomys hutchisoni* gen. et sp. nov.

Position	N	Observed range	Mean
M1			
A-P Length	3	1.31–1.52	1.42
Width	2	1.40–1.64	1.52
M2			
A-P Length	5	1.42–1.61	1.51
Width	5	1.72–2.01	1.85
M3			
A-P Length	9	1.33–1.55	1.48
Width	9	1.63–1.87	1.81
M4			
A-P Length	3	1.13–1.27	1.22
Width	3	1.57–1.64	1.61

Table 2. Dental measurements (in mm) of lower premolars and molars in UAMES 35327, a dentary of *Unnuakomys hutchisoni* gen. et. sp. nov.

Position	A-P Length	Width/WTri	WTal
p2	1.05	0.51	———
m1	1.21*	0.71*	0.80
m2	1.49	0.94	1.04
m3	1.49	1.02	1.09
m4	—	0.94	0.92

*minimum measurement due to incompleteness.

Table 3. Dental measurements (in mm) of lower premolars and molars of *Unnuakomys hutchisoni* gen. et. sp. nov.

Position	N	Observed range	Mean
p2			
A-P Length	2	1.03–1.05	1.04
Width	2	0.48–0.52	0.50
p3			
A-P Length	3	1.12–1.15	1.13
Width	3	0.55–0.59	0.57
m1			
A-P Length	5	1.21–1.34	1.26
WTri	5	0.64–0.73	0.69
WTal	5	0.69–0.80	0.74
m2/m3			
A-P Length	21	1.37–1.55	1.46
WTri	21	0.73–1.02	0.88
WTal	21	0.82–1.09	0.95
m4			
A-P Length	6	1.33–1.47	1.41
WTri	7	0.75–0.94	0.85
WTal	7	0.71–0.92	0.79

Upper molars

The molars are three-rooted. The M1 is smaller than M2 and M3 (which overlap in size), and M4 is the smallest of the four. Upper molars at each position are described below.

M1. Whereas the holotype DMNH 21353 lacks M1, an isolated complete and two incomplete M1s have been recovered from Pediomys Point. UAMES 34471 (Fig. 5B), a worn LM1, has a transverse width that slightly exceeds its length. On M1s of *Unnuakomys hutchisoni*, the parastylar process is large, projects anteriorly, and is either connected to the paracone by a low preparacrista (UAMES 34471, 34450; Fig. 5B, C) or is isolated (UAMES 34474). The stylar cusp A on M1 is anterior and slightly lingual to the apex of the paracone. M1 of *U. hutchisoni* has a distinct cusp posterolabial to the paracone. We agree with Davis (2007) that this cusp is not a stylar cusp B because it is located slightly posterior to the paracone. As noted above, for brevity we refer to this cusp as an anterior stylar cusp C, which is followed by another, similarly sized cusp here referred to as posterior stylar cusp C. A very shallow depression, the ectoflexus, is flanked by the anterior and posterior stylar cusp Cs.

Posterior to the posterior stylar cusp C is a long, blade-like stylar cusp D, the largest of the stylar cusps on M1. The connection of the posterior cusp C with cusp D varies. On UAMES 34471, these cusps are separated by a deep notch, while on UAMES 34474 and 34450, the posterior cusp C is barely delimited from cusp D. Although wear on UAMES 34471 obscures the relative heights of the paracone and metacone, on UAMES 34474 (an incomplete M1), these cusps are subequal in height and connected by a straight centrocrista. The postmetacrista is high and blade-like.

On the single, nearly complete M1 in which the conules are not worn off (UAMES 34450; Fig. 5C), a small though distinct paraconule is present, with a preparaconule crista extending labially from it to join the lingual side of the parastylar process. An internal conular crista extends from the paraconule to the base of the paracone. Similarly small, the metaconule has an internal conular crista extending from it to the base of the metacone. The postmetaconule crista extends labially, forming a narrow cingulum along the posterior wall of the metacone, but dying out before reaching the posterolabial corner of the tooth. The paraconule and metaconule on UAMES 34450 are relatively small, and they lie approximately equidistant between the protocone and the paracone and metacone, respectively. A short, weak cingulum occurs on the anterior face of the protocone, but there is no posterolingual cingulum. On UAMES 34471, wear has eroded the apices of the paracone and metacone as well as the crest of the postmetacrista. The blunted protocone, pre- and postprotocristae, and the conules form a continuous wear surface around the trigon basin.

M2. The M2s of *Unnuakomys hutchisoni* differ from M1s in their greater transverse width and the occlusal outline of the labial margin of their crowns (see Fig. 4A, 5A). Unlike M1s, which have a relatively straight labial margin with a very shallow ectoflexus, the labial

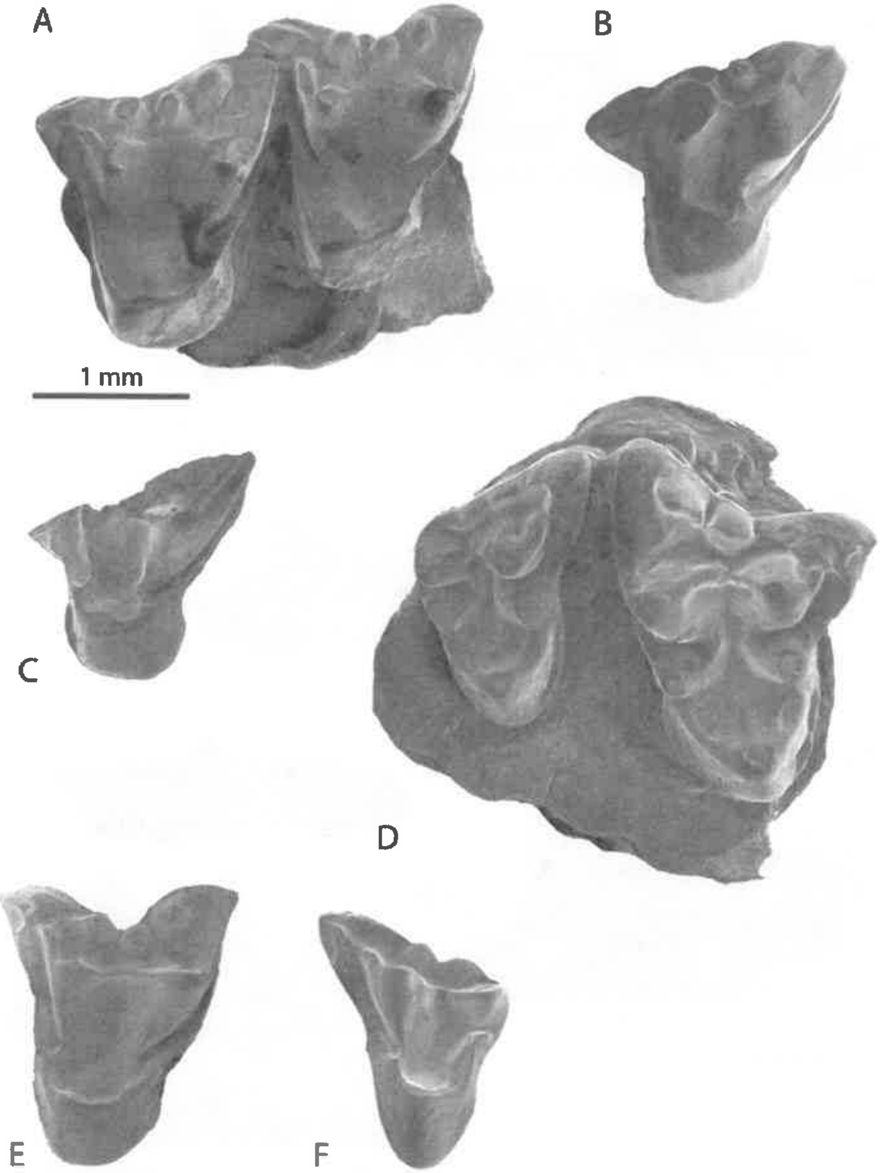

Figure 5. *Unnuakomys hutchisoni* from the Pediomys Point locality in the Prince Creek Formation, AK and *Pediomys elegans* from the Lance Formation, WY. SEM images of **A,** DMNH 21353 (holotype of *U. hutchisoni*), left maxillary fragment with M2–M3, in occlusal view; **B,** UAMES 34471, LM1 of *U. hutchisoni* in occlusal view; **C,** UAMES 34450, LM1 of *U. hutchisoni* in occlusal view; **D,** UCMP 47049, right maxillary fragment with M3–M4 of *P. elegans* in occlusal view; **E,** UAMES 34434, LM3 of *U. hutchisoni* in occlusal view; and **F,** UAMES 34470, LM4 of *U. hutchisoni* in occlusal view. Scale bar equals 1 mm.

margin of M2 is divided into two symmetrical lobes. Their outer margins meet at a distinct ectoflexus. Anterolabial to the apex of the paracone, a blade-like parastylar process projects anteriorly, connected to the former by a preparacrista. Presence of a carnassial notch between the end of the preparacrista and the stylar cusp A is variable on M2s, with some teeth (e.g. UAMES 34469, DMNH 21353) lacking it, whereas on other teeth it is narrow (UAMES 34435). Labial and slightly posterior to the apex of the paracone is an anterior stylar cusp C, which is followed by a similar-sized cusp, the posterior stylar cusp C. These two cusps flank the deepest part of the ectoflexus. More posteriorly along the stylar margin is a slightly larger stylar cusp D. On unworn M2s and M3s, the metacone is somewhat taller than the paracone. A long continuous postmetacrista originates near the apex of the metacone and is slightly concave as it slopes down to the posterolabial corner of

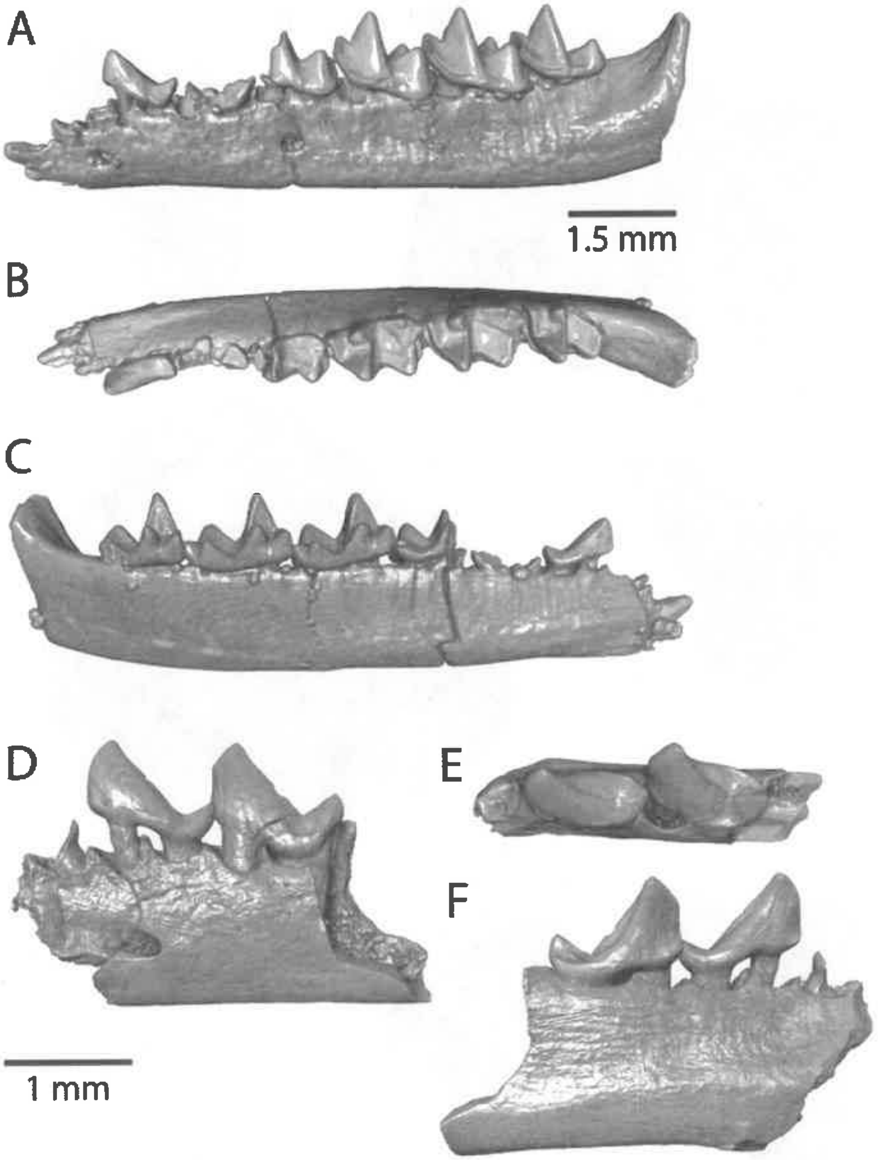

Figure 6. *Unnuakomys hutchisoni* from Pediomys Point locality. Micro-CT scans of UAMES 35327, left dentary in **A**, labial; **B**, occlusal; and **C**, lingual views; DMNH 21349, left dentary fragment with p2–p3 in **D**, labial; **E**, occlusal; and **F**, lingual views. Note: A–C share a scale (under A), and D–F share a scale (under D).

the tooth. The conules are heavily worn on most of the M2s. On two relatively unworn specimens (UAMES 34435, 34458), the conules are small and located approximately equidistant between the protocone and the paracone and metacone. The internal conular cristae and postprotocrista are similar in development to those on M1. The preparaconule crista on the less worn M2s extends labially as in M1, but widens just lingual to the parastylar process to form a shelf. A short, weak cingulum occurs on the anterior face of the protocone on M2 of the holotype of *U. hutchisoni* (DMNH 21353; Fig. 4A, 5A) as well as the other M2s, but all lack a cingulum on the posterior face of the protocone.

M3. The M3 on the holotype and several isolated M3s overlap with the M2s in their length and width measurements. However, the M3s differ from M2s in having a deeper ectoflexus and a large carnassial notch separating the labial end of the blade-like preparacrista from a large, anteriorly-projecting parastylar process that supports a large stylar cusp A. On two M3s (UAMES 34452, 34427), a tiny cuspule is present posterior to the stylar cusp A, connected to it by a short ridge. This cuspule is neither directly labial to the paracone nor at the labial extreme of the preparacrista. Following Davis (2007) it is therefore not interpreted as a stylar cusp B. As in M1–M2, large anterior and posterior stylar cusp Cs flank the deepest part of the ectoflexus; on some M3s the anterior stylar cusp C is slightly larger than the posterior one. In unworn M3s of *Unnuakomys hutchisoni*, the posterior stylar cusp C is separated by a notch from an ovate cusp D (DMNH 21353 holotype), although with wear their bases fuse (e.g. UAMES 34454, 34409). Stylar cusp D is variable in size, ranging from small and lower than posterior stylar cusp C (UAMES 34427) to larger than posterior stylar cusp C on most M3s (e.g. UAMES 34454, 34434). On one tooth (UAMES 34434; Fig. 5E), there are two small cusps in the D position; their bases are fused, and the anterior of the two has its base fused to the posterior stylar cusp C. As in M2s, the M3 paracone is lower than the metacone, and they are linked by a straight centrocrista. On DMNH 21353 (holotype; Figs 4A, 5A), the centrocrista is worn down, leaving an elongate wear facet; however, on UAMES 34434 (Fig. 5E), a straight centrocrista is preserved. Lingual to these cusps, the morphology of the crown shows few differences from those of the more anterior molars. On all but one of the M3s, the conules are worn off. On UAMES 34498, the paraconule and metaconule are tiny and located equidistant between the low protocone and the paracone and metacone. The protocone bears small, irregular depressions or a short, narrow cingulum on its anterior face.

M4. The outline of M4 of *Unnuakomys hutchisoni* approximates an isosceles triangle (Fig. 5F). The three M4s from Pediomys Point bear a large, anterolabially projecting parastylar process and anterior and posterior stylar cusp Cs, but the posterior end of the stylar shelf is greatly reduced and there is no stylar cusp D. Labial to the preparacrista and paracone, the surface of the stylar shelf forms a shallow basin. The paracone is larger and taller than the metacone. The protocone is anteroposteriorly narrower than the protocone on M1–M3. While the metaconule is worn off all three M4s, UAMES 34470, a LM4, bears a tiny paraconule that is located approximately midway between the protocone and paracone (Fig. 5F). M4 of *U. hutchisoni* has a long preprotocrista that extends labially to the lingual margin of the parastylar process, forming a narrow cingulum along the anterior side of the paracone. On UAMES 34470, a notch occurs between the labial end of the postprotocrista and the metacone (Fig. 5F). Only one of the three M4s bears a short, weak cingulum on the anterior face of the protocone; all three lack a cingulum on the posterior face of the protocone.

Dentary

UAMES 35327 and DMNH 21349 are a left and incomplete dentary, respectively (Fig. 6). UAMES 35327 also preserves the roots of p1, an incomplete canine, p2, an incomplete p3, and m1–m3. Two mental foramina occur on UAMES 35327, one ventral to the p1 and the second ventral to the trigonid of m1 (Fig. 6A). DMNH 21349 preserves p2–p3. A mental foramen is ventral to p2 (Fig. 6D).

Canine

The incomplete canine on UAMES 35327 indicates that this tooth was relatively small and projected anteriorly.

Premolars

All three premolars are two-rooted. The p2 and p3 are smaller and narrower than the molars, bearing a tall protoconid with a narrow ridge running posteriorly from it to a central cusp on the talonid. The p2 differs from p3 in being slightly smaller and narrower, with a weaker posterior ridge and a smaller talonid cusp (Fig. 6D–F).

Lower molars

Whereas the majority of specimens from Pediomys Point are isolated teeth, UAMES 35327 contains an incomplete m1, complete m2 and m3, and a m4 missing its posterolingual corner (Fig. 6A–C). With regard to relative size, m1 is the smallest and narrowest molar, m2 is slightly narrower than m3 (the largest of the molars), and m4 is smaller than m3. Morphologically, the lower molars closely resemble one another. The metaconid is slightly taller than the paraconid, which has a shallowly concave anterolabial wall; both are lower than the protoconid and aligned anteroposteriorly with the entoconid. On the rim of the broad talonid basin, the hypoconulid and higher entoconid are twinned, and the hypoconid is lower and well separated labially. The cristid obliqua contacts the posterior wall of the trigonid labial to the notch in the protocristid, approximately at the midline of the protoconid.

On all molars, basal cingulids are present on the anterior labial face of the trigonid and the posterior wall of the talonid. There is variable development of a continuous basal cingulid labial to the protoconid and hypoconid. On some teeth, there is a rugosity but not a continuous cingulid, while others bear a continuous labial cingulid (e.g. UAMES 35317). All of the lower molars have two roots. Based on comparison to UAMES 35327 in the framework of characters that typically distinguish the lower molars of Cretaceous pediomyids and peradectids, the isolated lower molars from

Pediomys Point have been placed into three categories – m1, m2/m3 (which are very similar and challenging to differentiate when not in a dentary), and m4, briefly discussed below.

m1. The m1 is the smallest of the lower molars. It is characterized by a more anteriorly placed paraconid (compared with the other molars) that is well separated from the metaconid, which results in the trigonid being relatively longer than the talonid. The trigonid also is narrower than the talonid. On the four isolated m1s from Pediomys Point, the labial basal cingulid is not continuous.

m2/m3. Unlike the m1s, the paraconid and metaconid on m2s and m3s are relatively closely approximated. On UAMES 35327, which bears both m2 and m3, the m3 is wider, the paraconid and metaconid appear slightly closer to one another, and the protoconid is farther from the metaconid than on m2, but otherwise the teeth are very similar. Consequently, isolated m2s and m3s cannot be definitively distinguished from one another. Anterior and posterior basal cingulids are present on all of the teeth, but development of the labial basal cingulid is variable.

m4. Based on an incomplete m4 (missing its posterolingual corner) on UAMES 35327, the m4 is narrower than the m3 and probably slightly shorter, although this cannot be definitively confirmed due to incompleteness of its talonid. Of the seven isolated teeth identified as m4s, all have a trigonid that is slightly wider than the talonid, in contrast to the other molars. However, like the m2s and m3s, the m4s have a closely approximated paraconid and metaconid, and their lengths overlap with the m2s/m3s. UAMES 35317 and 34453 have a continuous labial basal cingulid, while on the other m4s, the labial basal cingulid is discontinuous around the hypoconid.

Remarks

In his revision of 'pediomyid' marsupials, Davis (2007) included dental characters of *Unnuakomys hutchisoni*, and dubbed it the Prince Creek 'pediomyid' in his phylogenetic analysis. His analysis suggested it was closely related to *Pediomys elegans*. Our analysis, presented below and based on more material, provides further clarification on the phylogenetic position of *Pediomys* and indicates that *U. hutchisoni* does not have a sister-group relationship to the former.

The larger sample of premolars and molars available now shows that the postcanine dentition of *Unnuakomys hutchisoni* is smaller than any other documented pediomyid. All of the upper molars of *U. hutchisoni* have anterior and posterior stylar cusp Cs. Molars of *P. elegans* have a large cusp in the posterior stylar cusp C position. Rarely, a cusp is present in the anterior stylar cusp C position. When present, this cusp is much smaller than its counterpart in *U. hutchisoni* (Fig. 5D). In contrast to both *P. elegans* and *U. hutchisoni*, *Protolambda* and *Leptalestes* lack a stylar cusp C (Davis 2007). Unlike *U. hutchisoni*, the parastylar processes and stylar cusp A on M2 and M3 of *P. elegans* and *Protolambda* are directly anterior to the paracone, not anterior and labial. The anterior stylar shelf on M2 and M3 of *U. hutchisoni* is broader and better developed than on M2 and M3 of *P. elegans*, *Protolambda* and *Leptalestes*. Further, M4s of *U. hutchisoni* have an anterolabially projecting parastylar process that is larger than on M4s of *P. elegans* (Fig. 5D) and *Protolambda* (Davis 2007, fig. 11). On M1 through M3 of *P. elegans*, *Protolambda* and *Leptalestes*, the ectoflexus of the molars is shallower and not as distinct as it is on their counterparts in *U. hutchisoni*. In contrast to *U. hutchisoni*, the paraconules and metaconules are relatively larger on molars of *P. elegans* and *Protolambda*, and they are closer to the paracone and metacone, respectively, than to the protocone (Davis 2007; JE pers. obs.). Like *U. hutchisoni*, *Leptalestes* has small conules, but they are closer to the protocone, as opposed to *U. hutchisoni* molars wherein the conules are approximately equidistant between the protocone and paracone and metacone.

In comparison to *Unnuakomys hutchisoni*, lower molars of *Pediomys elegans* have distinctly larger talonid basins. Further, on molars of *P. elegans* the cristid obliqua is more labially directed, reaching the posterior wall of the trigonid at nearly the labial side of the protoconid. On lower molars of *Leptalestes* and *Protolambda*, the cristid obliqua meets the posterior wall of the trigonid labial to the protocristid notch, at the midline of the protoconid (Davis 2007), as in *U. hutchisoni*.

M2 and M3 of *Unnuakomys hutchisoni* have a relatively well-developed anterior stylar shelf that is unusual for pediomyids and reminiscent of '*Alphadon*' and lower Cretaceous (Albian) primitive metatherian *Kokopellia*. In fact, in his diagnosis of Pediomyidae, Davis (2007) indicated that upper molars have a suppressed anterior stylar shelf. However, the anterior stylar shelf on molars of *U. hutchisoni* is reduced compared to molars of '*Alphadon*' and *Kokopellia*, wherein the anterior and posterior stylar shelves are comparable to one another in development. Molars of the Aquilan *Iqualadelphis lactea*, shown to be a primitive pediomyid in the phylogenetic analysis of Williamson *et al.* (2012, 2014), also have an anterior stylar shelf that is better developed than that of other pediomyids (Fox 1987; Davis 2007), but reduced relative to *Kokopellia*. In comparing the M3 on the holotype of *U. hutchisoni* (DMNH 21353) with UALVP 29676, a left maxillary fragment of *I. lactea* with a complete M3 (see Johanson 1993, fig. 1D), the anterior stylar shelf is comparable in development in these two M3s. The genus '*Alphadon*', found to be paraphyletic in recent phylogenetic analyses (Williamson *et al.* 2012, 2014), shows several differences from *U. hutchisoni* in molar morphology, including presence of a deeper ectoflexus, large stylar cusp B, preparacrista that runs between the stylar cusp B and the paracone, the paracone and metacone are subequal in height, and large conules that are closer to the paracone and metacone than to the protocone (Clemens 1966; Johanson 1996; Williamson *et al.* 2012, appendices 1, 2). Therefore, the development of the anterior stylar shelf in *U. hutchisoni* and *I. lactea* appears morphologically intermediate between the primitive, unreduced condition on molars of basal metatherians such as *Kokopellia* and that of more derived Pediomyidae, as opposed to indicating any close evolutionary ties to '*Alphadon*'.

Phylogenetic analysis

Previous studies have referred *Unnuakomys hutchisoni* to the genus *Pediomys*, and closely related to *P. elegans* (Clemens & Nelms 1993; Clemens 1992; Davis 2007, fig. 24, identified as Prince Creek Pediomyid). In light of extensive new data described here from both the upper and lower dental elements of *U. hutchisoni*, we re-examine the systematic relationships of this taxon. Specifically, we reassess the referral of *Unnuakomys* to Pediomyidae *sensu* Williamson *et al.* (2012, 2014) and test its sister-group relationships within the clade, particularly with respect to *P. elegans*. *Unnuakomys hutchisoni* was scored into the character matrix of Williamson *et al.* (2014), the most recent comprehensive phylogenetic analysis of Cretaceous and early Palaeogene metatherians. Their analysis includes 95 taxa (four of which are non-metatherian) and 83 dental characters, and uses the Jurassic basal eutherian *Juramaia sinensis* as the outgroup. As noted by Williamson *et al.* (2014), the majority of Cretaceous and early Palaeogene metatherians are known only from teeth, so only dental characters were included in the analysis. *Unnuakomys hutchisoni* was scored for the 83 dental characters used in the analysis of Williamson *et al.* (2014; see Supplemental Appendix 1). Characters were treated as unweighted and 19 characters are additive. The data matrix (see Supplemental material) was analysed using TNT version 1.5 (Goloboff & Catalano 2016). To ensure consistency with the analysis of Williamson *et al.* (2014), the matrix was first analysed under the 'New Technology Search' with Sectorial Search, Rachet, Drift, and Tree Fusing, finding the minimum length tree 10 times. The 19 retained trees were then analysed under the 'Traditional Search' with tree bisection reconnection (TBR) branch-swapping. Bremer support values were calculated following the protocol of Williamson *et al.* (2014) that uses a pool of 30,000 suboptimal trees of up to 10 steps longer than the shortest trees. Williamson *et al.* (2014) used TNT version 1.1 for their phylogenetic analysis, whereas we used TNT version 1.5. There are some differences in Bremer support values that are, in part, due to the different versions of TNT.

Results

The analysis returned 270 most parsimonious trees of 507 steps (consistency index = 0.207; retention index = 0.701). The time-calibrated phylogeny of the Pediomyidae based on the strict consensus tree is shown in Figure 7. The entire strict consensus of the 270 trees can be found in Supplemental Appendix 3. The low ensemble consistency index suggests considerable homoplasy in the dataset, probably a result of the large amounts of missing data for some taxa and the nearly 1:1 ratio of taxa to characters (Williamson *et al.* 2014). On the whole, the topology is similar to that of Williamson *et al.* (2014), save for the inclusion of *Unnuakomys hutchisoni* within those authors' Pediomyidae. A notable difference in our results is that the clade containing the Lancian North American species *Glasbius intricatus* and *G. twitchelli*, and the early Paleocene Bolivian species *Roberthoffstetteria nationalgeographica*, was found to be the sister group of Pediomyidae. Characters that unite *Glasbius* spp. + *Roberthoffstetteria* with the Pediomyidae included the shape of stylar cusp D, the buccal extension of the postprotocrista beyond the base of the metacone, the distal expansion of the protocone, and, on the lower molars, the talonid is either subequal to, or wider than, the trigonid, and the cristid obliqua contacts the posterior trigonid wall labial to the protocristid notch (the last three characters were also noted by Davis 2007).

Here, we focus our discussion on the intragroup relationships of *Unnuakomys hutchisoni* within Pediomyidae (Fig. 7). Notably, our results do not recover a sister-group relationship between *U. hutchisoni* and *Pediomys elegans*, in contrast to the analysis of Davis (2007). Our topology indicates there is a basal split in the pediomyid tree, with *U. hutchisoni* as sister to the Aquilan species *Iqualadelphis lactea*, a clade that is in turn sister to another Aquilan taxon, ?*Aquiladelphis laurae*. Here, *P.*

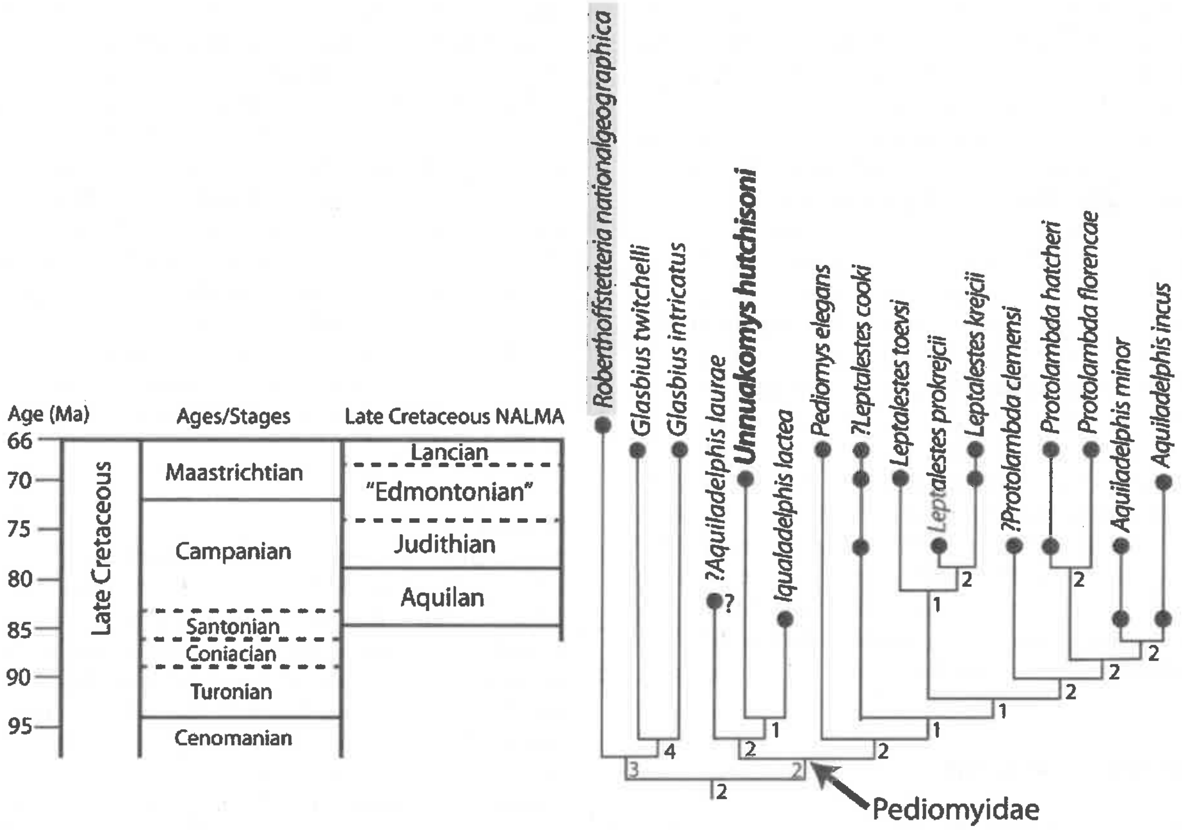

Figure 7. Temporally calibrated phylogeny of the Pediomyidae and its outgroup, based upon the strict consensus of 270 trees of 507 steps in Supplemental Appendix 3. Numbers at each node correspond to Bremer branch supports calculated from a pool of 30,000 suboptimal trees of up to 10 steps longer than the shortest trees. The South American polydolopimorphan *Roberthoffstetteria nationalgeographica* (shaded) is of early Paleocene age. It is known from a fauna of Tiupampan South American Land Mammal Age, which is approximately correlative with the Puercan 3 and Torrejonian 1 NALMAs (Woodburne *et al.* 2014; Goin *et al.* 2016). Timescale after Gradstein *et al.* (2012); temporal boundaries and durations of NALMA from Cifelli *et al.* (2004). Pattern of branching is from our phylogenetic analysis; the timing of branching prior to the Aquilan is not documented in the fossil record.

elegans is recovered as the basal member of a larger clade that includes species of *Leptalestes*, *Protolambda* and *Aquiladelphis*. However, Bremer support for this topology is low (see Figure 7), in part due to large amounts of missing data. For example, both *I. lactea* and *?A. laurae* are known only from isolated upper molars. Therefore, our results should be considered with caution until more material of poorly represented taxa is recovered.

The characters uniting *Iqualadelphis lactea* and *Unnuakomys hutchisoni* are largely plesiomorphic with respect to other pediomyids. In both species, development of the anterior stylar shelf, ectoflexus and preparacrista appears morphologically intermediate between basal metatherians such as *Kokopellia* and the other pediomyids. Both *I. lactea* and *U. hutchisoni* have a carnassial notch along the preparacrista and flat to concave buccal faces on the paracone and metacone, whereas other pediomyids lack a carnassial notch along the preparacrista and the buccal face of the paracone is convex, while that of the metacone is flat. However, in contrast to *U. hutchisoni*, *I. lactea* lacks a cusp in the stylar cusp C position, and retains a stylar cusp B.

?Aquiladelphis laurae is based on two upper molars (?M2 and M4) from Upper Cretaceous (?lower Campanian) rocks in Cedar Canyon, south-west Utah that Eaton (2006) described and questionably assigned to *Aquiladelphis*. *?Aquiladelphis laurae* suffers from considerable missing data (i.e. it was scored for only 34 of the 83 dental characters by Williamson *et al.* 2014). However, Eaton (2006) indicated that the presence of an anterior cingulum on the molar protocone, a character shared with most (but not all) upper molars of *U. hutchisoni*, made referral of *?A. laurae* to *Aquiladelphis* questionable. The ?M2 also appears to have two cusps in the stylar cusp C position – a larger one positioned just posterior to the deepest part of the shallow ectoflexus and a tiny cusp directly anterior to the larger cusp, between it

and the stylar cusp B (see Eaton 2006, fig. 13C, D). Eaton (2006) initially identified this tiny cusp as the posterior of two stylar cusps B, but given its position posterolabial to the paracone apex and no connecting preparacrista, we suggest it is an anterior stylar cusp C, an interpretation also made by Williamson *et al.* (2014, supplementary material 2). It should be noted, however, that the ?M2 of ?*A. laurae* is worn, making comparisons with other taxa challenging. ?*Aquiladelphis laurae*, *I. lactea* and *U. hutchisoni* also share other plesiomorphic characters, such as a better developed preparacrista and internal cristae than other pediomyids, and a moderately developed stylar cusp D. ?*Aquiladelphis laurae* differs from both *I. lactea* and *U. hutchisoni* in having a reduced anterior stylar shelf comparable to other pediomyids. Although more material is needed, our analysis suggests that Eaton (2006) was right to question referral of the taxon to *Aquiladelphis*.

Davis (2007) and Rigby & Wolberg (1987) independently concluded that the presence of a cusp in the stylar cusp C position was not a reliable character for diagnosing pediomyids, and we agree with this conclusion. In our analysis, taxa in both branches of the pediomyid tree lack the cusp (i.e. *Iqualadelphis lactea*, *Leptalestes* spp. and *Protolambda* spp.), others have a well-developed cusp (i.e. *Aquiladelphis* spp.), while still other taxa, including *U. hutchisoni*, *P. elegans* and tentatively ?*A. laurae*, variably or consistently have two cusps in the stylar cusp C position.

Discussion

Although metatherians are abundant at Late Cretaceous North American mid-latitude localities, *Unnuakomys hutchisoni* is the first metatherian to be described from above the Arctic Circle. That teeth of *U. hutchisoni* greatly outnumber those of other mammals at Pediomys Point is not unlike Lancian localities in the Hell Creek Formation of NE Montana where metatherians are among the most abundant mammalian fossils, comprising 26–61% of the individuals at each locality (Wilson 2014). However, what differs between Late Cretaceous mid-latitude localities and the Alaskan North Slope is metatherian richness. Up to 11 species of metatherian are known from Lancian localities in the Hell Creek Formation (Wilson 2014), and at least a dozen species are documented from 'Edmontonian' mid-latitude North American assemblages (Cifelli *et al.* 2004). In contrast to these Late Cretaceous mid-latitude localities, all of the more than 60 metatherian teeth found at Pediomys Point appear to belong to a single species. A taphonomic or sampling bias might be responsible. It is also possible that the extremes of darkness and cold experienced by animals on Alaska's North Slope during the Late Cretaceous (Spicer & Herman 2010) acted as a biogeographical filter, limiting others to mid-latitude existence. This hypothesis will be tested through continued collection and sorting of sedimentary matrix from Pediomys Point as well as through prospecting for additional microvertebrate localities in the Prince Creek Formation.

The Pediomyidae is thus far a North American clade whose mid-latitude members range from southern Alberta in the north (Fox 1971, 1987) to southern Utah (Eaton & Cifelli 2013) and New Mexico in the south (Davis 2007). *Unnuakomys hutchisoni* greatly expands the geographical range of the clade north by over 2000 km. Given that deposition of the Prince Creek Formation (and Pediomys Point) occurred on Cretaceous Beringia, a terrestrial corridor that intermittently connected North American and Asian faunas (Beard 1998; Wen *et al.* 2016), it is plausible that pediomyids will also be discovered in Asia. Another clade of Cretaceous metatherians, the Deltatheroidans, was present in North America, but is best known from the Late Cretaceous of Asia. Some workers have suggested the clade originated in North America and subsequently dispersed to Asia (Davis *et al.* 2008), while others have hypothesized an Asian origin and subsequent dispersal to North America (Wilson & Riedel 2010). That lineages of metatherians were dispersing between Asia and North America during the Late Cretaceous is quite probable (Williamson *et al.* 2014). The abundance of *U. hutchisoni* at the Pediomys Point locality suggests that these pediomyids successfully occupied Arctic environmental extremes during the Late Cretaceous (i.e. shutdown of photosynthesis during the long dark winter), thereby increasing the probability of trans-Beringian dispersal.

Endemic taxa of pachycephalosaur (Sullivan 2006), ceratopsid (Fiorillo & Tykoski 2012), tyrannosaurid (Fiorillo & Tykoski 2014) and hadrosaur (Mori *et al.* 2015) dinosaurs from the Prince Creek Formation support the presence of a distinctive, northern high-latitude early Maastrichtian dinosaurian fauna, initially coined the Paaŋaqtat Province (Erickson & Druckenmiller 2011). As the first mammal to be described from the Prince Creek Formation, *Unnuakomys hutchisoni* indicates the Arctic also hosted at least one endemic species of mammal. When considered alongside recent discoveries of a mammalian fauna in Early Cretaceous strata of East Siberia, Russia that contains novel species of docodont and eutriconodont (Averianov *et al.* 2018), there is growing evidence suggesting that endemism amongst vertebrates in the Cretaceous Arctic may have been more the rule than the exception.

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Supplemental material

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