

A revision of “pediomyid” marsupials from the Late Cretaceous of North America

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“Pediomyids” are a diverse group of small- to medium-sized marsupials which comprise a significant portion of many Late Cretaceous North American mammalian faunas. Known almost exclusively from isolated teeth and jaw fragments, “pediomyids” exhibit far more diversity than any other contemporaneous group of North American mammals. This has led some to suggest that the family “Pediomyidae” is an artificial, polyphyletic assemblage composed of multiple lineages that independently acquired various traditionally-recognized “pediomyid” molar characters, such as a reduction of the anterior stylocone, reduction of the stylocone and a labial shift in the attachment of the cristid obliqua. The present study seeks to elucidate the interrelationships of “pediomyid” marsupials and test the monophyly of the group using cladistic methodology, including a broad sampling of Late Cretaceous North American taxa and a comprehensive set of qualitative molar characters. Results suggest that the family “Pediomyidae” and the genus “*Pediomys*” are both polyphyletic and are in need of systematic revision. *Iqualadelphis lactea* (Aquilan) appears to be unrelated to the “pediomyid” radiation, and rests as a stem taxon near the base of the cladogram. The large Aquilan *Aquiladelphis* nests in a trichotomy with a strictly-defined “Pediomyidae” and the enigmatic Lancian taxon *Glasbius*, suggesting the possibility of a distant relationship (above the familial level). Three clades are recognized within the “Pediomyidae”: a restricted *Pediomys*, *Leptalestes* gen. nov. (containing the three smallest species), and *Protolambda* (containing the remaining three larger species). Results suggest that “*Pediomys*” *exiguus* is a stem taxon lacking a close relationship to *Pediomyidae sensu stricto*, and is removed to permit recognition of the family as monophyletic. The results carry implications for the role “pediomyids” might have played in the initial North American marsupial radiation sometime prior to the Campanian, and the pattern of molar evolution throughout major Late Cretaceous lineages.

Key words: Marsupialia, Pediomyidae, systematics, Late Cretaceous, United States, Canada.

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Introduction

“Pediomyidae” Simpson, 1927a are diverse, biotically significant marsupials known only from the Late Cretaceous (late Santonian–Maastrichtian) of North America. “Pediomyids” make up large portions of the mammalian faunal record from that time period, occasionally as the numerically dominant taxa (e.g., Clemens 1966). Though possible “pediomyids” have been reported from the late Eocene of Texas (Slaughter 1978) and the Maastrichtian of Peru (Sigé 1972), and previous phylogenetic work indicates the possibility of close relationships with some Paleocene South American taxa (Marshall 1987), thorough evaluation of these hypotheses is beyond the scope of this project. For simplicity of outgroup comparison and the need to keep temporal and geographic disparity at a minimum, this study is restricted to Late Cretaceous North American taxa and will not address proposed relationships of “pediomyids” to Tertiary groups or other marsupial radiations.

Known principally from dental remains (although isolated tarsals from the Lance and “Oldman” formations have been tentatively referred to “*Pediomys*” Marsh, 1889; see Szalay 1982, 1994), “pediomyids” range in size from some of the

smallest Late Cretaceous marsupials to approaching some of the largest. “Pediomyids” have a generally opossum-like dentition; presumed apomorphies recognized by previous investigations include reduction of the anterior stylocone and reduction to loss of the stylocone on upper molars; and attachment of the cristid obliqua labial to the protocristid notch on lower molars (Fig. 1). Herein, I revise the family “Pediomyidae”, modifying its diagnostic characters and providing a definition in the form of included taxa, in addition to addressing the taxonomic relationships of other marsupials currently thought of as “pediomyids”. The concept of Marsupialia used in this study is taxon-based, including *Kokopellia juddi* Cifelli, 1993a and all descendants, and includes all taxa traditionally considered as marsupials. Alternatively, this taxon may be defined as stem-based, including all mammals more closely related to marsupials than to eutherians, deltatheroidans, or other stem metatherians (e.g., *Sinodelphys* Luo, Ji, Wible, and Yuan, 2003; see Kielan-Jaworowska et al. 2004).

The family “Pediomyidae”, as currently understood, contains two genera and twelve species (Table 1). Owing to their distinctive molar specializations (among Late Cretaceous North American marsupials), the “Pediomyidae” have long

Table 1. Classifications of included taxa. Left, from Kielan-Jaworowska et al. (2004); right, revised from results of this study.

<p>Class Mammalia Linnaeus, 1758 Infraclass Metatheria Huxley, 1880 Cohort Marsupialia Illiger, 1811 Order and family <i>incertae sedis</i> <i>Kokopellia juddi</i> Cifelli, 1993a Order "Didelphimorphia" Gill, 1872 Family <i>incertae sedis</i> <i>Iqualadelphis lactea</i> Fox, 1987b Family "Alphadontidae" Marshall, Case, and Woodburne, 1990 <i>Aenigmadelphys archeri</i> Cifelli and Johanson, 1994 <i>Alphadon jasoni</i> Storer, 1991 <i>Alphadon wilsoni</i> Lillegraven, 1969 <i>Turgidodon praesagus</i> (Russell, 1952) <i>Turgidodon russelli</i> (Fox, 1979) <i>Varalphadon wahweapensis</i> (Cifelli, 1990b) Family "Pediomyidae" Simpson, 1927a <i>Aquiladelphis incus</i> Fox, 1971 <i>Aquiladelphis minor</i> Fox, 1971 <i>Aquiladelphis paraminor</i> Rigby and Wolberg, 1987 "<i>Pediomys</i>" <i>elegans</i> Marsh, 1889 "<i>Pediomys</i>" <i>clemensi</i> Sahni, 1972 "<i>Pediomys</i>" <i>cooki</i> Clemens, 1966 "<i>Pediomys</i>" <i>exiguus</i> Fox, 1971 "<i>Pediomys</i>" <i>fassetti</i> Rigby and Wolberg, 1987 "<i>Pediomys</i>" <i>florencae</i> Clemens, 1966 "<i>Pediomys</i>" <i>hatcheri</i> (Osborn, 1898) "<i>Pediomys</i>" <i>krejci</i> Clemens, 1966 "<i>Pediomys</i>" <i>prokrejci</i> Fox, 1979 Family Stagodontidae Marsh, 1889 <i>Eodelphis cutleri</i> (Woodward, 1916) Order Paucituberculata Ameghino, 1894 Family Glasbiidae Clemens, 1966 <i>Glasbius intricatus</i> Clemens, 1966</p>	<p>Class Mammalia Linnaeus, 1758 Infraclass Metatheria Huxley, 1880 Cohort Marsupialia Illiger, 1811 Order and family <i>incertae sedis</i> <i>Kokopellia juddi</i> Cifelli, 1993a Order "Didelphimorphia" Gill, 1872 Family <i>incertae sedis</i> <i>Aenigmadelphys archeri</i> Cifelli and Johanson, 1994 <i>Apistodon exiguus</i> (Fox, 1971) <i>Iqualadelphis lactea</i> Fox, 1987b <i>Varalphadon wahweapensis</i> (Cifelli, 1990b) Family "Alphadontidae" Marshall, Case, and Woodburne, 1990 <i>Alphadon jasoni</i> Storer, 1991 <i>Alphadon wilsoni</i> Lillegraven, 1969 <i>Turgidodon praesagus</i> (Russell, 1952) <i>Turgidodon russelli</i> (Fox, 1979) Family Stagodontidae Marsh, 1889 <i>Eodelphis cutleri</i> (Woodward, 1916) Superfamily <i>Pediomyoidea</i> Simpson, 1927a, new rank Family <i>Pediomyidae</i> Simpson, 1927a <i>Pediomys elegans</i> Marsh, 1889 <i>Protolambda hatcheri</i> (Osborn, 1898) <i>Protolambda florencae</i> (Clemens, 1966) ?<i>Protolambda clemensi</i> (Sahni, 1972) <i>Leptalestes krejci</i> (Clemens, 1966) <i>Leptalestes prokrejci</i> (Fox, 1979) ?<i>Leptalestes cooki</i> (Clemens, 1966) Family <i>Aquiladelphidae</i> nov. <i>Aquiladelphis incus</i> Fox, 1971 <i>Aquiladelphis minor</i> Fox, 1971 Family <i>Glasbiidae</i> Clemens, 1966 <i>Glasbius intricatus</i> Clemens, 1966</p>
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been recognized as a monophyletic group (Clemens 1966), although they were initially regarded as a subfamily of the "Didelphidae" (*sensu* Simpson 1945; the term "Didelphidae", traditionally used in reference to *Alphadon*-like taxa, is replaced with "Alphadontidae" Marshall, Case, and Woodburne, 1990; see Kielan-Jaworowska et al. 2004 for a brief summary). However, an hypothesis proposed by Fox (1987a) suggests that the family is instead an artificial assemblage, comprised of at least two lineages that independently acquired "pediomyid"-like molar characteristics. Central to this hypothesis is the Aquilan taxon *Iqualadelphis* Fox, 1987b, which retains several plesiomorphies and has been postulated by Fox to be related to a specific lineage of later "pediomyids". The morphological diversity seen within the "Pediomyidae" is uncontested, and invites testing of Fox's hypothesis.

Institutional abbreviations.—AMNH, American Museum of Natural History, New York, New York, USA; CM, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, USA; OMNH, Oklahoma Museum of Natural History, Norman, Oklahoma, USA; UALVP, University of Alberta Laboratory for Vertebrate Paleontology, Edmonton, Alberta, Canada; UCMP, University of California Museum of Paleontology,

Berkeley, California, USA; UM, University of Minnesota, Minneapolis, Minnesota, USA; UNM, University of New Mexico, Albuquerque, New Mexico, USA; YPM, Yale Peabody Museum, New Haven, Connecticut, USA.

Other abbreviations and conventions.—I follow the general practice of abbreviating molars and premolars with the letters "M" and "P", respectively; teeth belonging to the lower dentition are indicated with a lower case letter. In referring to stylar cusps, the term "stylocone" is equivalent to "stylar cusp B", "parastyle" is equivalent to "stylar cusp A", and the term "stylar cusp in the C position" will be used instead of "stylar cusp C" to denote topographic position and not necessarily homology. To indicate taxonomic uncertainty, quotation marks will be used when referring to groups or groupings that are proposed as polyphyletic, following Fox (1987a) and Johanson (1993). To avoid confusion between current systematics and the revisions proposed herein, the term *sensu lato* (s.l.) is applied to a group when referring to its current, polyphyletic composition (see Table 1), as is the case with "Pediomyidae" and "*Pediomys*". The term *sensu stricto* (s.s.) modifies the group to include only the taxa indicated by the present study. Additionally, quotation marks will be dropped from the names of groups that become monophyletic under a restricted

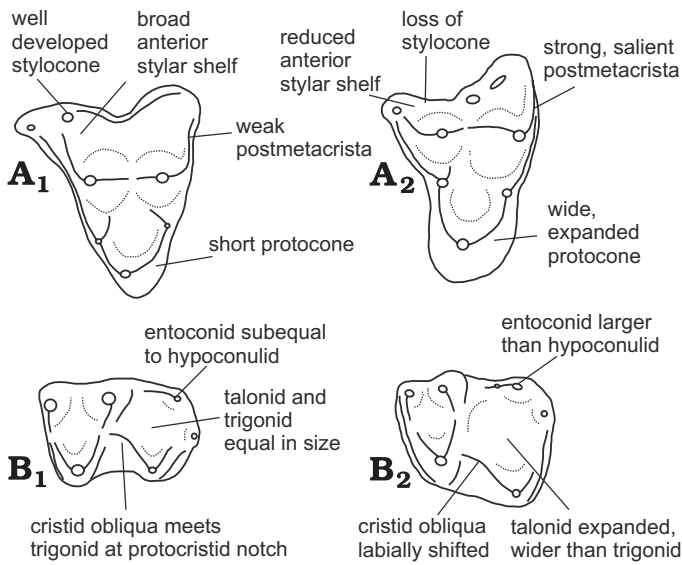


Fig. 1. Illustration of important “pediomyid” upper (A) and lower (B) molar characters. Line drawings based on *Kokopellia juddi* (A₁, B₁) and *Pedimys elegans* (A₂, B₂).

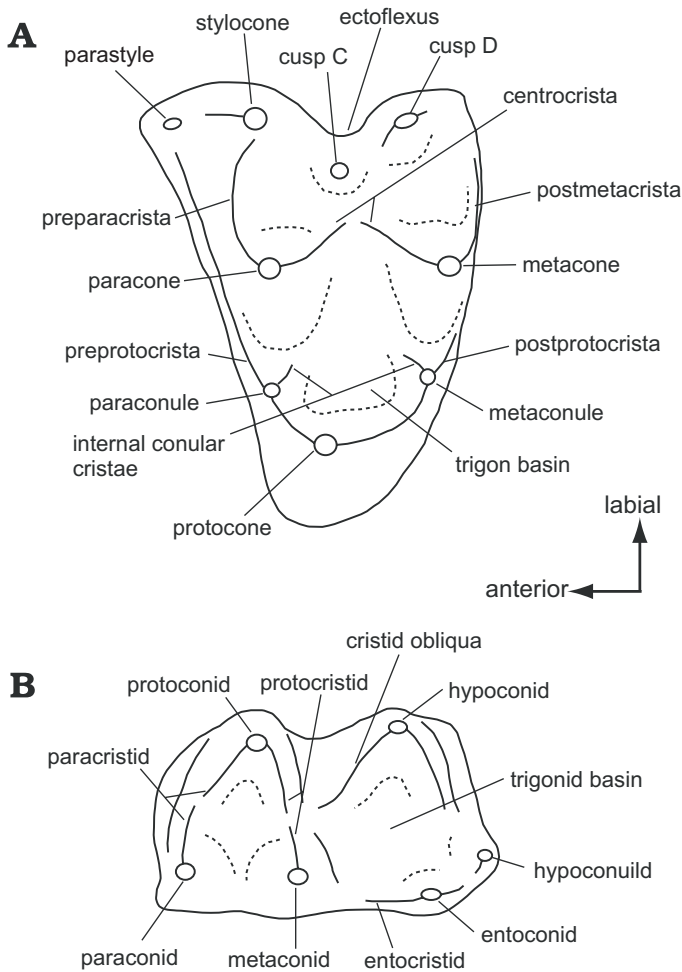


Fig. 2. Illustration of terminology for upper (A) and lower (B) marsupial molars, based on *Alphasodon jasoni* (Lillegraven 1969).

definition (e.g., *Pediomyidae* s.s., *Pedimys* s.s.), but they are retained when referring to traditional definitions. See the “Systematic paleontology” section for detailed morphological descriptions and revisions of these groups. North American Land Mammal Ages (NALMAs) are used in place of the European Marine Stages when referring specifically to the distribution of Late Cretaceous taxa (and not the age of a formation). Definitions of the NALMAs follow Lillegraven and McKenna (1986). Molar terminology is illustrated in Fig. 2.

Historical background

The genus “*Pedimys*” was established by Marsh (1889), based on an upper third molar described from the Lance Formation (late Maastrichtian) of Wyoming. He named the type species *Pedimys elegans*, after its tiny size relative to many other mammalian remains recovered from that formation. A second, much larger genus from the Lance Formation, *Protolambda hatcheri* Osborn, (1898), was moved to “*Pedimys*” by Simpson (1927b). Simpson (1927b) then erected the subfamily *Pediomyinae* (within the family “*Didelphidae*”), noting it likely represented the primitive morphology for the family and possibly even all marsupials (Simpson 1927a, 1929). Included in the subfamily was a number of additional genera that later turned out to be synonymous with other taxa or were otherwise unrelated (see Clemens 1966: 34 for explanation).

The current concept of “*Pediomyidae*,” and, for that matter, of all other Late Cretaceous mammal groups of North America, originated in William A. Clemens’ landmark studies (Clemens 1964, 1966, 1973a) of the fauna from the type Lance Formation, Wyoming. Clemens (1966) promoted the “*Pediomyinae*” to family status and produced a revised diagnosis. He restricted the family to “*Pedimys*” and added to the known diversity of the genus by describing three new species: “*Pedimys cooki*,” “*P. krejci*,” and “*P. florenceae*.” Clemens (1966) demonstrated that the five known species of “*Pedimys*” were bimodally distributed in size and that the larger taxa shared, to varying extent, inflation of the ultimate upper premolar (Clemens 1966: 54). Clemens also proposed a hypothetical association of upper and lower dentitions for the Lance marsupials, which had not been attempted until then and which proved to be enormously useful (e.g., Lillegraven 1969). Although only one Late Cretaceous North American marsupial fossil has been found with upper and lower dentition in association (a specimen of *Alphasodon jasoni* Storer, 1991; see Lillegraven 1969: fig. 15), Clemens’ referrals have been uncontested in the four decades since publication of his now classic study. Clemens’ insight provided precedent for what is now routine assignment of lower molars to Late Cretaceous marsupials based on the upper dentition (e.g., Fox 1979; Lillegraven and McKenna 1986; Cifelli 1990a, b).

Clemens (1966) also addressed “pediomyid” ancestry, proposing the then novel and now widely accepted interpre-

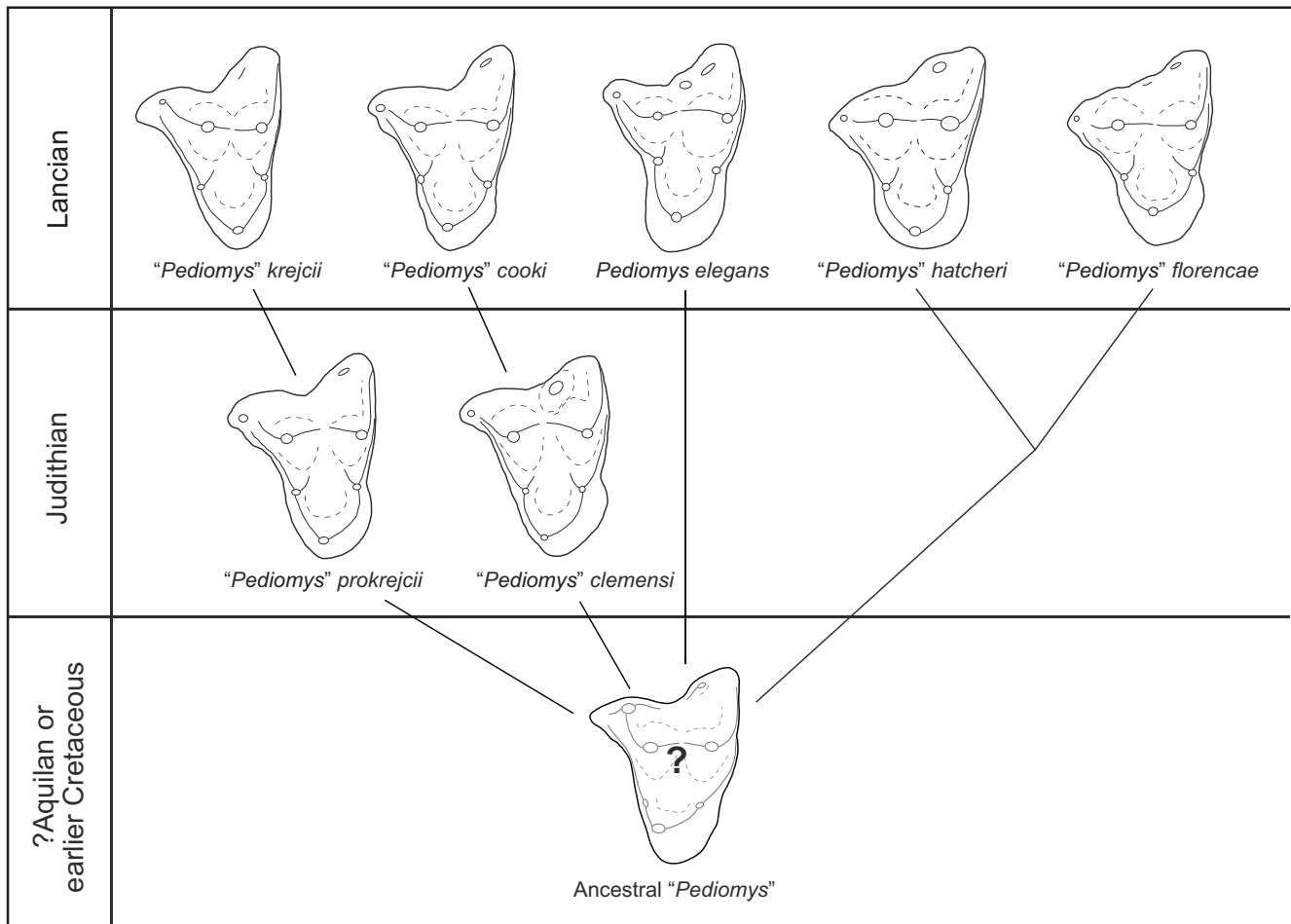


Fig. 3. Model of "pediomyid" species succession and upper molar evolution as illustrated in Fox (1979), derived from a hypothetical Milk River taxon (line drawing based on *Iqualadelphis lactea*). Modified from Fox (1979: fig. 4).

tation that the group was derived in its suppression of the anterior styler shelf and stylocone. According to Clemens' model, "*Pediomys*" evolved from a marsupial with an *Alphadon*-like molar configuration, with upper molars bearing a wide styler shelf and five styler cusps, as suggested by the slightly less suppressed anterior styler shelf and prominent cusp C of *Pediomys elegans*. He also recognized the morphological diversity represented within the genus, suggesting that some of the various species referred to "*Pediomys*" may in fact belong in separate genera (Clemens 1966: 54).

Until 1971, "pediomyid" marsupials were known only from the Lancian of Wyoming and Alberta (see Lillegraven 1969 for "pediomyids" from what is now known as the Scollard Formation). Fox (1971) extended the temporal range of the "Pediomyidae" when he described three taxa from the Milk River Formation of Alberta (Aquilan NALMA, initially thought to be of early Campanian age and now considered to be more probably late Santonian; see Leahy and Lerbekmo 1995 and Payenberg et al. 2002). "*Pediomys*" *exiguus*, the smallest member of the genus, exhibits a relatively primitive morphology, possessing a large stylocone on its upper molars. Lower molars are unknown. Fox (1971) proposed a second "pediomyid" genus, *Aquiladelphis*, which also pos-

sesses a stylocone, although in general its species (*A. incus* and *A. minor*) are closer in size to the large "pediomyids", "*P.*" *hatcheri* and "*P.*" *florencae*. Despite the supposed primitive dental morphology and older geologic age of these taxa, Fox (1971) described them as unique and divergent from other "pediomyids" later in the Cretaceous, making them poor candidates for ancestry of the group. However, Fox would later state (Fox 1987a: 166) that "*P.*" *exiguus* is not, in fact, pediomyid-like at all.

In his comprehensive description of the vertebrate fauna of the Judith River Formation (late Campanian) of central Montana, Sahni (1972) added a new "pediomyid", "*Pediomys*" *clemensi*, based on some fragmentary upper molars and complete lower molars. He noted morphological similarities between his new species and the Lancian *P. elegans*. Fox (1979) argued against this proposed relationship in his description of "*Pediomys*" from the contemporaneous Dinosaur Park Formation ("upper Oldman Formation" of older literature; see Eberth and Hamblin 1993; Eberth 2005). Based on description of more complete fossils (dentigerous jaws) than those available to Sahni, Fox instead recognized a closer relationship between "*Pediomys*" *clemensi* and "*P.*" *cooki*, based on configurations of the styler shelf and styler cusps.

He also described a new species, “*P.*” *prokrejicii*, clearly named for its hypothesized ancestry to the Lancian “*P.*” *krejicii* (Fig. 3). As for the ancestry of the group, Fox (1979) contradicted Clemens (1966, 1968), hinting that unpublished material from the Milk River Formation indicated the ancestral “pediomyid” morphology was somewhat different than what is seen in *Alphadon*.

Fox (1987b) elaborated on some of the Milk River taxa and their role in “pediomyid” evolution, with the description of *Iqualadelphis lactea* from the Milk River Formation of southern Alberta. Though not referring to the taxon as a true “pediomyid”, he nonetheless cited several features it shared with later taxa, most notably “*P.*” *prokrejicii* (Judithian) and “*P.*” *krejicii* (Lancian). These include a transversely wide crown, well-developed stylar cusp D and a lack of a stylar cusp in the C position; however, *Iqualadelphis* retains a distinct stylocone and moderately-developed anterior stylar shelf. These similarities led him to propose that *Iqualadelphis* approximates the ancestral morphology for “pediomyids” (and likely the condition for the earliest marsupials as well; Fig. 4). Additionally, he suggested that various species of “*Pediomyis*” represent separate lineages, some of which never went through an *Alphadon*-like stage in which cusp C was present (Fox 1987a, b). *Pediomyis*, Fox suggested, should be restricted to the type species *P. elegans*, with the remainder classified as Marsupicarnivora, family *incertae sedis*. He did not specify how they were to be divided into genera, but it would likely reflect his three proposed lineages: “*P.*” *krejicii*–*prokrejicii*, “*P.*” *cooki*–*clemensi*, and “*P.*” *hatcheri*–*florenceae* (see Fig. 3).

The crux of Fox’s (1987a) polyphyly hypothesis was the argument that the inconsistent presence of a stylar cusp in the C position among species of “*Pediomyis*” must be indicative of ancestries from separate primitive marsupials, some of which did not possess a cusp C and each of which independently acquired advanced “pediomyid” characters (such as suppression of the stylocone and the anterior stylar shelf). However, more recent discoveries (Cifelli 1993a; Cifelli and Muizon 1997) indicate a somewhat different situation. *Kokopellia* appears to represent the primitive condition for marsupials, which is characterized by a wide anterior stylar shelf, moderate-sized stylocone and parastyle and a lack of any other stylar cusps. Therefore, it is conceivable that all families of Late Cretaceous marsupials that possess a stylar cusp in the C position derived it independently, suggesting that the presence or absence of this cusp is unreliable in determining phylogenetic relationships.

The most recently described “pediomyids” are those from the upper Fruitland and lower Kirtland formations in the San Juan Basin, New Mexico (Rigby and Wolberg 1987; see Clemens 1973b for initial work in the region). Though often ascribed to the problematic “Edmontonian” NALMA, the mammalian assemblage (Hunter Wash local fauna) from this stratigraphic zone is now considered to be of Judithian age (Cifelli et al. 2004). Rigby and Wolberg (1987) described two “pediomyids” from this fauna: “*Pediomyis*” *fasseti* and *Aqui-*

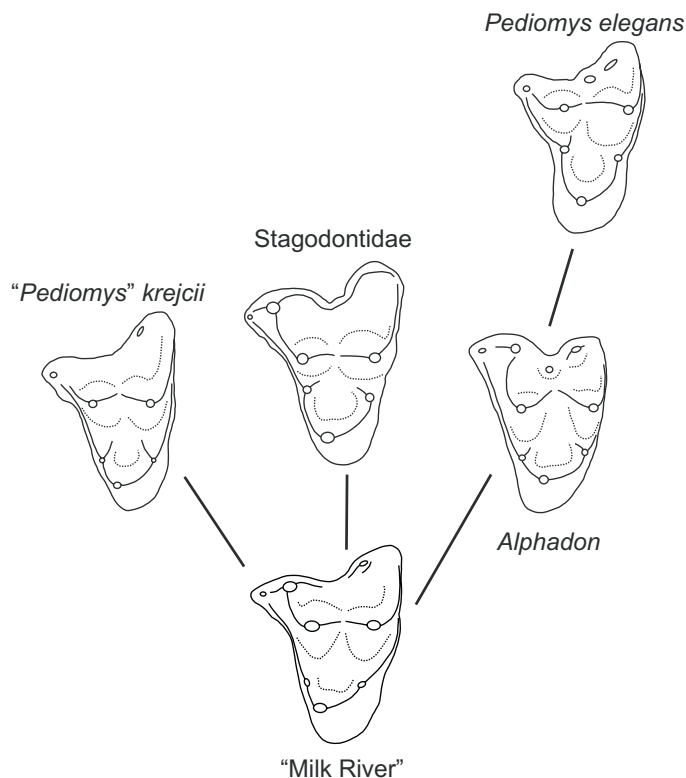


Fig. 4. Diagram showing alternative hypothesis of upper molar evolution in primitive Upper Cretaceous marsupials, from an ancestral molar anatomy (“Milk River”) in which cusp B and D were developed, but not cusp C, which is added later. This model hypothesized that each Late Cretaceous lineage (including various “pediomyids”) was derived independently from Milk River taxa, such as *Iqualadelphis*. Modified from Fox 1987a: fig. 6.

adelphis paraminor. Neither is represented by a complete upper molar, though one can be reconstructed for “*P.*” *fasseti* using the type and one additional referred specimen. These species are herein considered to be synonyms of other taxa, and they have been excluded from the analysis (see the Systematic paleontology section for detailed comments). It is noteworthy that Rigby and Wolberg (1987: 68) recognized the difficulties of utilizing the presence of cusp C as a diagnostic character for “pediomyids” or other marsupials, since it “...seems to appear and disappear frequently within accepted lineages”, a conclusion relevant to the present study.

Several additional studies have dealt with the relationships of the “Pediomyidae” to other families of North and South American marsupials (Marshall 1987; Reig et al. 1987; Marshall et al. 1990). None of these works made an effort to resolve the proposed polyphyly of the group as, understandably, it was beyond their scope. However, the interrelationships of “pediomyid” marsupials bear directly on their ancestry and thus their relationships to other major groups of North American marsupials, such as *Glasbius* and the “alphadontids”. These groups have often been treated so differently as to be classified in different orders. For example, Aplin and Archer (1987) demoted the “Pediomyidae” to a subfamily and placed it within the Microbiotheriidae, as did Reig et al. (1987) and Marshall (1987). Marshall et al. (1990) retained the taxon as a

family and allied it with the Microbiotheriidae under the order Microbiotheria. McKenna and Bell (1997) allied the “Pediomyidae” with the Stagodontidae in the order Archimetatheria and further removed *Iqualadelphis* to a stem position in a different order, the “Didelphimorphia”. If these studies and classifications are to be followed, perhaps some members of the “Pediomyidae” belong in separate orders.

Materials and methods

As previously noted, this study is necessary to refine our understanding of the diversity and relationships of “pediomyid” marsupials. To achieve this goal, it is crucial to include evidence from a multitude of representative taxa across the Late Cretaceous North American Marsupialia. Given the nature of the fossil record, the character set is based almost entirely on molar morphology. For consistency, all characters were coded using upper and lower third molars (unless the character specifies a different tooth locus). The penultimate molar is generally the most species-specific locus in the molar series in Late Cretaceous marsupial taxa. The diagnoses of these and other North American Cretaceous mammals have been based almost exclusively on molar morphology. Premolars, though arguably significant, tend to be too generalized in morphology across Late Cretaceous marsupial taxa (with notable exceptions, such as the bulbous third premolar of *Didelphodon*). With the vast majority of the North American record consisting of isolated teeth, premolars become very difficult to confidently assign to the generic level, let alone the species level (with some exceptions; see Cifelli 1990a). A single character was included, dealing with inflation of the ultimate premolar.

Twenty-two taxa were included in this analysis, representing all families of Late Cretaceous North American marsupials, plus two undescribed taxa (Table 1). When dealing with a group as morphologically and taxonomically diverse as the “pediomyids”, it is appropriate to sample a morphologically and taxonomically diverse set of other taxa. I felt it necessary to include such broad a sample to help ensure that major morphological differences were reflected in the cladogram topology. The outgroup selected was *Kokopellia juddi*, because it is generally regarded as the oldest true marsupial (Cifelli 1993a; Cifelli and Muizon 1997; Kielan-Jaworowska et al. 2004) and is illustrative of the primitive dentition of the group (the recently-described *Sinodelphys szalayi* Luo, Ji, Wible, and Yuan, 2003, some 25 my older, represents an even more primitive stem metatherian lineage, but its molar morphology is not yet well known). One additional taxon, *Aenigmadelphys archeri* Cifelli and Johanson, 1994, was included based on its generally primitive and unspecialized molars (despite being retained in the “Alphadontidae” by Kielan-Jaworowska et al. 2004). These two taxa help establish character polarity.

Representatives of the family “Alphadontidae” were included to test Fox’s (1987a) hypothesis on upper molar evolu-

tion. Previously, the suppression of the anterior styler shelf and the stylocone were thought of as apomorphic “pediomyid” characters (e.g., Clemens 1966). However, Fox (1987a) implicated some sort of *Alphadon*-like stage in the ancestry of at least some “pediomyid” marsupials and an independent acquisition of traditional “pediomyid” characters, focusing on styler cusp C as another important morphological feature. It is therefore essential to include “alphadontids” representing a variety of different morphologies and geologic ages in the analysis.

Glasbius, the sole member of the Glasbiidae, was included primarily because its relationships are highly enigmatic. It is a distinctive taxon that suddenly appeared in the Lancian with no obvious morphological antecedents. This leaves open the possibility of a relationship between *Glasbius* and “pediomyids” (as suggested, for example, by Rougier et al. 1998), especially given that both have a labial attachment of the cristid obliqua, a traditional “pediomyid” character. *Glasbius intricatus* Clemens, 1966 is included in the analysis because it is the better known of the two species.

Stagodontids have been postulated by some authors to represent one of the earliest-diverging groups of Late Cretaceous metatherians (Marshall and Kielan-Jaworowska 1992), with a contested first appearance at the Early–Late Cretaceous boundary in central Utah (Cifelli and Eaton 1987; Cifelli 2004). Fox and Naylor (1995) proposed that the Stagodontidae are instead nested deeply within the Marsupialia. The group is nonetheless important in that, like *Glasbius*, stagodontids have a labially-attaching cristid obliqua, making them relevant for exploring the homoplasy of traditionally accepted “pediomyid” characters. *Eodelphis* is well represented in northern faunas of Judithian age that include diverse “pediomyids” (Fox 1981).

Finally, every North American species classified in the genera assigned to the family “Pediomyidae” (*sensu* McKenna and Bell 1997) was included. Two taxa from the San Juan Basin are notable exceptions, however; *Aquiladelphis paraminor*, known only by poorly preserved material, and “*Pediomyis*” *fassetti* are synonymized with *Aquiladelphis minor* and “*Pediomyis*” *prokrejcii*, respectively. This is explained in detail in the Systematic paleontology section. Two undescribed “pediomyids” were also included, one from the Prince Creek Formation on the North Slope of Alaska and another from the St. Mary River Formation of Montana. Both are important not only for their morphology, but their stratigraphic position is potentially intermediate between the well known faunas of the Judithian and Lancian North American Land Mammal ages (Cifelli et al. 2004). The important Milk River “pediomyid”-like taxon *Iqualadelphis lactea* was also included, for obvious reasons stemming from its proposed position as a bridge between primitive marsupials and certain lineages of “pediomyids”.

For this analysis, 57 qualitative morphological characters were compiled based on a thorough examination of upper and lower molar series for all taxa involved. The character set was restricted to qualitative features due to the difficulties and arbi-

trariness encountered in assigning states to morphology with a continuous range of variation. Though many of these characters stem from new observations, a number of them were derived from previous studies of Cretaceous mammal evolution (e.g., Clemens 1979; Clemens and Lillegraven 1986; Cifelli 1993b; Johanson 1996a). Character polarity is based primarily on the condition seen in *Kokopellia juddi*. Various characters that heavily influence the patterns of topologic distribution of taxa are discussed in the text; a complete, detailed list of all characters and states is given in Appendices 1 and 2. The analysis was run using PAUP* 4.0b (Swofford 2003).

Results

The results of this analysis clearly indicate that the taxa currently assigned to the “Pediomyidae” s.l. represent an artificial, polyphyletic assemblage, as shown in Fig. 5. At first glance, this appears to support Fox’s (1987a) central hypothesis regarding the relationships of “pediomyid” marsupials. However, the specific manner in which the taxa segregate and the distribution of important characters differ significantly from Fox’s hypothesis on “pediomyid” evolution. The analysis upholds Fox’s hypothesis that the family “Pediomyidae” s.l. and the genus “*Pediomys*” s.l. are polyphyletic, but the only taxa confounding the systematics were the Milk River forms, *Aquiladelphis* and “*Pediomys*” *exiguus*. Removal of these taxa from the “Pediomyidae” s.l. and exclusion of “*P.*” *exiguus* from “*Pediomys*” s.l. restores monophyly of the group.

Of central importance to Fox’s (1987a) views on evolution of the “Pediomyidae” is the Aquilan taxon *Iqualadelphis lactea*. Though he stopped short of calling it a “pediomyid”, he suggested that it represents an ancestral form for the “*Pediomys*” *krejci-prokrejci* lineage (Fox 1987b). His basis for this association is clear—there is some resemblance between the three taxa (see Fig. 3), and *I. lactea* exhibits some “pediomyid”-like characters, such as a slight suppression of the anterior stylocone, since stylocone is somewhat taller on at least some specimens (Fox 1971; Johanson 1993). Given Fox’s hypothesis, it would be expected that *Iqualadelphis* would settle as a sister taxon to at least some “pediomyids”, even under a more inclusive definition. However, the analysis places it in a position on the cladogram basal to nearly all other ingroup taxa (Fig. 5). These results suggest it is a stem marsupial that evolved features that approach certain traditional “pediomyid” molar characters through parallelism. This result is consistent with the findings of several other recent analyses (e.g., Rougier et al. 1998, 2004; Wible et al. 2001). This phylogenetic position must be interpreted with some caution, since knowledge of *Iqualadelphis* is limited to upper molars, and its position could change with the discovery of more complete fossils (but see discussion below on the effect of restricting the analysis to upper molar data). At present, however, this taxon appears to have had no role in the evolutionary history of “pediomyid” marsupials, and only

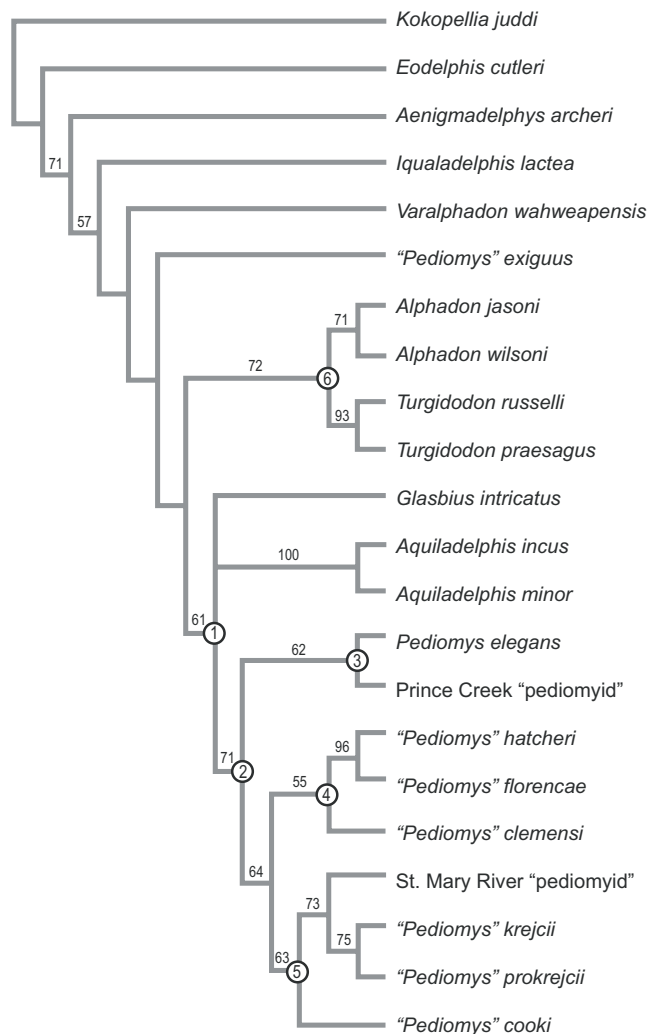


Fig. 5. Strict-consensus cladogram of three equally-parsimonious cladograms, resulting from a heuristic search of 22 taxa and 57 characters. All characters are unordered and unweighted, and no topologic constraints were applied. Numbers above branches indicate bootstrap support values (>50% only). Numbers in circles indicate major taxonomic nodes discussed in the text: 1, Pediomyoidea (new rank); 2, Pediomyidae s.s.; 3, *Pediomys* s.s.; 4, *Leptalestes* gen. nov.; 5, *Protolambda*; 6, “Alphadontidae”. Tree length = 181; consistency index = 0.46.

serves to illustrate the high degree of homoplasy exhibited by Late Cretaceous North American marsupial taxa.

The strict consensus cladogram distributes “pediomyid” (s.l.) taxa among three clades (Fig. 5). The most basal of the three is “*Pediomys*” *exiguus*, which branches off the main marsupial stem only slightly higher than its Milk River contemporary, *Iqualadelphis*, and nowhere near the remainder of the species referred to “*Pediomys*” (this, however, is not a surprising result since Fox (1987a) rescinded his original assessment of “*P.*” *exiguus* as a “pediomyid”). “*P.*” *exiguus* not only retains a wide anterior stylocone and a large stylocone connected to the paracone via a strong preparacrista, it has a small protocone (plesiomorphy). This species has no features that can be considered remotely “pediomyid” (perhaps with the exception of broad pre- and postprotocristae); removal of it

from the "Pediomyidae" and *Pediomys* restores monophyly for the family and genus, respectively. As is the case in *Iqualadelphis*, only upper molars are known for "*P.*" *exiguus*. However, the morphological disparity between this taxon and other "pediomyids", together with the lack of shared, derived characters, makes it highly unlikely discovery of lower molar data would restore its position within (or proximal to) the "Pediomyidae".

The second lineage of "pediomyids" contains another Aquilan taxon, the genus *Aquiladelphis*. *Aquiladelphis* was originally referred to the "Pediomyidae" s.l. (Fox 1971) based on its narrow anterior styler shelf, reduction of the stylocone, and labial shift in the attachment of the cristid obliqua. However, my analysis places *Aquiladelphis* in a trichotomy with the *Pediomyidae* s.s. and *Glasbius* (Fig. 5, node 1), so a monophyletic relationship with other "pediomyid" taxa cannot be supported without the inclusion of *Glasbius* (it should be noted that *Glasbius* is the sister taxon to either *Aquiladelphis* or the *Pediomyidae* s.s. in all other equally parsimonious cladograms, and in no case is a traditional, genus-level composition of the "Pediomyidae" s.l. supported). Given size, degree of morphological specialization, and hypothesized relationship to two family-level taxa (*Pediomyidae* s.s. and *Glasbiidae*), I consider *Aquiladelphis* to be sufficiently unique to warrant placement in its own monotypic family, the *Aquiladelphidae* fam. nov.

An interesting relationship exists between the *Pediomyidae* s.s., the *Glasbiidae*, and the *Aquiladelphidae* fam. nov. The three taxa sit at an unresolved node (Fig. 5, node 1) supported by numerous characters, many of which are traditional "pediomyid" features (see the Systematic paleontology section). These characters serve as the basis for the erection of a new superfamily to house these three families, the *Pediomyoidea* Simpson, 1929 (new rank). The fact that *Glasbius*, a taxon that has never been associated with the "Pediomyidae" s.l., except dubiously by Reig et al. (1987), appears related to traditional "pediomyid" taxa suggests that some of these features are derived relative to Late Cretaceous marsupials in general, but rather plesiomorphic for "pediomyids" in particular. On the other hand, another traditional "pediomyid" feature, the labial shift of the cristid obliqua, shows some degree of homoplasy, since it is present in both pediomyoids and stagodontids (such as *Eodelphis*), two phylogenetically disparate groups (Fig. 5). Interestingly, this feature is also seen in South American peradectines and "didelphoids" (Muizon and Cifelli 2001), suggesting it might be a poor character on which to base diagnosis of a higher group.

All species referred to "*Pediomys*" s.l., with the exception of "*P.*" *exiguus*, are monophyletic (Fig. 5, node 2). This group of seven named and two unnamed taxa comprises a restricted *Pediomyidae*, united by numerous characters related to postvallum/prevallid shear and expansion of the protocone/trigonid basin crushing mechanism. The internal geometry of the *Pediomyidae* s.s. is interesting in that three separate clades can be recognized, two of which were hypothesized by Fox (1987a). The basal-most clade contains *Pedio-*

mys elegans and an unnamed taxon from the Prince Creek Formation of northern Alaska (William A. Clemens, personal communication 2003; Fig. 5, node 3). The other two clades of pediomyid (s.s.) marsupials are, at their core, composed as predicted by Fox (1987a). "*Pediomys*" *hatcheri* and "*P.*" *florenceae* are closely related (Fig. 5, node 4), as are "*P.*" *krejicii* and "*P.*" *prokrejicii* (along with an undescribed taxon from the St. Mary River Formation (Ronald E. Heinrich, personal communication 2003; Fig. 5, node 5). However, the third of Fox's (1987a) species lineages is incongruent with the results of this study. Instead of being most closely related to each other, "*P.*" *clemensi* belongs in the "*P.*" *hatcheri* clade, and "*P.*" *cooki* is a member of the "*P.*" *krejicii* group. There is considerable character support for the "*P.*" *krejicii*–*prokrejicii* and "*P.*" *hatcheri*–*florenceae* clades, though the primary difference at first glance between the two is size.

One of the principal features used by Fox (1987a) to characterize the evolution of "pediomyid" molars is a styler cusp in the C position. The distribution of this cusp, as exemplified by the differences between pediomyoids and "alphadontids", has significant implications for previous theories of molar evolution in North American marsupials (e.g., Clemens 1966; Fox 1987a). The arrangement and presence of the various cusps on the styler shelf is of particular importance to this study. Stem marsupials, such as *Kokopellia*, *Sinbadelphys*, and *Adelpdelphys* (Cifelli and Muizon 1997; Cifelli 2004) clearly demonstrate the primitive dentition for all Late Cretaceous marsupials, possessing a well-developed stylocone but lacking all other styler cusps. Styler cusp D was likely added first, in ancestral stagodontids and basal "didelphimorphians" such as *Aenigmadelphys*.

The topologic distribution of a styler cusp in the C position is very relevant to the hypotheses of "pediomyid" molar evolution proposed by Fox (1987a; Fig. 4 herein; see also Marshall et al. 1990 for an alternative evolutionary scenario of styler cusp C in marsupials). The results suggest a styler cusp in the C position evolved only once in Late Cretaceous North American marsupials. However, it is important to note that small cusps are variably present at positions roughly correlative to cusp C in some stem taxa [e.g., *Aengimadelphys* (Cifelli and Johanson 1994) and *Varalphadon creber* (Johanson 1996a)] though it is unclear whether any of these are homologous to structures in other taxa. Parsimony requires that this cusp first appeared posterior to the deepest part of the ectoflexus in the common ancestor of "*P.*" *exiguus*, the "Alphadontidae", and the *Pediomyoidea* as a conical, well-developed cusp, and later migrated anteriorly to the midline of the crown in the "alphadontids". This conclusion is supported by the presence of a styler cusp in the C position in numerous taxa from the Milk River Formation, notably "*Pediomys*" *exiguus*, *Aquiladelphis*, and *Albertatherium* (an interesting "alphadontid"; see Fox 1971; Johanson 1994). These taxa, of Aquilan age, are considerably older than other members of their clades, and all three possess well-developed cusps in the C position. Additionally, *Alphadon clemensi* and *A. lillegraveni*, both from the Cenomanian of Utah (Eaton 1993),

possess a styler cusp in the C position posterior to the deepest part of the ectoflexus, possibly demonstrating the ancestral condition for the “Alphadontidae”. Also noteworthy is the fact that this cusp varies in the two species referred to *Glasbius*—it is present in the type, *G. intricatus*, but absent in contemporaneous *Glasbius twitchelli*. The distribution of this cusp suggests it might be a poor diagnostic character.

Given the already obvious limitations of a cladistic analysis of diverse taxa represented almost exclusively by isolated teeth, this study is further hampered in that some significant species are known by upper molars alone (e.g., *Iqualadelphis lactea*, “*P.*” *exiguus*, and the St. Mary River “pediomyid”). This eliminates any possibility for lower molar character support for evolutionary relationships between these and other taxa. However, the balance of morphological support for the overall results of this study comes from upper molars. When all lower molar characters are removed from the analysis, the topology of the strict consensus tree does not change appreciably (see Appendix 3). The internal geometry of the *Pediomyidae* s.s. shifts slightly, but the three taxa known only from upper molars do not change in position. This should not be interpreted as indicative of any weakness of lower molar features in characterizing relationships—instead, the absence of lower molar data (a relatively small number of characters) has little effect on relatively robust results built upon a much larger body of diverse upper molar characters. In other words, this is not a reflection of the nature of the data, but of how the morphology was sampled. It should be noted, however, that the discovery of more complete fossils of these three taxa (and, of course, any other poorly-known taxa) could provide new data that could have a significant effect on tree topology and interpretation of the evolution of “pediomyid” marsupials.

To assess directly what effects *a priori* assumptions of a monophyletic “*Pediomyidae*” s.l. would have on cladogram statistics, two topological constraint trees were constructed (see Appendix 3). The first constrains all taxa currently referred to the “*Pediomyidae*” into a clade (“*Pediomys*” and *Aquiladelphis*, as well as all species therein). Interestingly, the contents and interrelationships of the *Pediomyidae* s.s. do not change. The Milk River “pediomyids” (*Aquiladelphis* and “*P.*” *exiguus*) take up positions as sister taxa, and *Iqualadelphis* remains near the base of the tree. The only systematic change given this scenario would be a revision of the genus “*Pediomys*”; however, this constraint requires five additional steps (approximately 2.8%), all of which are associated with the inclusion of “*P.*” *exiguus*. Regardless, even traditional “pediomyid” characters (such as suppression of the stylocone and anterior styler shelf, and expansion of the protocone) would best define the family at the same node as the unconstrained consensus tree, leaving the taxonomy as proposed in this study.

The second constraint tree (see Appendix 3) also utilizes a monophyletic “*Pediomyidae*” s.l., but adds the “pediomyid”-like Milk River taxon *Iqualadelphis* to the mandatory clade. The results are somewhat similar to the first constraint, except most resolution is lost from within the “*Pediomyidae*”. Addi-

tionally, *Iqualadelphis* nests with “*Pediomys*” *krejci*, as part of a clade Fox (1987a, b) postulated it might be ancestral to. However, the position of *Iqualadelphis* would be far too derived relative to the other members of its clade to support an ancestral hypothesis (not to mention its older geologic age). This constraint requires eight additional steps (approximately 4.4%). Despite the interesting results provided by these constraint cladograms, the original unmodified one is the shortest and preferred cladogram. The results derived from the original strict consensus cladogram (Fig. 5) will be used to revise the systematics of “pediomyid” marsupials and related taxa in the next section.

Systematic paleontology

Cohort Marsupialia Illiger, 1811

Remarks.—Following Kielan-Jaworowska et al. (2004), the cohort Marsupialia is defined as a stem-based taxon, containing Crown Marsupialia plus all extinct taxa more closely related to the crown group than to deltatheroidans or eutherians. This is preferable to a traditional, strictly crown-based definition, which would leave in limbo the large number of Cretaceous stem taxa that are clearly closer to marsupials than other groups. These stem taxa would otherwise require the erection of a paraphyletic group, situated close to but just outside of the crown Marsupialia. It is therefore more convenient to refer to all taxa herein as marsupials, a tradition of North American paleomammalogy with over one hundred years of use. Furthermore, the ordinal classifications of all included taxa follow Kielan-Jaworowska et al. (2004), with the notable exception of *Glasbius*, which is removed from the otherwise wholly South American Paucituberculata and placed in the “Didelphimorphia”. All other taxa are also included in this order, except *Kokopellia*, which remains order and family *incertae sedis* (see Cifelli and Muizon 1997 and Kielan-Jaworowska et al. 2004 for comments regarding a possible relationship between *Kokopellia* and the Asiadelphia).

Superorder “Ameridelphia” Szalay, 1982

Order “Didelphimorphia” Gill, 1872

Remarks.—In the previous section, it was noted that the family “*Pediomyidae*” and the genus “*Pediomys*” appear to be polyphyletic and are thus invalid as currently defined. In this section, I propose revisions to the taxonomy of “pediomyid” marsupials to preserve monophyly at both the familial and generic levels. The stem marsupial *Iqualadelphis* is retained as family *incertae sedis*, though it has been referenced as “pediomyid”-like (Fox 1987a, b; Johanson 1993). “*Pediomys*” *exiguus*, from the Milk River Formation, is placed in a separate genus, *Apistodon* gen. nov., and also treated as family *incertae sedis*. The other Milk River “pediomyid”, *Aquiladelphis*, is placed in its own monotypic family, the Aquiladelphidae fam. nov. However, a phylogenetic relationship is retained between *Aquiladelphis* and the *Pediomyidae* s.s., with the addition of

Glasbius, under the superfamily Pediomyoidea (new rank). The remainder of the genus “*Pediomys*” s.l. is divided into three genera: *Pediomys* s.s., *Leptalestes* gen. nov., and *Protolambda*. See the “Results” and “Conclusions” sections for comments regarding other groups, such as the “alphadontids” and other stem marsupials.

Family *incertae sedis*

Genus *Apistodon* nov.

Derivation of the name: From the Greek *apistos*, meaning untrustworthy, in reference to the type species’ supposed superficial resemblance to *Pediomys* and long-standing incorrect classification; and the Greek *odontos*, meaning tooth.

Type species: *Apistodon exiguus* (Fox, 1971); UALVP 5536 (holotype), Veregris Coulee, Aquilan: Canada, Alberta (Milk River Formation).

Included species.—Type and only species.

Diagnosis.—Very small marsupial similar to other primitive marsupials in having a paracone taller than the metacone, and a poorly-developed protocone. Differs from primitive marsupials (such as *Kokopellia* and *Iqualadelphis*) in having very strongly developed shearing crests, including well-developed pre- and postprotocristae, and a large stylar cusp in the C position. Differs from “alphadontids” in having greater height differential between paracone and metacone, placement of the stylar cusp in the C position posterior to the ectoflexus, and shallower ectoflexus. Differs from all pediomyids in retention of a wide anterior stylar shelf, a large stylocone, and an unexpanded protocone.

Remarks.—The type species for this genus is removed from the genus *Pediomys*. It was initially described as a species of “*Pediomys*” based on Fox’s (1971) interpretation of a narrow stylar shelf labial to the paracone and a small stylocone. Fox (1987a) later commented that this species does not appear to be pediomyid-like at all, a conclusion strongly supported by the present study. The stylar shelf is not at all reduced, and the taxon retains a large stylocone and a weak, unexpanded protoconal region. In Fox’s original description of “*P.*” *exiguus*, the stylar cusp he called D is more likely a stylar cusp in the C position, based on its location just posterior to the deepest portion of the ectoflexus. The small, blade-like cusp situated further posteriorly corresponds better to cusp D. This is not the same condition seen in “*Pediomys*” *clemensi* Sahni, 1972, because in that species the cusp on the first molar is in a typical location for cusp D. Its position migrates anteriorly through the molar series into one more typical of cusp C. The cusp in question on “*P.*” *exiguus* remains in the same relative position throughout the molar series. Nothing is known of the lower dentition, but it can be inferred that the talonid was not expanded relative to the trigonid as is the case in pediomyids. Not only is the protoconal region relatively small, the paracone is taller than the metacone, as in primitive marsupials, indicating a relatively shorter talonid (Johanson 1996b). Until the discovery of additional, more complete material, *Apistodon* appears to be a generally primitive marsupial with no specific relation to other taxa at the familial level.

Also interesting to note, the Milk River Formation has yielded some of the smallest known Cretaceous marsupial taxa (*Apistodon* and *Varalphadon creber*) along with some of the largest (*Eodelphis* and *Aquiladelphis*). This serves to highlight the high degree of morphological diversity achieved by marsupials as early as the latest Santonian, at least in terms of body size (though cusp morphology hints at strong dietary differences as well).

Stratigraphic and geographic range.—Aquilan: Canada, Alberta (Milk River Formation).

Apistodon exiguus (Fox, 1971)

Fig. 6A–C.

Holotype: UALVP 5536, a RM1.

Included specimens.—See Fox (1971).

Emended diagnosis.—As for the genus.

Stratigraphic and geographic range.—As for the genus.

Genus *Iqualadelphis* Fox, 1987b

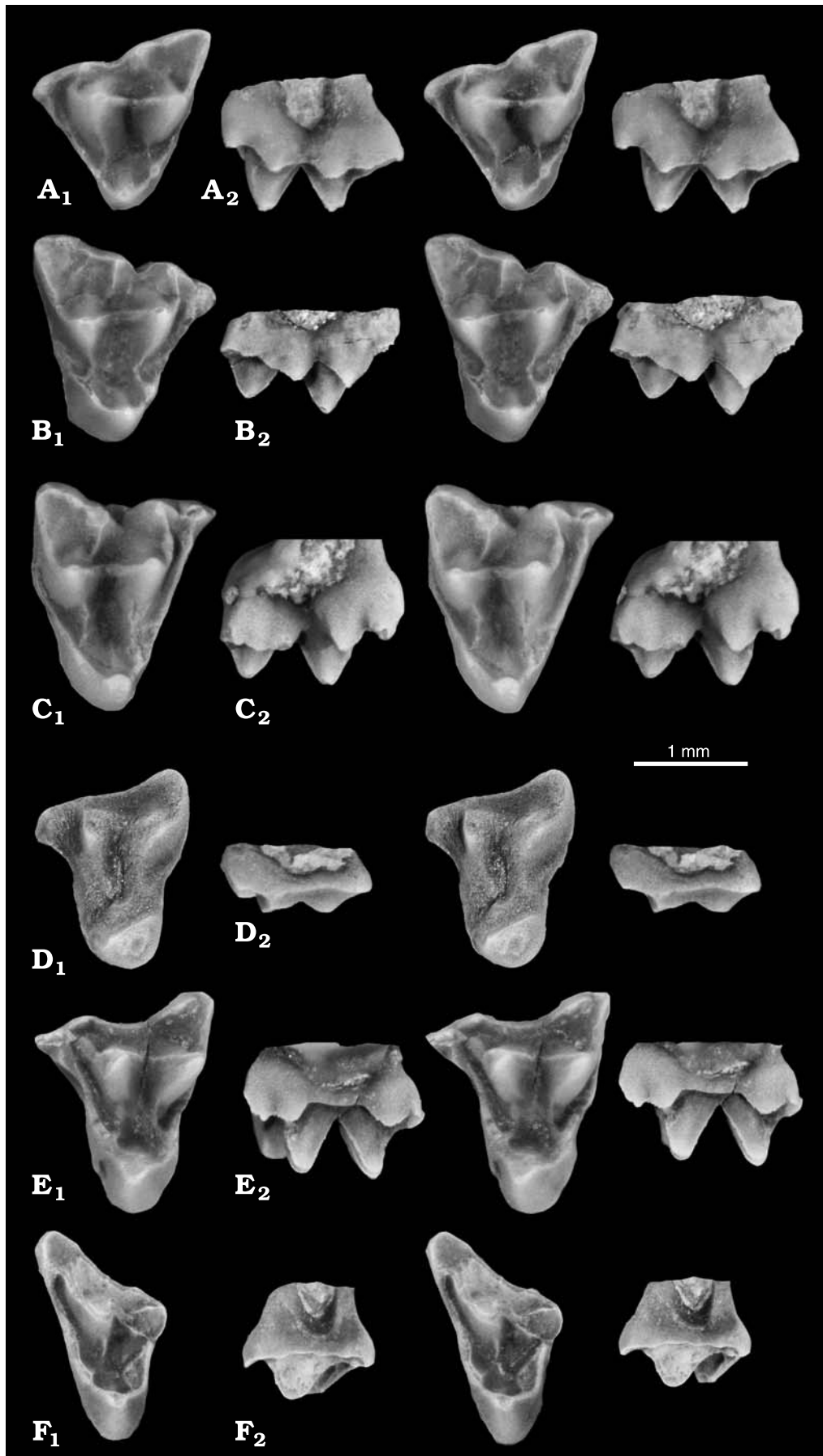
Type species: *Iqualadelphis lactea* Fox, 1987b; UALVP 22823 (holotype), Verdegris Coulee, Aquilan: Canada, Alberta (Milk River Formation).

Included species.—Type and only species.

Emended diagnosis.—Small, generally primitive marsupial with upper molars differing from other basal marsupials (such as *Kokopellia* and *Aenigmadelphys*) in having a lingually placed parastyle, somewhat reduced anterior stylar shelf and corresponding shallowing of the ectoflexus (though not to the degree seen in the PEDIOMYIDAE s.s.), metacone taller than the paracone, protocone subequal in height to the principal cusps, well-developed preprotocrista, and a postprotocrista that extends labially past the base of the metacone. Differs from “alphadontids” in close approximation of paracone and metacone, slight reduction in width of anterior stylar shelf, and absence of a stylar cusp in the C position. Differs from pediomyids (s.s.) in retention of a stylocone, moderate width of the anterior stylar shelf, and a strong preparacrista oriented towards the stylocone. Differs from *Leptalestes* gen. nov. specifically in retaining a well-developed stylar cusp D on M3.

Remarks.—Traditionally, this taxon has been informally allied with the “PEDIOMYIDAE” s.l. based on presumed synapomorphies, but classified as family *incertae sedis* or in a different order (e.g., Fox 1987a, b; Johanson 1993; McKenna and Bell 1997). However, some authors have placed *Iqualadelphis* formally within the “PEDIOMYIDAE” (e.g., Marshall et al. 1990; Kielan-Jaworowska et al. 2004). Though *Iquala-*

Fig. 6. Upper molars (stereophotographs) of *Apistodon exiguus* (Fox, 1971) (A–C) and *Iqualadelphis lactea* Fox, 1987b (D–F), in occlusal (A₁–F₁) and labial (A₂–F₂) views. A. UALVP 29677, LM1. B. UALVP 29691, RM2. C. UALVP 29695, RM3. D. UALVP 22828, LM2. E. 22823, LM3. F. 22829, LM4. All from Verdegris Coulee, Milk River Formation, Alberta, Canada (see Kielan-Jaworowska et al. 2004: fig. 2.19). D, E, figured in Johanson (1993); E, also figured in Fox (1987a, b). →



delphis may superficially resemble some pediomyids (specifically species of *Leptalestes* gen. nov.), I herein exclude it from the Pediomyidae s.s. based on a number of features. It retains a somewhat broad styler shelf with a moderately developed stylocone, a strong preparacrista, and an unexpanded protocone. Eaton et al. (1999) assigned a specimen to cf. *Iqualadelphis* sp., from a unit in southwestern Utah of uncertain affinities. It seems very likely that the specimen does in fact belong to this taxon. The unit was tentatively placed in the Santonian, based on palynomorphs, though Kielan-Jaworowska et al. (2004) suggested some parts of the fauna are more similar to assemblages of Judithian age. Cifelli (1990a) erroneously referred specimens from the Kaiparowits Formation of Utah to this genus, due to difficulties in making comparisons with original material (Richard L. Cifelli, personal communication 2003). Cifelli and Johanson (1994) later corrected this mistake, referring the specimens in question to a new genus and species, *Aenigmadelphys archeri*.

Stratigraphic and geographic range.—Aquilan: Canada, Alberta (Milk River Formation); and ?Aquilan: United States, Utah (uncertain unit).

Iqualadelphis lactea Fox, 1987b

Fig. 6D–F.

Holotype: UALVP 22823, a LM3.

Included specimens.—See Fox (1987b), Johanson (1993), Eaton et al. (1999).

Emended diagnosis.—As for the genus.

Remarks.—As for the genus.

Stratigraphic and geographic range.—As for the genus.

Superfamily Pediomyoidea Simpson, 1927a, new rank

Included families.—Pediomyidae (s.s.) Simpson, 1927a (type family), Aquiladelphidae fam. nov., and Glasbiidae Clemens, 1966.

Diagnosis.—Small to very large, morphologically diverse marsupials distinctive in exhibiting a shallowing of the ectoflexus on all upper molars, a styler cusp in the C position posterior to the deepest part of the ectoflexus, rounding of the labial face of the paracone, reduction in the strength of the internal conular cristae, and basal posterior expansion of the protocone. Lower molars are characterized by a lingual shift of the paraconid into alignment with the metaconid and entoconid (a character shared with the “Alphadontidae”), and a talonid wider than the trigonid. Pediomyoids differ further from all North American Late Cretaceous marsupials, besides the Stagodontidae, in the anterior attachment of the cristid obliqua, which is labially shifted to the midline of the protoconid.

Remarks.—A relationship between *Aquiladelphis* and the Pediomyidae s.s. lends some support to the original inclusion of the genus in that family (Fox 1971). However, the results of this study suggest this relationship cannot be monophyletic without the inclusion of *Glasbius*, making a superfamily the most appropriate level at which to associate the groups.

Though this node is the only polytomy in the strict consensus cladogram (Fig. 5, node 1), all the equally-parsimonious trees suggest *Aquiladelphis* is more closely related to *Glasbius* than to the Pediomyidae s.s. Fox (1979) noted that the most important functional similarity between *Aquiladelphis* and “*Pediomyis*” is an emphasis on crushing, and it is clear crushing was also important in *Glasbius* (though this invites the possibility of convergence). *Glasbius* appeared suddenly in the Lancian, and no good candidates for morphological ancestry are present in the fossil record. This leaves open the possibility that *Aquiladelphis*, species of which have been reported from geographically and geologically wide-ranging localities (Fox 1971; Rigby and Wolberg 1987; Diem 1999), could be an early member of a lineage that diversified in North America, terminating with *Glasbius*. This would not exclude any speculation that *Glasbius* is related to later South American groups, such as the Caroloameghiniinae (Marshall 1987), but it would lend doubt to initial evolution of the group on the southern continent, with later emigration to North America.

The position of the paraconid (in alignment with the metaconid and entoconid) is a feature held in common between the Pediomyoidea and the “Alphadontidae” (this character is mentioned in the diagnosis of the latter group by Kielan-Jaworowska et al. 2004). Though it is lacking in one sampled species of *Alphadon* and, more conspicuously, in *Glasbius*, it was likely present in the common ancestor of the two groups. A lingual position of the paraconid has also been linked to a reduction in the height of the paracone (Johanson 1996b), but the principal upper molar cusps are of subequal height in all but two pediomyoid lineages (*Glasbius* and *Pediomyis* s.s.).

Stratigraphic and geographic range.—Aquilan–Lancian: United States and Canada.

Family Pediomyidae Simpson, 1927a

Included genera.—*Pediomyis* s.s. Marsh, 1889 (type genus), *Leptalestes* gen. nov., and *Protolambda* Osborn, 1898.

Emended diagnosis.—Small to large, morphologically distinctive marsupials differing from other Late Cretaceous North American marsupials in having upper molars characterized by strong suppression of the anterior portion of the styler shelf, loss of the stylocone, lingually shifted parastyle, reduction of the preparacrista, a tall, salient postmetacrista, and strong development of the postprotocrista labial to the metaconule. Lower molars characterized by a more directly labial orientation of the protocristid, and a significant lowering in the height of the hypoconid relative to the entoconid.

Remarks.—The members of the Pediomyidae s.s. (Fig. 5, node 2) are united on the basis of a number of unique features, many of which are linked to a departure from prevallum/postvallid shear (prevalent in primitive marsupials), and an emerging reliance upon postvallum/prevallid shear. Pediomyids have a reduced preparacrista and a lingually shifted parastyle, a change that effectively shortens the preprotocrista, which would reduce *en echelon* shear (Fox 1975). Additionally, the postmetacrista is tall and salient and is paired with a wide postprotocrista, pro-

viding *en echelon* shear on the posterior edge of the upper molar. The reduction of the anterolabial portion of the upper molar and corresponding reduction of prevallum/postvallid shear were likely the cause of a shortening of the protoconid, which is accomplished in pediomyids by a shift of the protoconid posteriorly so that the protoconid approximates a right angle with the lingual margin of the crown. An additional change of uncertain significance is a lowering in height of the hypoconid relative to the entoconid. This would be expected in taxa with a shallow trigon basin, which occludes with the hypoconid (Crompton 1971), but this feature is also present in pediomyids that retain a deep trigon basin.

The basal-most clade of the *Pediomyidae* contains the members of *Pediomys* s.s. (*P. elegans* and an unnamed taxon from the Prince Creek Formation of Alaska; Fig. 5, node 3). This result corroborates Clemens' (1966) speculation that *P. elegans* best represents the primitive dental morphology for all pediomyids (at least those known at the time of his publication), but the fact that it sits at the base of a monophyletic grouping of pediomyid clades contradicts Fox's (1987a) hypothesis that each lineage independently suppressed the stylocone and anterior styler shelf, with no other “pediomyids” passing through a *P. elegans*-like stage. This implies instead that a cusp in the C position, which was present in the ancestral pediomyid (as well as the common ancestor of the other two families in the *Pediomyoidea*), was maintained only in the lineage leading to *P. elegans* and was lost in the other taxa. Strong suppression of the anterior styler shelf and loss of the stylocone are synapomorphies, not homoplasies, for species assigned to “*Pediomys*” s.l. (minus “*P.*” *exiguus*), and the presence of styler cusp in the C position in *P. elegans* only serves to anchor it to the base of the *Pediomyidae*.

Several unnamed pediomyid-like specimens have been figured in the literature (Fox 1987a: fig. 5; Montellano 1992: figs. 32–35; Eaton et al. 1999: fig. 3). While these resemble pediomyid marsupials in many regards, most of these specimens appear to retain a small stylocone on their reduced anterior styler shelves. Further systematic work might demonstrate these specimens represent taxa situated at the very base of the *Pediomyidae* or might link pediomyids to other groups of Late Cretaceous marsupials.

Stratigraphic and geographic range.—Judithian–Lancian: United States and Canada.

Genus *Pediomys* Marsh, 1889

Type species: *Pediomys elegans* Marsh, 1889; YPM 11866 (holotype), V-5003, Lancian: United States, Wyoming (Lance Formation).

Included species.—*Pediomys elegans* Marsh, 1889 (type species) and undescribed taxon from the Prince Creek Formation (William A. Clemens, personal communication 2003).

Emended diagnosis.—Very small- to medium-sized pediomyids differing from all other pediomyids in having a notably reduced paracone, resulting in a large height difference between the paracone and metacone; presence of an accessory cusp posterior to the styler cusp C position but anterior

to the deepest point of the ectoflexus; reduction in the height of the postmetacrista; metaconid significantly taller than paraconid; a talonid significantly wider and with its base lower than that of the trigonid; and a larger height difference between the entoconid and hypoconid, such that the talonid slopes strongly labially.

Remarks.—*Pediomys elegans* and the Prince Creek taxon are the only members of a restricted *Pediomys* (Fig. 5, node 3). The genus is redefined based on the presence of a number of derived features that, despite its basal position within the *Pediomyidae* s.s., likely distance *P. elegans* from the morphology of the actual ancestral pediomyid, such as a significantly lowered paracone, reduced postmetacrista, and a broadly expanded talonid. These features, along with well-developed conules, may suggest a departure from a shearing-based diet, though both species are very small. Both taxa also exhibit (though variably in *P. elegans*) a small accessory cusp anterior to the styler cusp in the C position, just posterolabial to the paracone. It is slightly larger in the Prince Creek form than in *P. elegans*, though it is unlikely that this cusp represents a vestigial stylocone (as suggested by Clemens 1966), since in no Late Cretaceous marsupial taxon is a stylocone located posterior to the paracone. More plausibly, it is a *de novo* feature of limited (if any) functional significance. Twinned cusps are also present in *Aquiladelphus*, though their position labial relative to the paracone, and their anterior connection with the preparacrista, make it more likely the cusps represent a reduced and split stylocone. Among Late Cretaceous marsupial taxa, only *Albertatherium* (Fox 1971) possesses both a stylocone and a preparacrista that runs anteriorly to the parastyle and not the stylocone.

Stratigraphic and geographic range.—“Edmontonian”: United States, Alaska (Prince Creek Formation), Lancian: United States, Wyoming (Lance Formation), South Dakota and Montana (Hell Creek Formation), Canada, Alberta (Scollard Formation), Saskatchewan (Frenchman Formation).

Pediomys elegans Marsh, 1889

Figs. 7, 8.

Neotype: CM 11658, a right fragmentary maxilla with M2–4 (holotype is YPM 11866, a LM2; see Simpson 1929; Clemens 1966).

Included specimens.—See Estes (1964), Sloan and Van Valen (1965), Clemens (1966, 1973a), Lillegraven (1969), Archibald (1982), Breithaupt (1982), Wilson (1983), Johnston and Fox (1984), Fox (1989), Storer (1991), Lofgren (1995), Hunter et al. (1997), Webb (2001), Hunter and Archibald (2002).

Emended diagnosis.—Distinctive from the Prince Creek form in larger size, stronger inflation of the paracone, greater transverse width of the protoconal region of upper molars, consistent presence of an accessory cuspule on the entocristid of lower molars, and more extreme labial placement of the attachment of the cristid obliqua (nearly to the labial edge of the protoconid).

Remarks.—This taxon was among the first Cretaceous mammals of North America to be described, and it remains highly

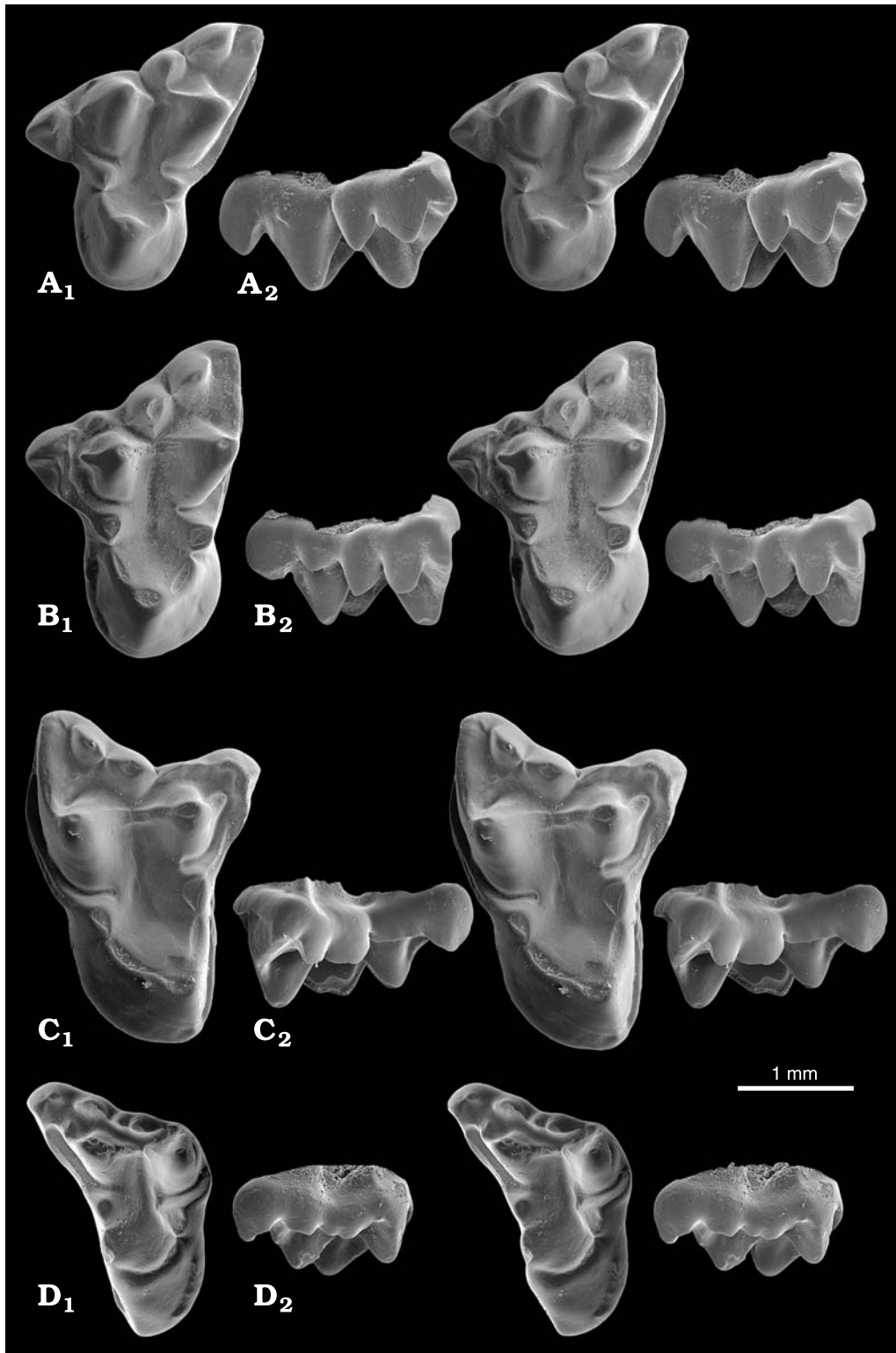


Fig. 7. Upper molars (stereomicrographs) of *Pedimys elegans* Marsh, 1889, in occlusal (A₁–D₁) and labial (A₂–D₂) views. A. OMNH 64262, LM1. B. OMNH 64263, LM2. C. OMNH 63402, RM3. D. OMNH 64265, LM4. All from OMNH V1209, Hell Creek Formation, Montana, USA (see Blacktail Creek local fauna, Kielan-Jaworowska et al. 2004: fig. 2.21).

important to our understanding of Late Cretaceous marsupial diversity. Though situated in the first lineage to branch within the Pediomysidae, *Pedimys elegans* exhibits many derived features that likely distance it from the morphology

expected for an ancestral pediomysid (contrary to earlier ideas by Clemens 1966 and Fox 1987a). *P. elegans* is the only pediomysid to have potentially survived beyond the K/T boundary, with a possible occurrence in the lower Ravenscrag

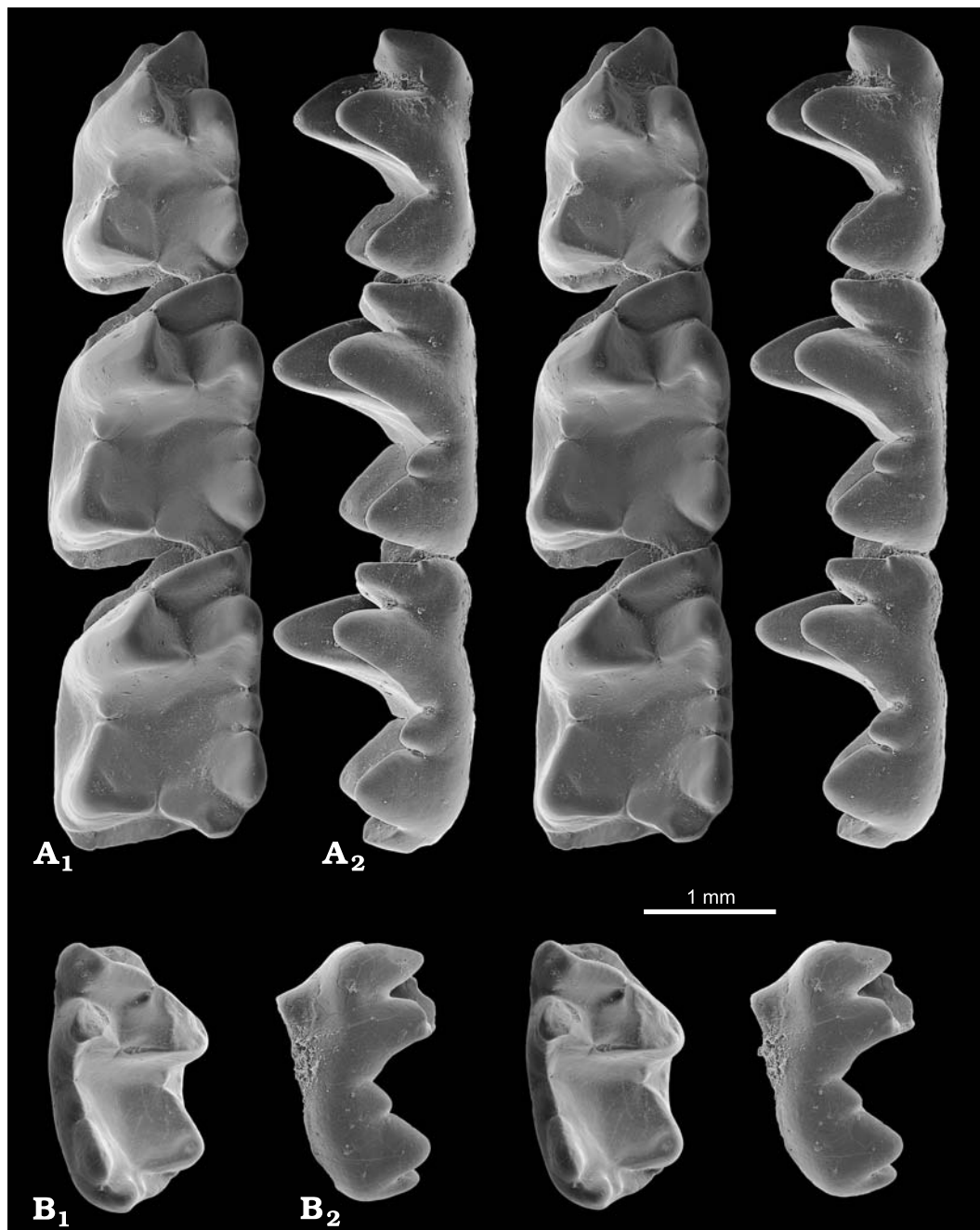


Fig. 8. Lower molars (stereomicrographs) of *Pedimys elegans* Marsh, 1889, in occlusal (A₁, B₁) and lingual (A₂, B₂) views. **A.** OMNH 64266, Lm1–m3. **B.** OMNH 64267, Rm4. All from OMNH V1209, Hell Creek Formation, Montana, USA (see Blacktail Creek local fauna, Kielan-Jaworowska et al. 2004: fig. 2.21). Anterior is up.

Formation (Puercan, Saskatchewan; Johnston and Fox 1984). Fox (1979: fig. 2a) figured a fragmentary upper molar from the Dinosaur Park Formation, described as *Pedimys* cf. *P. elegans*. It is very likely a new species; though very similar to *P. elegans*, the specimen (UALVP 14813) is not only Judithian in age (*P. elegans* is unknown from rocks older than Lancian in age), but it exhibits a stylar cusp D that is smaller than the cusp in the C position, as well as an additional stylar cusp posterior to D. A small pediomysid from the Prince Creek Formation of Alaska has been assigned to *P. elegans*, but it likely belongs to a new, closely related taxon (Clemens

and Nelms 1993; Clemens 1995; William A. Clemens, personal communication 2003).

Stratigraphic and geographic range.—As for the genus.

Genus *Protolambda* Osborn, 1898

Type species: *Protolambda hatcheri* Osborn, 1898; AMNH 2202 (lectotype), Lance Creek, Lancian:United States, Wyoming (Lance Formation).

Included species.—Type species; *Protolambda florencae* (Clemens, 1966); and, tentatively, ?*P. clemensi* (Sahni, 1972).

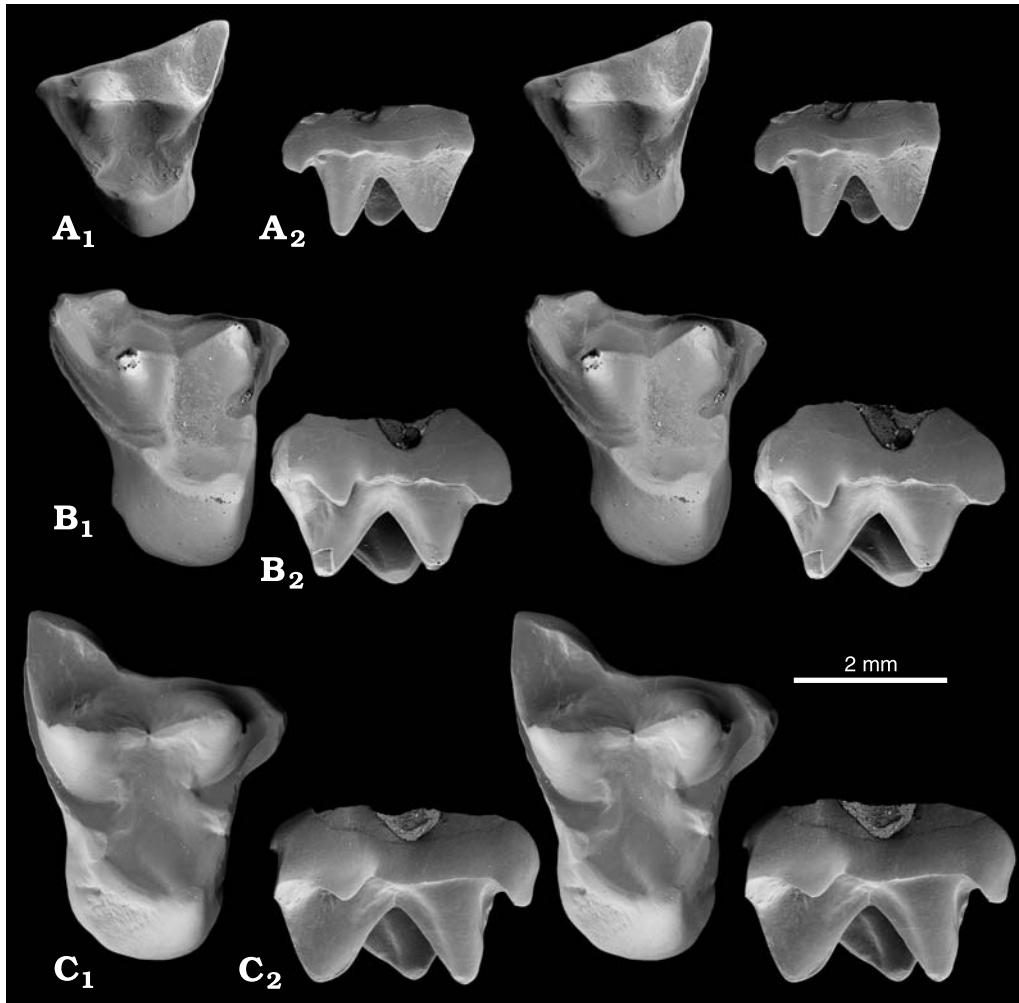


Fig. 9. Upper molars (stereomicrographs) of *Protolambda hatcheri* Osborn, 1898, in occlusal (A₁–C₁) and labial (A₂–C₂) views. A. UCMP 47265, LM1. B. UCMP 52982, RM2. C. UCMP 53199, RM3. A–C, from UCMP V5620, V5818, and V5711 (respectively), Lance Formation, Wyoming, USA (see Clemens 1966: fig. 1).

Diagnosis.—Moderate to large pediomysids differing from all other pediomysids in possessing upper molars with an extremely lingually shifted parastyle (in-line with the apices of the paracone and metacone), near complete reduction of the preparacrista, little change in the shallow depth of the ectoflexus between M1 and M3, inflation of the paracone, a strongly developed centrocrista, and anteroposterior elongation of the trigon basin. Lower molars are characterized by equal height and length of the paraconid and metaconid (plesiomorphies), and robustness of all cusps. The P3 is inflated and robust. Differs specifically from *Pediomys* in loss of a stylar cusp in the C position.

Remarks.—The genus *Protolambda* is resurrected from Osborn (1898), after being merged with “*Pediomys*” by Simpson (1927b). All three of the above species are assigned to *Protolambda*, as *P. hatcheri* remains the type species. This group (Fig. 5, node 4) is characterized by a further lingual shift in the parastyle (beyond that which characterizes pediomysids in general), as well as features that give their molars a relatively broad appearance. The ectoflexus re-

tains a shallow depth posteriorly through the molar series, the preparacrista is nearly absent (though the centrocrista is strong), the paracone is inflated, and the trigon basin is anteroposteriorly long. The lower molars are also robust. The paraconid and metaconid are subequal in height, a reversal from the basal pediomysoid condition, where the metaconid is taller. Most notably, the taxon exhibits an inflated P3, though the ultimate premolar of the lower dentition is only slightly larger than in other taxa. This is significant in that it differs from the condition seen in stagodontids and *Aquiladelphus*, where both the upper and lower ultimate premolars are inflated (presumably, the P3 of *Aquiladelphus* would have been inflated, based on comparisons with stagodontids, though this tooth is unknown in *Aquiladelphus*). These characters are almost certainly adaptations in the direction of durophagy (though possibly just general omnivory), which is reasonable given the large size attained by *P. hatcheri* and *P. florencae*.

Stratigraphic and geographic range.—Judithian–Lancian: United States and Canada.

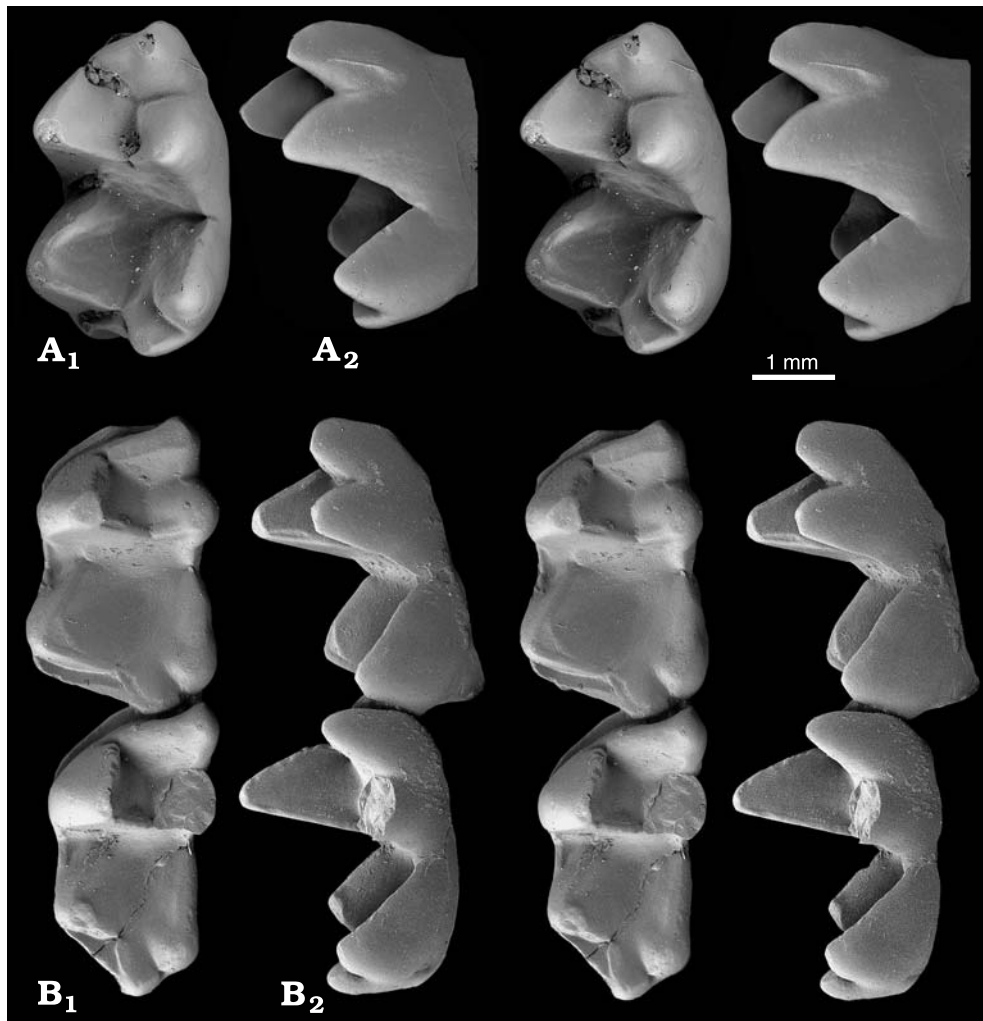


Fig. 10. Lower molars (stereomicrographs) of *Protolambda hatcheri* (Osborn, 1898), in occlusal (A₁, B₁) and lingual (A₂, B₂) views. A. UCMP 46920, Lm2. B. UCMP 46847, Lm3–m4. A, B, from UCMP V5620 and V5711 (respectively), Lance Formation, Wyoming, USA (see Clemens 1966: fig. 1).

Protolambda hatcheri Osborn, 1898

Figs. 9, 10.

Lectotype: AMNH 2202, a right fragmentary maxilla with M3 (see Clemens 1966; paralectotype is AMNH 2203, a M2; see Simpson 1929).

Included specimens.—See Clemens (1961, 1966), Estes (1964), Sloan and Van Valen (1965), Lillegraven (1969), Archibald (1982), Wilson (1983), Whitmore (1985), Lofgren (1995), Hunter et al. (1997), Cifelli et al. (1999), Hunter and Archibald (2002).

Emended diagnosis.—Differs from *Protolambda florencae* in smaller size (though still significantly larger than ?*P. clemensi*), a metacone broader than the paracone (in labial view), and lack of protoconal rugosities. Differs from ?*P. clemensi* in possession of all apomorphies of the genus, except for inflation of both the paracone and P3.

Remarks.—Among pediomyids, *Protolambda hatcheri* is second in size only to *P. florencae*. See Clemens (1966: 45, 49–50) for comments regarding the taxonomic history of this

long-known pediomyid. Specimens left in open nomenclature (hereafter to mean, for example, specimens identified as “*Pediomys*” sp. cf. “*P.*” *hatcheri*) were described by Fox (1979), Storer (1991), and Hunter and Archibald (2002).

Stratigraphic and geographic range.—Judithian: Canada, Alberta (Dinosaur Park Formation); and Lancian: United States, Utah (North Horn Formation); Wyoming (Lance Formation); South Dakota and Montana (Fox Hills and Hell Creek formations); Canada, Alberta (Scollard Formation).

Protolambda florencae (Clemens, 1966)

Figs. 11, 12.

Holotype: UCMP 51440, a left fragmentary maxilla with M2–3.

Included specimens.—See Clemens (1966), Archibald (1982), Wilson (1983), Lofgren (1995), Hunter et al. (1997), Webb (2001).

Distribution.—Lancian: United States, Wyoming (Lance Formation); South Dakota, North Dakota, and Montana (Hell Creek Formation).

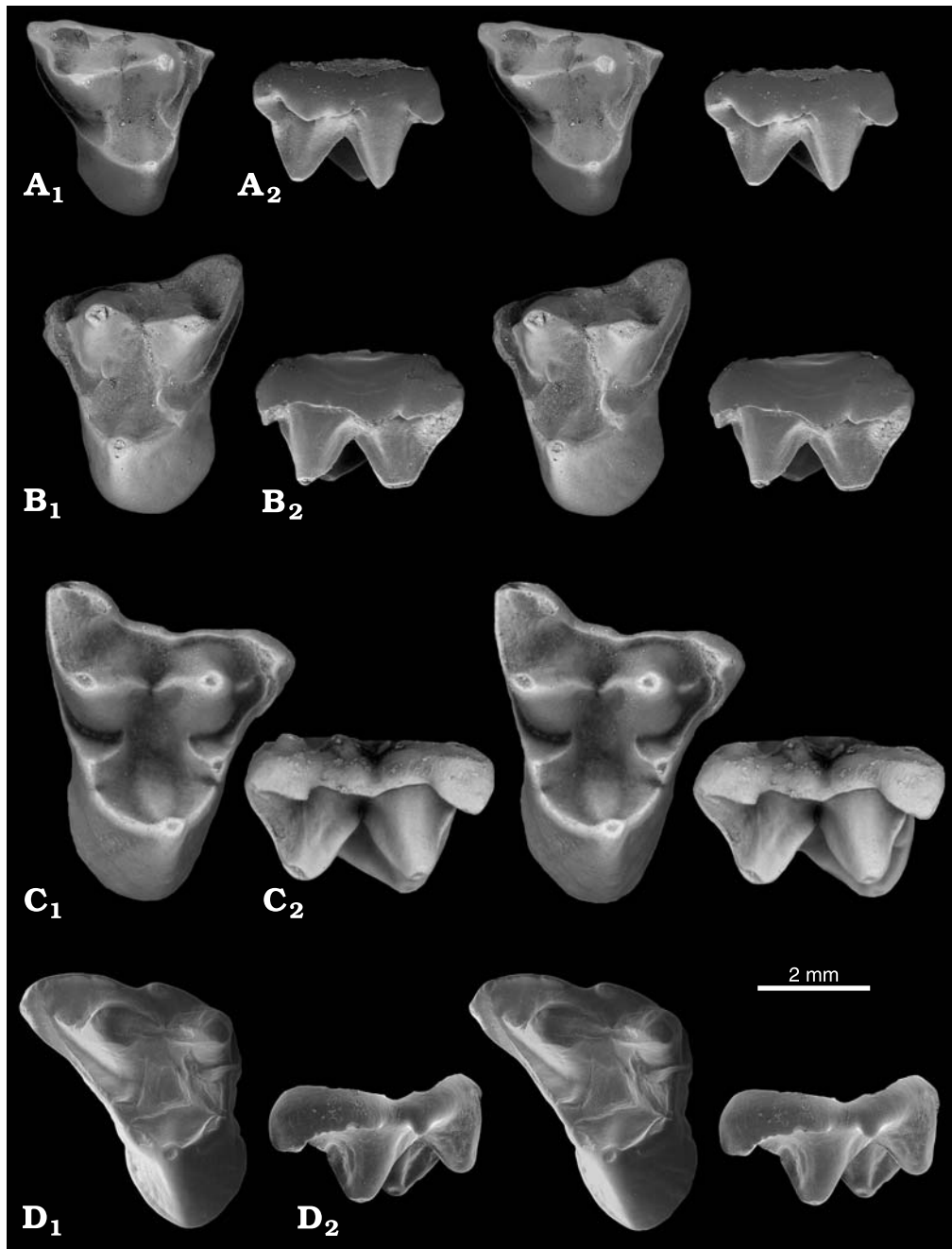


Fig. 11. Upper molars (stereomicrographs) of *Protolambda florencae* (Clemens, 1966), in occlusal (A₁–D₁) and labial (A₂–D₂) views. **A.** UCMP 52338, RM1. **B.** UCMP 47087, LM2. **C.** UCMP 48331, RM3. **D.** UCMP 47283, LM4. A, B, D, from UCMP V5620; C, from UCMP V5711, all Lance Formation, Wyoming, USA (see Clemens 1966: fig. 1); D, figured in Clemens (1966).

Emended diagnosis.—Differs from other species of *Protolambda* in significantly larger size, and an anterior shift in the protoconid, resulting in an obtuse angle between the entoconid and protoconid (reversal of a character diagnostic of the family). Differs from *?Protolambda clemensi* in possession of all apomorphies of the genus, except for inflation of both the paracone and P3.

Remarks.—Most notable about *Protolambda florencae* is its size (largest of all pediomyids), and the fact that it is the only pediomyid completely restricted to the Lancian. Specimens

left in open nomenclature were described by Archibald (1982), Russell (1987), Hunter and Pearson (1996), and Hunter and Archibald (2002).

?Protolambda clemensi (Sahni, 1972)

Figs. 13, 14.

Holotype: AMNH 77373, a fragmentary LM1.

Included specimens.—See Sahni (1972), Fox (1979), Montellano (1992).

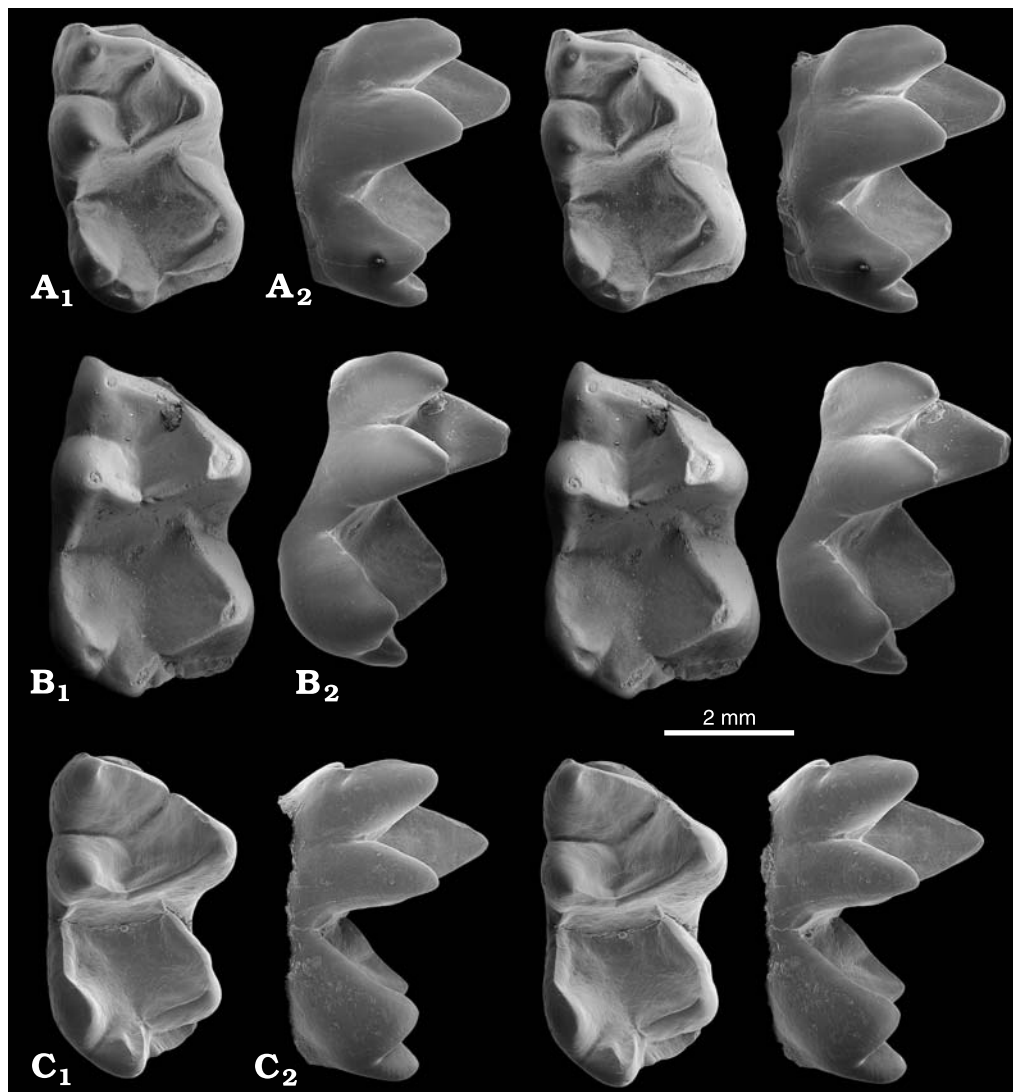


Fig. 12. Lower molars (stereomicrographs) of *Protolambda florencae* (Clemens, 1966), in occlusal (A₁–C₁) and lingual (A₂–C₂) views. A, UCMP 46338, Rm2; B, UCMP 46329, Rm3; C, UALVP 27268, Rm4. All from UCMP V5620, Lance Formation, Wyoming, USA (see Clemens 1966: fig. 1). Anterior is up.

Emended diagnosis.—Differs from *Protolambda hatcheri* and *P. florencae* in styler cusp D positioned anteriolabial relative to the metacone (autapomorphy), a lower postmetacrista, and a broader paracone than metacone (in labial view). Also lacks all apomorphies of the genus, except for inflation of both the paracone and P3.

Remarks.—The referral of this species is tentative due to the absence of many of the diagnostic characters of the genus. However, the upper molars of ?*Protolambda clemensi* share some general similarities to those of the other two species in the genus, with inflated cusps and broad, somewhat deep basins. Based on inferred dietary similarities, which are reached in a similar manner, this species is included in *Protolambda*.

Stratigraphic and geographic range.—Judithian: United States, Montana (Judith River Formation); Canada, Alberta (Dinosaur Park Formation).

Genus *Leptalestes* nov.

Derivation of the name: From the Greek *leptaleos*, meaning thin and delicate, in reference to the very small and slender form of the upper molars of the type species, and the Greek *lestes*, meaning thief, a common suffix for Cretaceous mammals.

Type species: *Leptalestes krejci* (Clemens, 1966); UCMP 51390 (holotype), V-5711, Lancian: United States, Wyoming (Lance Formation).

Included species.—Type species; *L. prokrejci* (Fox, 1979) (equal to or including “*Pediomys*” *fassetti* Rigby and Wolberg, 1987); and, tentatively, ?*L. cooki* (Clemens, 1966); and an undescribed taxon from the St. Mary River Formation (Ronald E. Heinrich, personal communication 2003).

Diagnosis.—Small, primitive pediomyids differing from all other pediomyids in possessing upper molars with a significant connection between the bases of the paracone and metacone, small conules, and lacking protoconal cingula (plesiomorphies). Reversals associated with lower molars consist of the equal width of the trigonid and talonid, equal height of

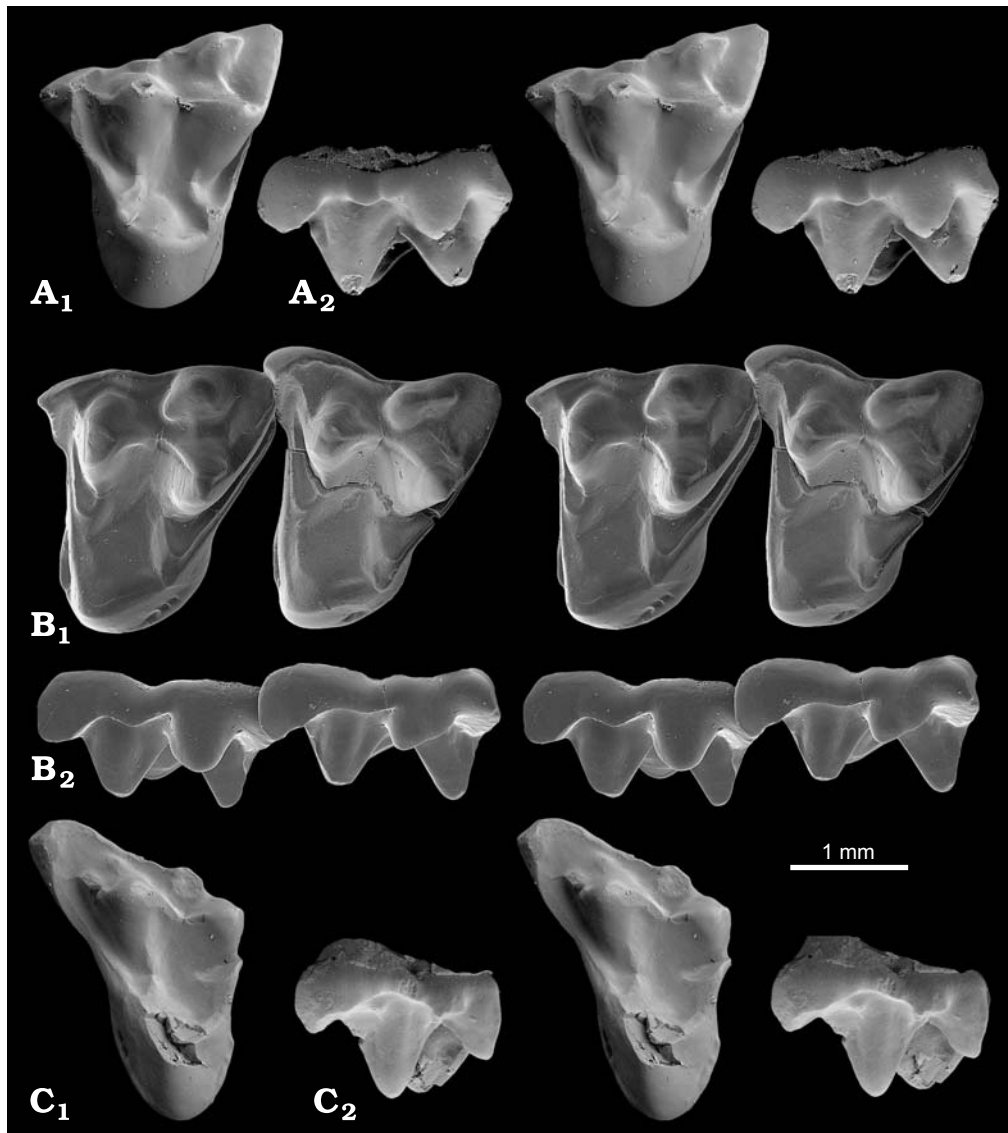


Fig. 13. Upper molars (stereomicrographs) of *?Protolambda clemensi* (Sahni, 1972), in occlusal (A₁–C₁) and labial (A₂–C₂) views. A. UALVP 4229, LM1. B. UALVP 4329, LM2–M3. C. UALVP 4635, LM4. All from UALVP Irvine Locality, Dinosaur Park Formation, Alberta, Canada (see Kielan-Jaworowska et al. 2004: fig. 2.19). B, figured in Fox (1979).

the paraconid and metaconid, and presence of a small entoconid. *Leptalestes* differs further from other pediomyids, and is derived, in exhibiting near complete reduction of stylar cusp D on M3, and possession of a tall postmetacrista and a transversely wide protocone. Differs specifically from *Pediomyis* in loss of a stylar cusp in the C position.

Remarks.—This group (Fig. 5, node 5) is united by a number of features that are plesiomorphic in general for Late Cretaceous North American marsupials, and is derived almost solely in features that place it within the *Pediomyidae* s.s. The taxa exhibit numerous characters seen primarily in stem marsupials, such as poor separation between the paracone and metacone, weak conules, an unexpanded talonid, and a small entoconid. The data suggest that these states are reversals instead of plesiomorphies, since the clade is nested deep within a derived group. However, apomorphies are present in

the group. These taxa show progressive suppression of stylar cusp D posteriorly through the upper molar series, with the cusp reduced to a small rugosity on M3 in some cases. The protoconal region is also transversely wider than in other pediomyids, though *P. elegans* does separately achieve a similar condition. Interestingly, this change does not appear to have a noticeable affect on lower molar morphology, such as a widening of the talonid basin. The St. Mary River taxon is likely referable to this genus, though nothing is known of its lower dentition, and a number of the diagnostic characters for *Leptalestes*, though plesiomorphic, are from the lower molars. The possible inclusion of the St. Mary River pediomyid would make this genus the most diverse in the *Pediomyidae*.

Stratigraphic and geographic range.—Judithian–Lancian: United States and Canada.

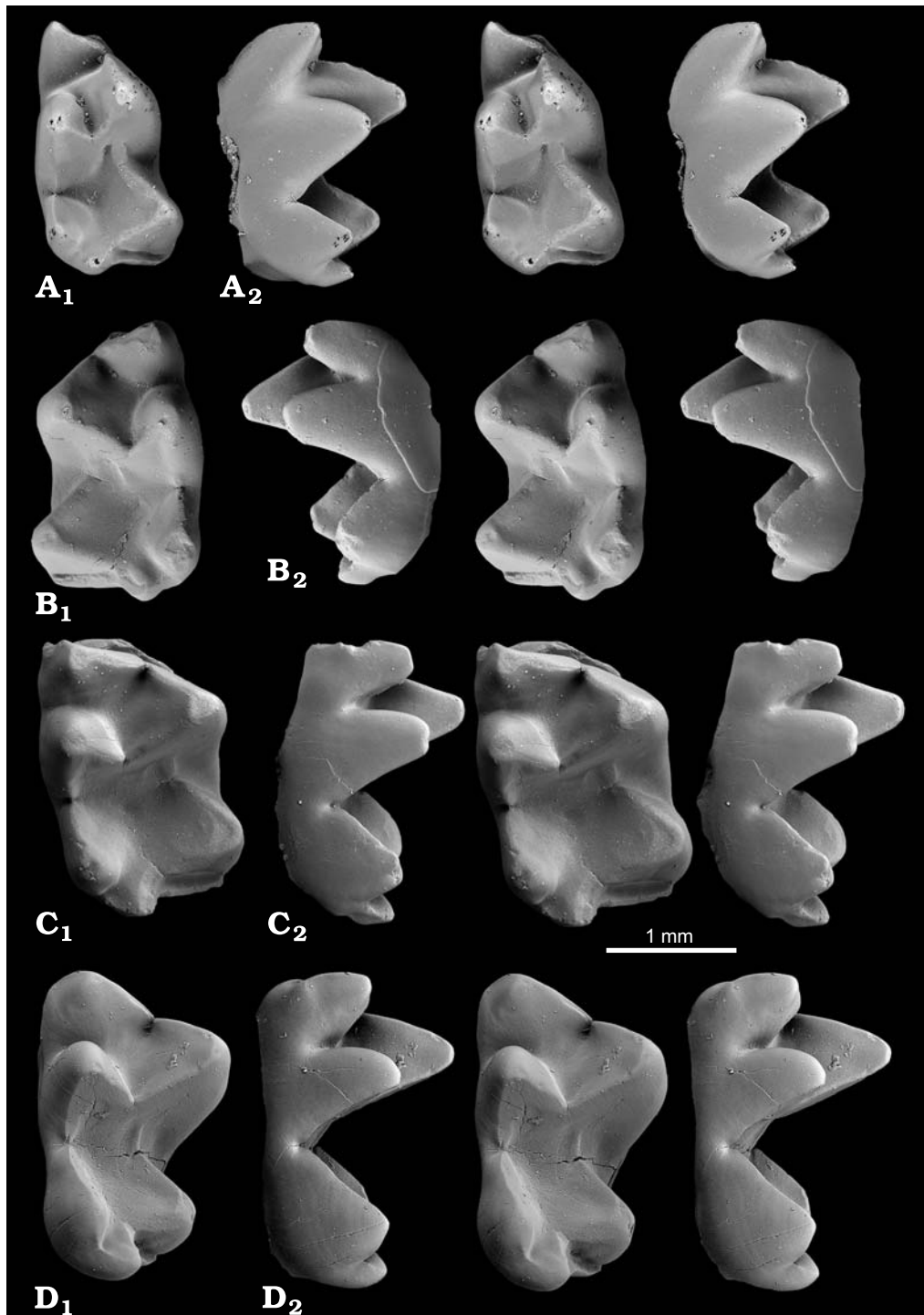


Fig. 14. Lower molars (stereomicrographs) of *Protolambda clemensi* (Sahni, 1972), in occlusal (A₁–D₁) and lingual (A₂–D₂) views. A. UALVP 45622, Rm1. B. UALVP 45630, Lm2. C. UALVP 45628, Rm3. D. UALVP 4203, Rm4. All from UALVP Irvine Locality, Dinosaur Park Formation, Alberta, Canada (see Kielan-Jaworowska et al. 2004: fig. 2.19). Anterior is up.

Leptalestes krejci (Clemens, 1966)

Figs. 15, 16.

Holotype: UCMP 51390, a left fragmentary maxilla with P3 and M1–3.

Included specimens.—See Clemens (1966), Lillegraven (1969), Archibald (1982), Wilson (1983), Storer (1991),

Lofgren (1995), Cifelli et al. (1999), Webb (2001), Hunter and Archibald (2002).

Emended diagnosis.—Differs from other species of *Leptalestes* in having a metacone both taller and broader (in labial view) than the paracone. Differs specifically from the St. Mary River form in having smaller conules that are placed closer to

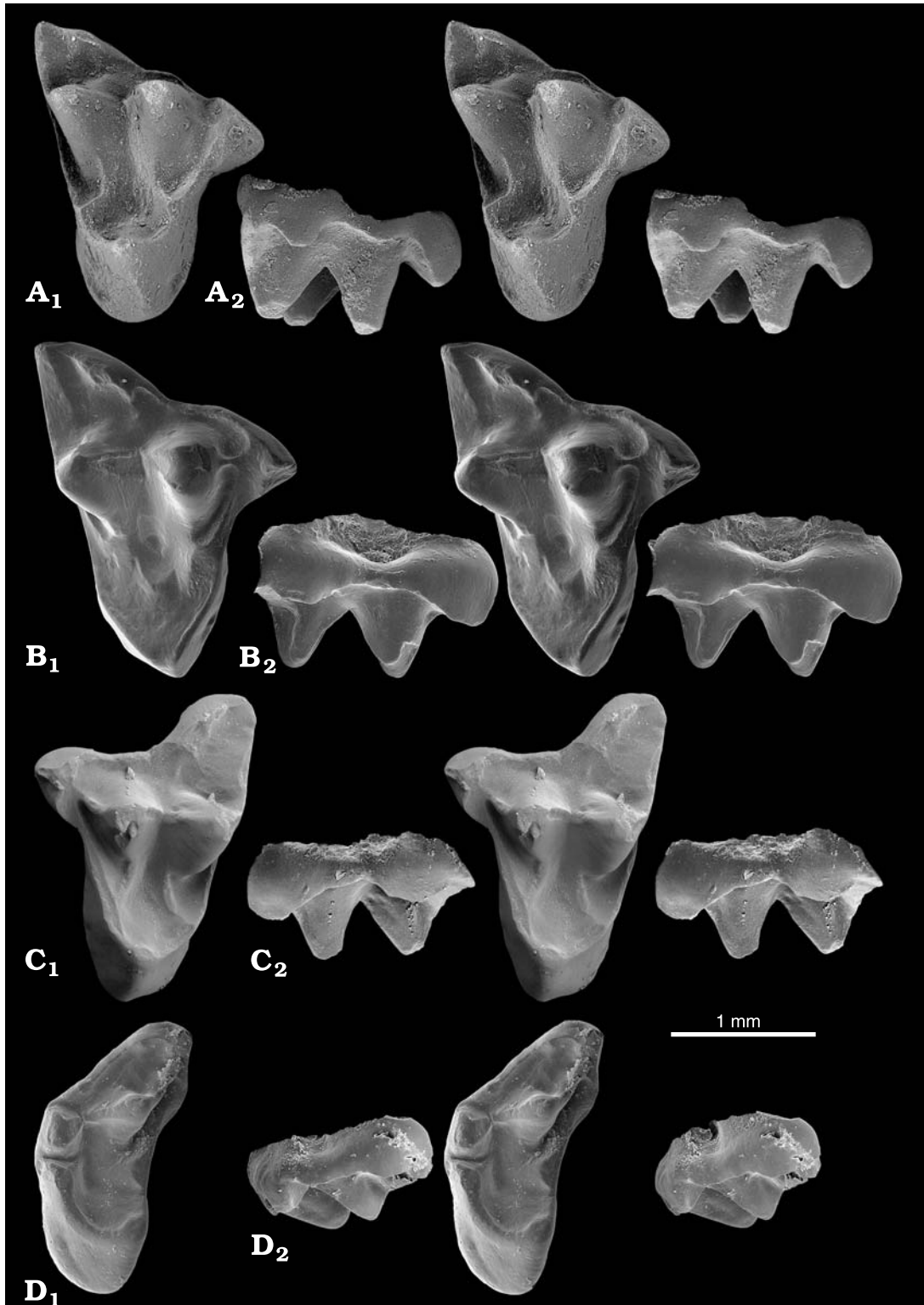


Fig. 15. Upper molars (stereomicrographs) of *Leptalestes krejci* (Clemens, 1966), in occlusal (A₁–D₁) and labial (A₂–D₂) views. A. UALVP 3804, RM1. B. UALVP 2410, RM1–M3 (M2 figured). C. UALVP 4059, LM3. D. UALVP 3812, RM4. All from UALVP KUA-1, Scollard Formation, Alberta, Canada (see Lillegraven 1969). B, figured in Lillegraven (1969); D, figured in Clemens and Russell (1965).

the protocone. Differs specifically from *?Leptalestes cooki* in weaker conules, absence of protoconal cingula, a talonid of equal width to the trigonid, and a metaconid of equal width to the paraconid (in lingual view).

Remarks.—As is the case for *Protolambda florencae*, specimens confidently assigned to *Leptalestes krejci* are known only from the Lancian. However, a lower molar was described from the lower St. Mary River Formation by Sloan

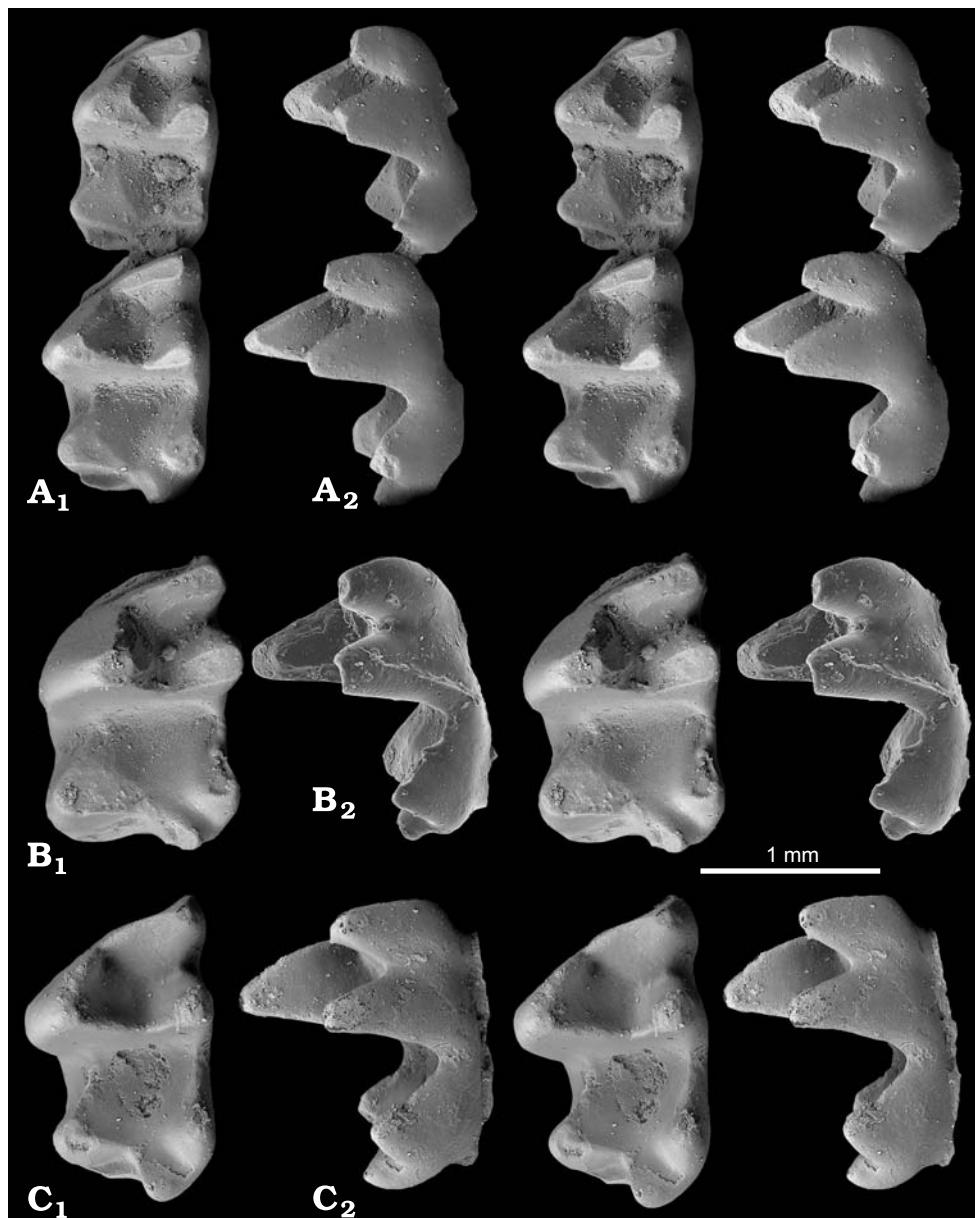


Fig. 16. Lower molars (stereomicrographs) of *Leptalestes krejci* (Clemens, 1966), in occlusal (A₁–C₁) and lingual (A₂–C₂) views. A. UCMP 47036, Lm1–m3 (m1–m2 figured). B. UCMP 46860, Lm2. C. UCMP 46487, Lm3–m4 (m4 figured). A–C, from UCMP V5620, V5711, and V5616 (respectively), Lance Formation, Wyoming, USA (see Clemens 1966: fig. 1). Anterior is up.

and Russell (1974) and referred to “*Pedimys*” cf. “*P.*” *krejci*, giving this taxon a possible “Edmontonian” occurrence. Other specimens left in open nomenclature were described by Wilson (1983), Hunter et al. (1997), and Hunter and Archibald (2002).

Stratigraphic and geographic range.—“Edmontonian”: Canada, Alberta (St. Mary River Formation); and Lancian: United States, Wyoming (Lance Formation); South Dakota and Montana (Hell Creek Formation); Utah (North Horn Formation); Canada, Alberta (Scollard Formation); Saskatchewan (Frenchman Formation).

Leptalestes prokrejci (Fox, 1979)

Figs. 17, 18.

Holotype. UALVP 14817, a left fragmentary maxilla with M1–2.

Included specimens.—See Sahni (1972), Fox (1979), Rigby and Wolberg (1987), Montellano (1992), Peng (1997).

Emended diagnosis.—Differs from other species of *Leptalestes* in frequent presence of an accessory cuspule along the entocristid. Differs specifically from the St. Mary River form in having smaller conules that are placed close to the protocone. Differs specifically from ?*L. cooki* in having weaker conules, absence of protoconal cingula, a talonid of equal width to the trigonid, and a metaconid of equal width to the paraconid (in lingual view).

Remarks.—This taxon is strikingly similar to *Leptalestes krejci*, leading Fox (1979; 1987a) to suggest a possible an-

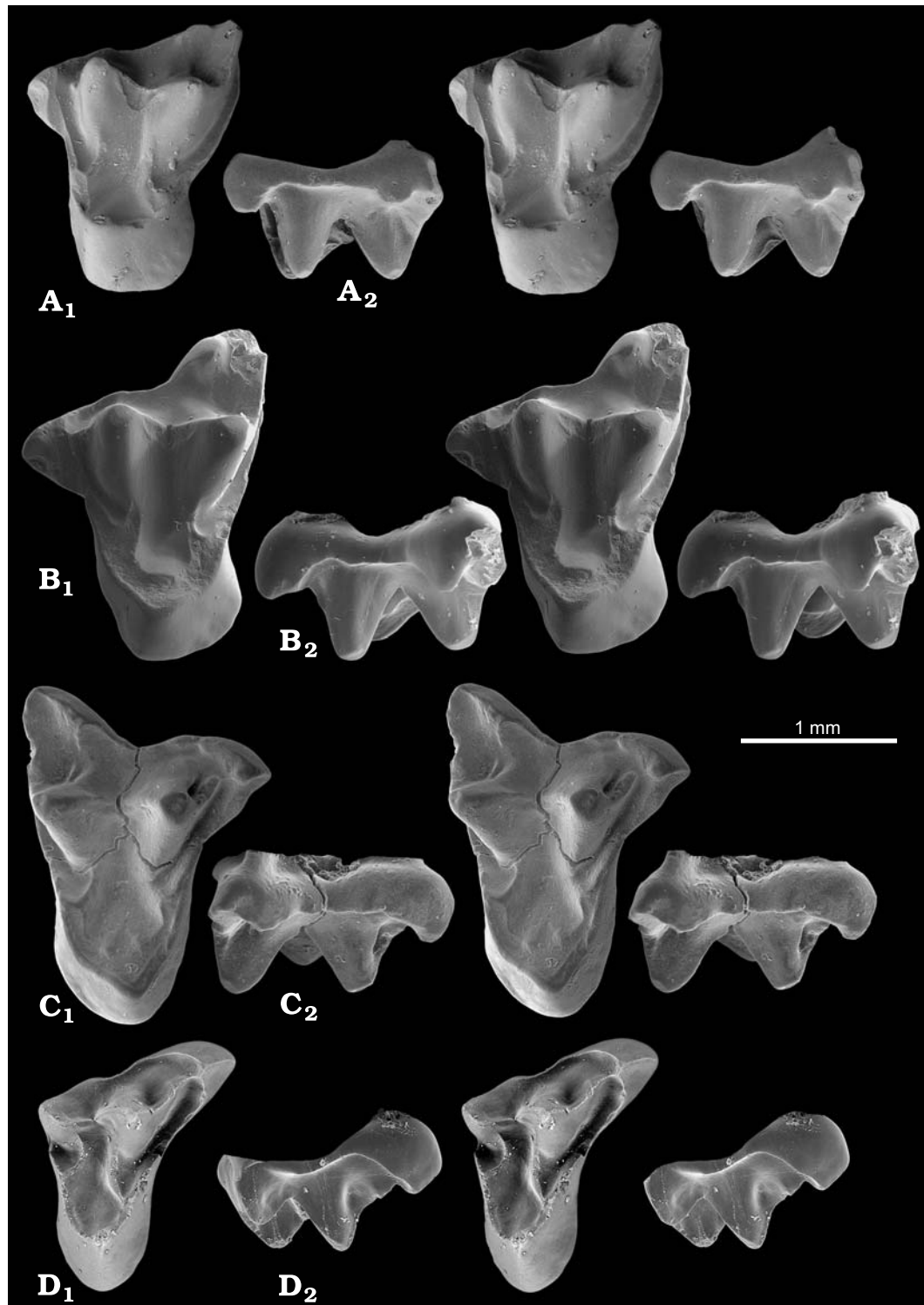


Fig. 17. Upper molars (stereomicrographs) of *Leptalestes prokrejicii* (Fox, 1979), in occlusal (A₁–D₁) and labial (A₂–D₂) views. A. UALVP 55587, LM1. B. UALVP 6850, LM2. C. UALVP 29764, RM3. D. UALVP 55588, RM4. All from UALVP Irvine Locality, Dinosaur Park Formation, Alberta, Canada (see Kielan-Jaworowska et al. 2004: fig. 2.19).

cestral-descendent relationship between the two. “*Pedionmys*” *fassetti*, the pediomyid species described by Rigby and Wolberg (1987) from the Lower Hunter Wash local fauna of the San Juan Basin, New Mexico, is synonymous with *L. prokrejicii* and not a new species. Rigby and Wolberg (1987)

described “*P.*” *fassetti* as most nearly resembling “*P.*” *exiguus*, with the exception of possessing a larger stylocone (“...about one-half the size of the paracone...” Rigby and Wolberg 1987: 67) and a smaller stylocone D. This description appears to be based primarily on a molar they designate

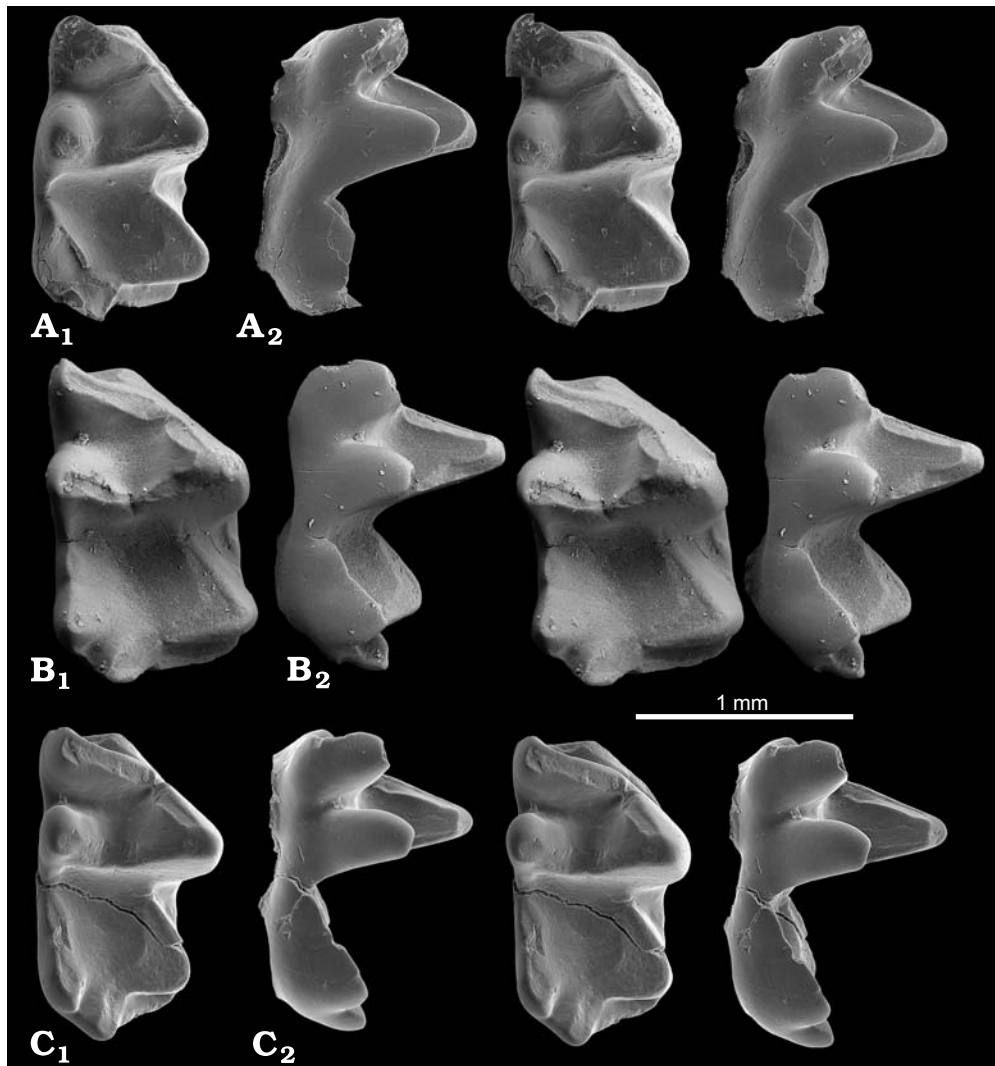


Fig. 18. Lower molars (stereomicrographs) of *Leptalestes prokrajcii* (Fox, 1979), in occlusal (A_1 – C_1) and lingual (A_2 – C_2) views. **A.** UALVP 6757, Rm2–m4 (m2 figured). **B.** UALVP 6760, Rm3. **C.** UALVP 55585, Rm4. All from UALVP Irvine Locality, Dinosaur Park Formation, Alberta, Canada (see Kielan-Jaworowska et al. 2004: fig. 2.19). Anterior is up.

as M1 (UNM B1738), yet this specimen is likely not referable to the taxon represented by the holotype. There is little evidence for a stylocone of any appreciable size on the holotype (a stylocone the size of the one on UNM B1738, even if in the process of suppression, would still be detectable on the penultimate molar). Additionally, the styler shelf of UNM B1738 is wider than that on the holotype, whereas the typical condition seen in pediomyids is for the styler shelf to increase in width through the molar series, as in all other dentally similar marsupials. The specimen designated as M1 is therefore more likely referable to a species of *Alphadon*, a taxon which is common in the fauna. Based on features of the composite upper third molar, a more probable conclusion is that the taxon represented by UNM B1734 (holotype) and UNM B1737 is *Leptalestes prokrajcii* and not a new species, making “*P.*” *fassetti* a junior subjective synonym. Also, referral of lower molars UNM B1724 and UNM B1725 to this taxon is questionable. The cristid obliqua meets the trigonid

barely labial to the protocristid notch, a condition more reminiscent of “alphadontids”. The assessment that *L. prokrajcii* is present in the Fruitland-Kirtland formations lends support to the idea that the Hunter Wash local fauna is of Judithian age, since this taxon is present in northern formations of that age.

Stratigraphic and geographic range.—Judithian: United States, Montana (Judith River Formation); New Mexico (Fruitland-Kirtland formations); Canada, Alberta (Judith River Group and Dinosaur Park Formation).

?Leptalestes cooki (Clemens, 1966)

Figs. 19, 20.

Holotype: UCMP 47738, a right fragmentary maxilla with P3 and M1–3.

Included specimens.—See Clemens (1966, 1973a), Diem (1999), Webb (2001), Hunter and Archibald (2002).

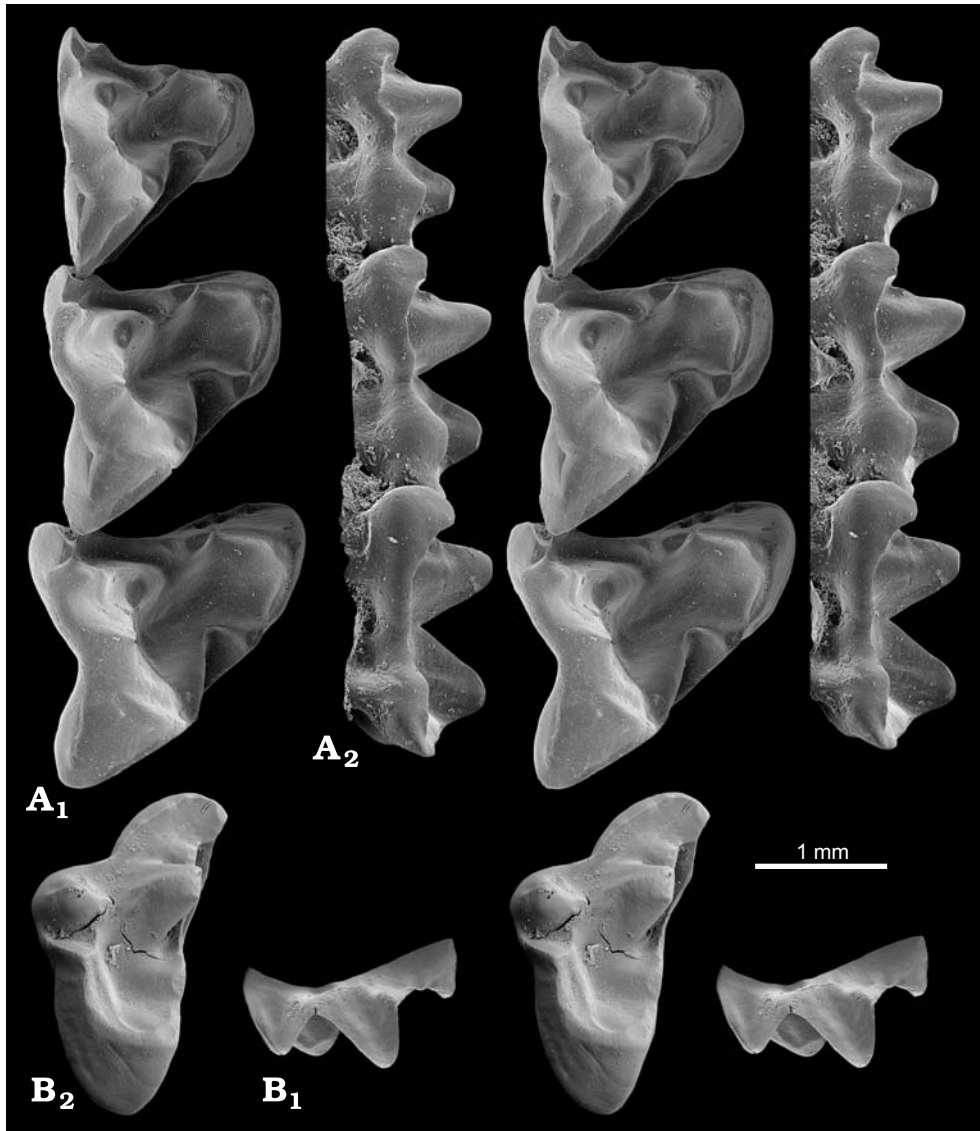


Fig. 19. Upper molars (stereomicrographs) of *?Leptalestes cooki* (Clemens, 1966), in occlusal (A₁, B₁) and labial (A₂, B₂) views. **A.** UCMP 47738, RP3, M1–M3 (M1–M3 figured). **B.** UCMP 53256, RM4. A, B, from UCMP V5711 and V5616 (respectively), Lance Formation, Wyoming, USA (see Clemens 1966: fig. 1). A, figured in Clemens (1966).

Emended diagnosis.—Resembles other species of *Leptalestes* in apomorphies characteristic of the genus, such as near complete reduction of styler cusp D on M3, possession of a tall postmetacrista, and loss of a styler cusp in the C position. Differs from other species of *Leptalestes* in having strong conules, protoconal cingula, a talonid wider than the trigonid, and a metaconid larger than the paraconid (in lingual view).

Remarks.—This species is tentatively referred to *Leptalestes*, based on a few synapomorphies, in the light of numerous character differences between it and the other two included and described species. *?L. cooki* more closely reflects the morphology of a typical stem pediomyid, as opposed to *L. krejci* and *L. prokrejci*, which exhibit several features more characteristic of stem marsupial taxa (such as, interestingly, *Iqualadelphis*). Additionally, the presence of *?L. cooki* in the Lower

Hunter Wash local fauna, along with *Aquiladelphis minor* and *L. prokrejci*, demonstrates that pediomyoids had achieved some degree of diversity in the southern United States at least by the Judithian, though their overwhelming diversity and sheer abundance in northern faunas from the Aquilan through the end of the Cretaceous still suggests that these taxa dispersed southward after an initial northern diversification. Specimens left in open nomenclature were described by Sloan and Russell (1974) and Archibald (1982).

Stratigraphic and geographic range.—Judithian: United States, New Mexico (Fruitland and Kirtland formations); “Edmontonian”: United States, Colorado (Williams Fork Formation); Canada, Alberta (St. Mary River Formation); and Lancian: United States, Wyoming (Lance Formation); South Dakota (Fox Hills Formation); Montana (Hell Creek Formation).

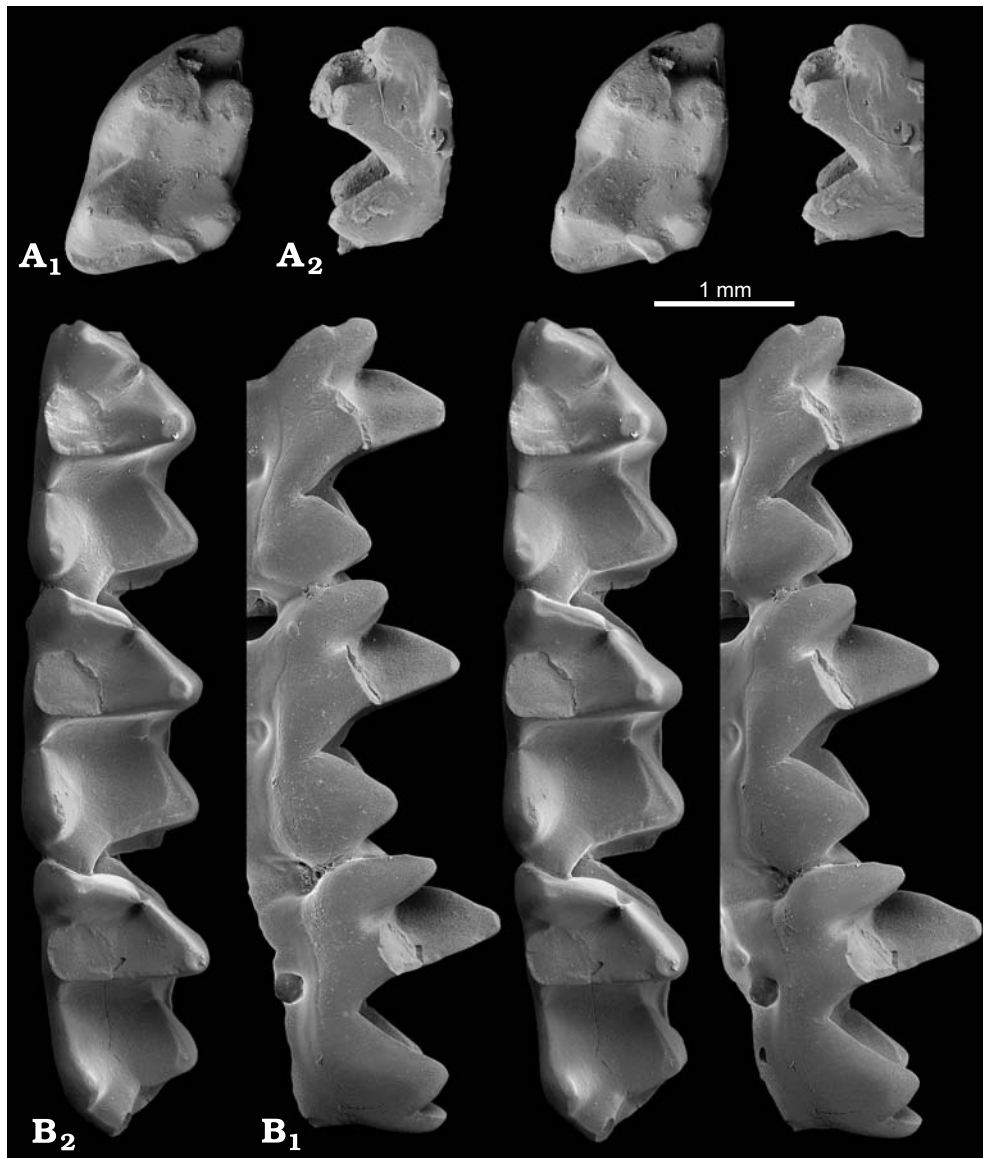


Fig. 20. Lower molars (stereomicrographs) of *?Leptalestes cooki* (Clemens, 1966), in occlusal (A₁, B₁) and lingual (A₂, B₂) views. A. UCMP 46883, Lm1–m3 (m1 figured). B. UCMP 51434, Rm2–m4. A, B, from UCMP V5620 and V5815 (respectively), Lance Formation, Wyoming, USA (see Clemens 1966: fig. 1).

Family Aquiladelphidae nov.

Included genera.—*Aquiladelphis* Fox, 1971 (type genus by monotypy).

Diagnosis.—As for the type and only genus.

Remarks.—The genus *Aquiladelphis* was originally allied with “*Pediomys*” s.l. in the “*Pediomyidae*” s.l. based on shared suppression of the anterior styler shelf and labial attachment of the cristid obliqua. However, it appears that these characters are somewhat wider distributed across Late Cretaceous marsupials, and that *Aquiladelphis* is not nearly as derived as the *Pediomyids* (s.s.) in either of these respects. There does appear to be some relationship between the two, but the data suggest it exists above the familial level (Fig. 5, node 1). However, the species of this genus are sufficiently derived and different from all other contemporaneous taxa to

warrant their placement in a monotypic family. See “Comments” on the *Pediomyoidea* (above) for discussion on a relationship between the *Aquiladelphidae* and the *Glasbiidae*.

Stratigraphic and geographic range.—As for the type and only genus.

Genus *Aquiladelphis* Fox, 1971

Included species.—*Aquiladelphis incus* Fox, 1971 (type species) and *A. minor* Fox, 1971 (equal to or including *A. paraminor* Rigby and Wolberg, 1987).

Emended diagnosis.—Very large marsupials differing from most Late Cretaceous contemporary taxa (exceptions including the *Stagodontidae* and *Glasbius*) in possessing numerous supposed adaptations for durophagy, such as heavy, robust cusps and broad, shallow basins on all molars. Differ

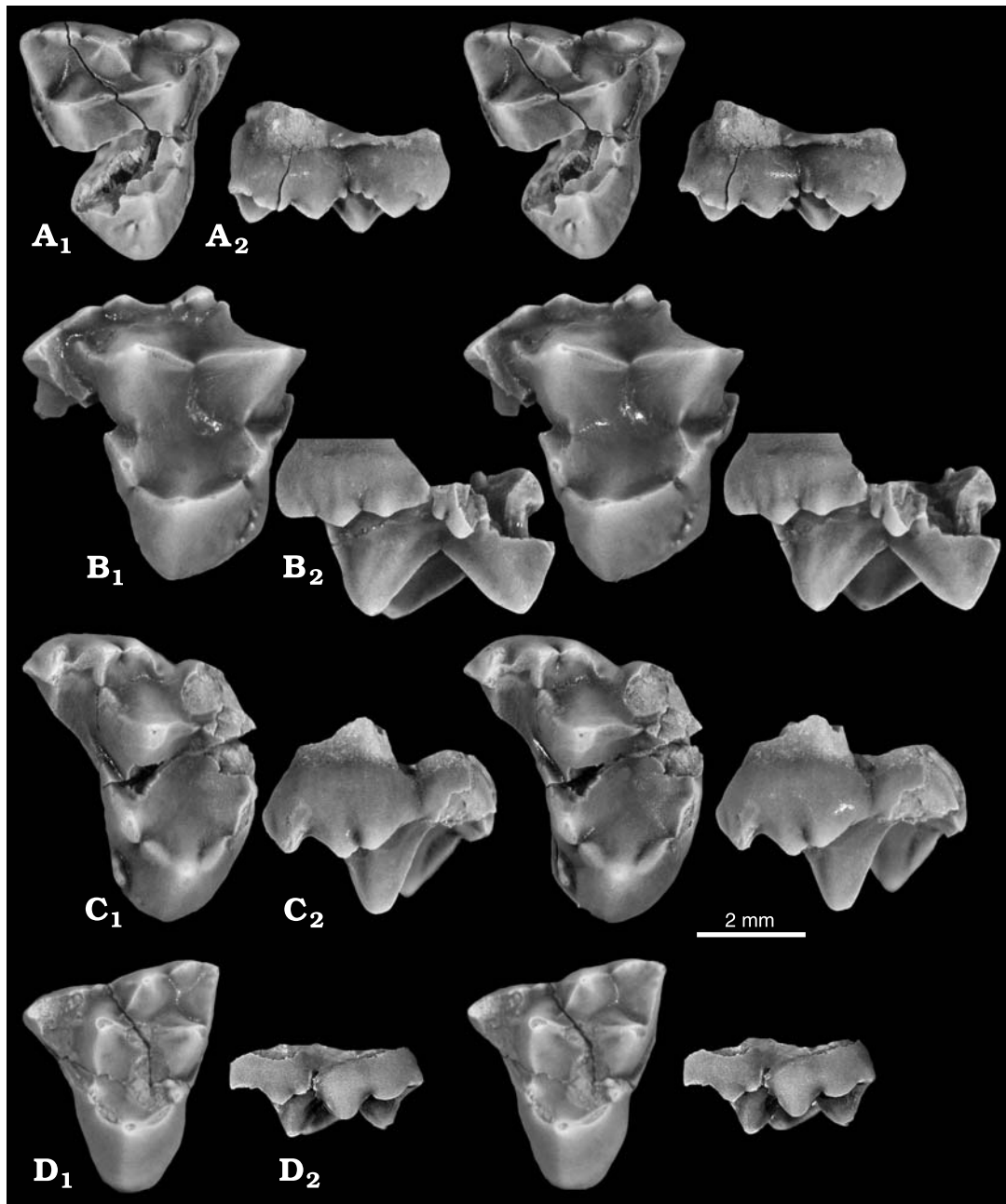


Fig. 21. Upper molars (stereophotographs) of *Aquiladelphis incus* Fox, 1971 (A–C) and *Aquiladelphis minor* Fox, 1971 (D), in occlusal (A₁–D₁) and labial (A₂–D₂) views. A. UALVP 29697, RM2. B. UALVP 5522, LM3. C. UALVP 5523, LM4. D. UALVP 29674, LM2. All from Verdigris Coulee, Milk River Formation, Alberta, Canada (see Kielan-Jaworowska et al. 2004: fig. 2.19). B, C, figured in Fox (1971).

from other pediomyoids in the very large size of the styler cusp in the C position. Similar to pediomyoids in reduction of the anterior styler shelf, but differ in retention of a stylocone (often in the form of a pair of small, broad cusps, though some specimens retain a single, moderately developed cusp), presence of a strong preparacrista, and a paracone taller than the metacone (plesiomorphies). Resemble stagodontids and *Protolambda* in inflation of the ultimate lower premolar.

Remarks.—The “Edmontonian” occurrence of this genus is based on specimens from the Williams Fork Formation, Col-

orado, described in the unpublished Master’s thesis of Diem (1999).

Stratigraphic and geographic range.—Aquilan: Canada, Alberta (Milk River Formation); Judithian: United States, New Mexico (Fruitland-Kirtland formations); and “Edmontonian”: United States, Colorado (Williams Fork Formation).

Aquiladelphis incus Fox, 1971

Figs. 21A–C, 22A.

Holotype: UALVP 5522, a fragmentary LM3.

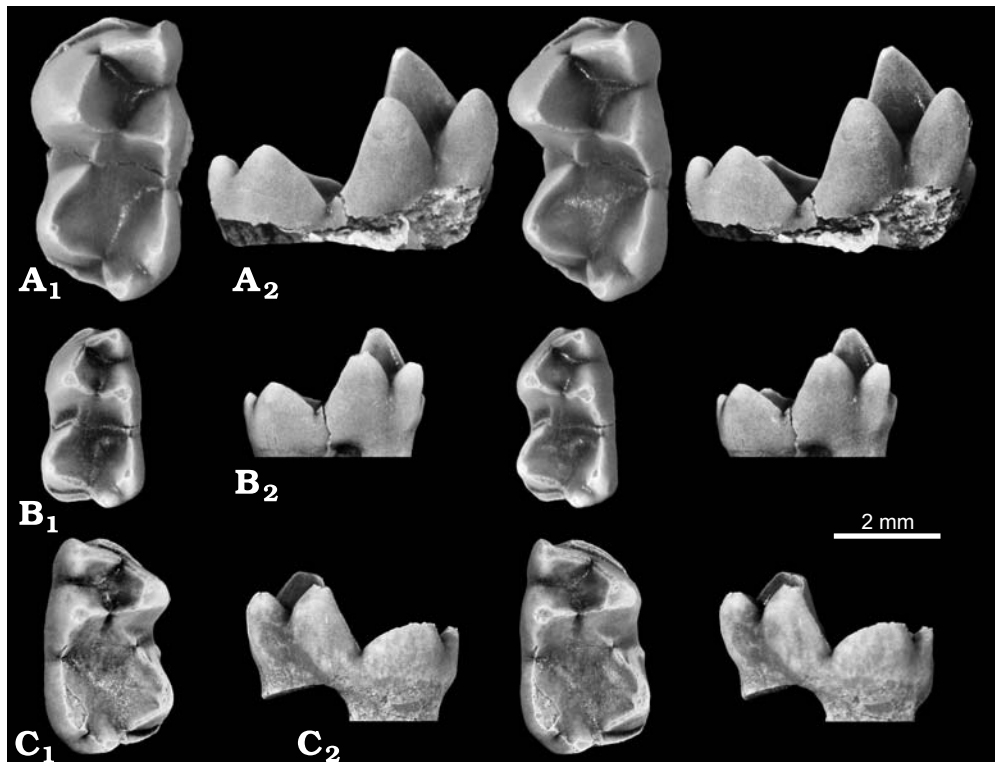


Fig. 22. Lower molars (stereophotographs) of *Aquiladelphis incus* Fox, 1971 (A) and *Aquiladelphis minor* Fox, 1971 (B, C), in occlusal (A₁–C₁) and lingual (A₂–C₂) views. A. UALVP 29711, Lm4. B. UALVP 5534, Lm2. C. UALVP 5531, Rm3. All from Verdigris Coulee, Milk River Formation, Alberta, Canada (see Kielan-Jaworowska et al. 2004: fig. 2.19). B, C, figured in Fox (1971).

Included specimens.—See Fox (1971), Diem (1999).

Stratigraphic and geographic range.—Aquilan: Canada, Alberta (Milk River Formation); and “Edmontonian”: United States, Colorado (Williams Fork Formation).

Diagnosis (from Fox 1971: 155).—“The larger species of *Aquiladelphis*. Known premolars strong but not bulbous; pre-ultimate upper molars longer anteroposteriorly than wide transversely; lower molars broad.”

Aquiladelphis minor Fox, 1971

Figs. 21D, 22B, C.

Holotype: UALVP 5539, a fragmentary RM2.

Included specimens.—See Fox (1971), Rigby and Wolberg (1987).

Diagnosis (from Fox 1971: 157).—“A species of *Aquiladelphis* smaller in dental dimensions than *A. incus*. Upper molars with two stylar cusps B; stylar cusp C very large and the largest stylar cusp; stylar cusp D large, cusp E small.”

Remarks.—Based on lower molars alone, a species of *Aquiladelphis* is certainly present in the Fruitland-Kirtland formations. However, it is not clear that the published specimens are sufficiently different from *A. minor* to warrant recognition of the separate species, *A. paraminor* Rigby and Wolberg, 1987. The differences between the two species cited by Rigby and Wolberg (1987) do not appear to correlate with the specimens, and it is likely the m1 they refer to for most of the significant

comparisons belongs to a different taxon (as appears to be the case in their other described “pediomyid”, “*Pediomys*” *fasseti*). However, the fragmentary upper molar assigned as the holotype for *A. paraminor* (Rigby and Wolberg 1987: fig. 4) departs somewhat from *A. minor*. The position of the parastyle and the cusp designated as C are problematic. In all other upper molars of *Aquiladelphis*, the parastyle is positioned much more lingually, nearly even with the paracone. Additionally, the stylocone, while often split into two cusps, is usually restricted to a portion of the stylar shelf directly labial to the paracone, while the cusp in C position is always positioned posterior to the deepest point of the ectoflexus. It is possible that this molar represents an M4, though the cusp posterolabial to the paracone does not agree well with the M4 of *A. incus* (Fox 1971: pl. 4B). However, in general form the holotype of *A. paraminor*, if it represents a species of *Aquiladelphis*, is most reminiscent of an M4. This locus is unknown in *A. minor*, and since the lower molars referred to *A. paraminor* are essentially not different from *A. minor*, I propose synonymizing the two species. *A. minor* has priority, making *A. paraminor* a junior subjective synonym. Rigby and Wolberg (1987) also refer a lower molar described by Fox (1979: fig. 3a) from the “Oldman” Formation to *A. paraminor*. Fox (1979) referred the specimen to “*Pediomys*” cf. *P. hatcheri*, and though all other specimens referred to *A. paraminor* likely belong to *A. minor*, Fox’s original assessment will not be questioned here.

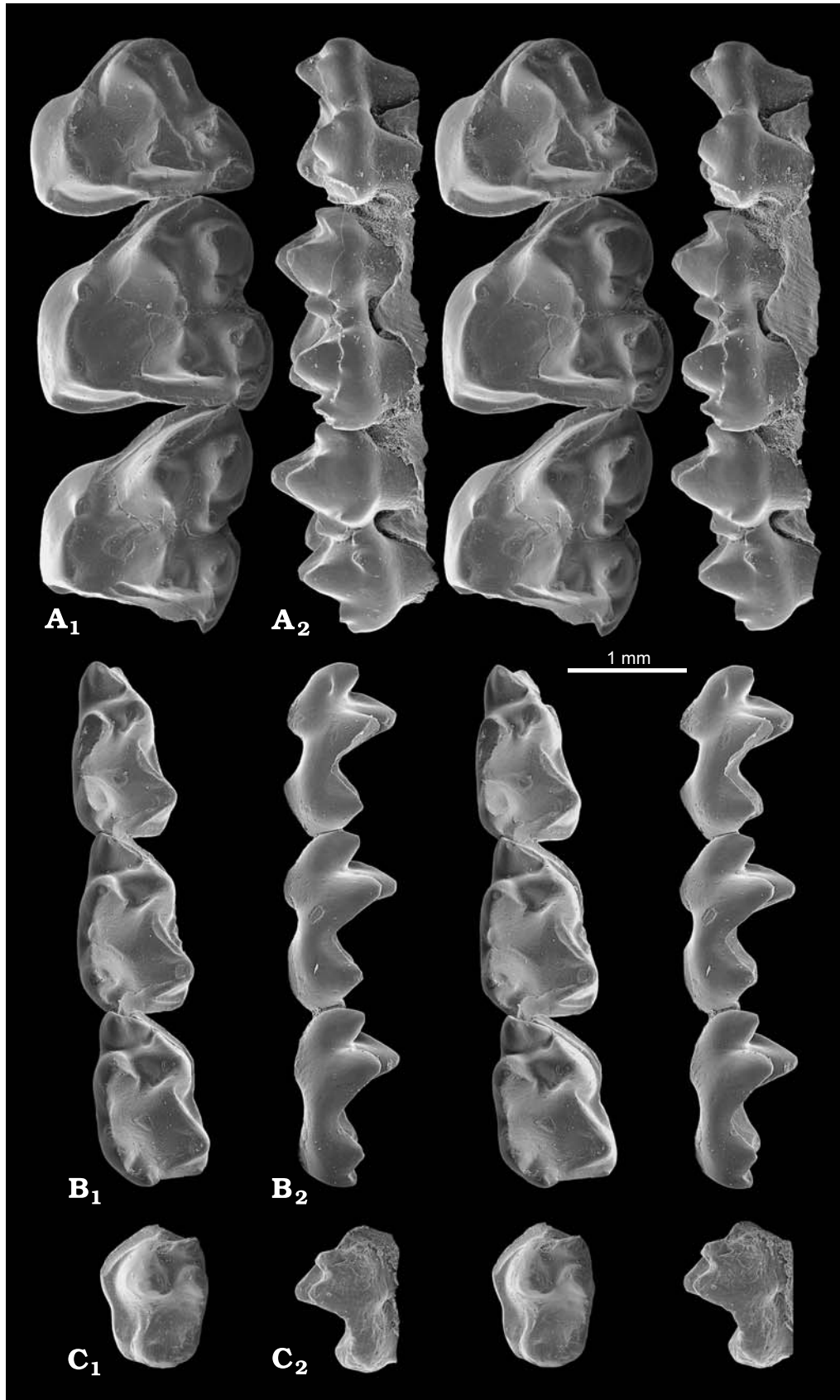


Fig. 23. Upper and lower molars (stereomicrographs) of *Glasbius intricatus* Clemens, 1966, in occlusal (A₁–C₁), labial (A₂), and lingual (B₂, C₂) views. **A.** UM VP1593, RP3, M1–M3 (M1–M3 figured). **B.** AMNH 58759, Rp2–p3, m1–m3 (m1–m3 figured). **C.** AMNH 57960, Lm4. All from UCMP V5711, Lance Formation, Wyoming, USA (see Clemens 1966: fig. 1). A, B, figured in Clemens (1966).

Stratigraphic and geographic range.—Aquilan: Canada, Alberta (Milk River Formation); and Judithian: United States, New Mexico (Fruitland Formation).

Family Glasbiidae Clemens, 1966

Included genera.—*Glasbius* Clemens, 1966 (type genus by monotypy).

Diagnosis.—As for the type and only genus.

Remarks.—This taxon was first erected by Clemens (1966) as a subfamily of the Didelphidae, and elevated to family status by Archer (1984). As noted earlier, the family Glasbiidae, represented solely by the genus *Glasbius*, is unique among all other Late Cretaceous marsupial taxa in its distinctive morphology and the suddenness of its appearance in the fossil record, without any plausible antecedents. This had led some authors to refer to it as an “alien” in the Lancian faunas (Weil and Clemens 1998; Clemens 2002; Cifelli et al. 2004), and others to classify it among endemic South American groups, such as the Caroloameghiniinae (Marshall 1987) or, more conservatively, the Paucituberculata (Kielan-Jaworowska et al. 2004). It appears that most of the similarities result from convergence on a bunodont molar pattern, and are unlikely to be phylogenetically significant. Additionally, the extreme reduction in the size of the fourth molar in *Glasbius* is unique among Cretaceous Metatheria (a similar condition occurs in some deltatheroidans; depending on how Metatheria is defined, this group may also be included). An incomplete dentary described by Clemens (1966: fig. 19, AMNH 58759) and referred to *Glasbius* cf. *intricatus* was dropped from the generic hypodigm by Archibald (1982). Nonetheless, the morphology of this specimen is strikingly similar to specimens of *Glasbius* (a fact which must have led Clemens (1966) to tentatively refer it in the first place), suggesting slightly higher diversity within this interesting and significant Lancian family. See “Comments” on the PEDIOMYOIDEA (above) for discussion on a relationship between the Glasbiidae and the Aquiladelphidae.

Stratigraphic and geographic range.—As for the type and only genus.

Genus *Glasbius* Clemens, 1966

Fig. 23.

Type species: *Glasbius intricatus*; UCMP 48047 (holotype), V-5711, Lancian: United States, Wyoming (Lance Formation).

Included species.—*Glasbius intricatus* Clemens, 1966 (type species) and *G. twitchelli* Archibald, 1982.

Diagnosis (from Archibald 1982: 137).—“Principal cusps on upper molars low relative to protofossa; metacone higher than paracone and metaconule larger than paraconule; stylar shelf broad; B large on M1–4; D higher than B on M1–2, smaller than B on M3, absent on M4; A and E small; C small or absent; m2 longer than other molars; talonid (including labial cingulum) wider than trigonid, except on m4; width of m3 > m2 > m1; cristid obliqua contacts trigonid on back of protoconid; trigonid short anteroposteriorly, paraconid and

metaconid closely approximated on m3–4; difference in height of trigonid over talonid not great and decreases from m1 to m4; lingual side of crown higher than labial, except on m1–2, where protoconid is subequal to metaconid; basal cingulum on anterior, labial, and posterior sides of m1–4 with variously developed cusps on some molars; M/m 4 much smaller than preceding molars; p1–3 double-rooted, increasing in size posteriorly; anteroposterior axis of p1 rotated at 30–45° angle to long axis of dentary.”

Stratigraphic and geographic range.—Lancian: United States, Wyoming (Lance Formation); Montana (Hell Creek Formation); and Canada, Saskatchewan (Frenchman Formation).

Conclusions

“Pediomyid” marsupials have long been a hallmark of Late Cretaceous North American terrestrial faunas, especially of the Western Interior. But ever since the diversity of the group was first recognized and described by Clemens (1966), “pediomyid” relationships have been in dispute. Richard C. Fox, who has perhaps done more than anyone else to increase our understanding of these important mammals (e.g., Fox 1971, 1979, 1987a, b), is also principally responsible for the controversy. His assignment to the family of unique and morphologically-disparate taxa from the early Campanian Milk River Formation of Alberta drove his ideas of “pediomyid” character polarity and evolution, especially with regard to the independent suppression of the stylocone and anterior stylar shelf and the importance of stylar cusp C.

The main issue at hand, it would seem, was outlined by Fox (1987a: 167–168) as his alternative hypotheses 3 and 4. Clemens (1966) had suggested stylar cusp C was lost in some lineages of marsupials prior to the Campanian. He also proposed that *Pediomys elegans* represents the primitive stylar shelf morphology for “pediomyid” marsupials, since it is reasonably complex and thus might indicate descent from some sort of *Alphadon*-like ancestor. Since none of what Fox described as the “Milk River forms” (which refers to *Iqualadelphis* and perhaps two still undescribed “pediomyids” resembling “*P.*” *florencae*; see Fox 1987a: fig. 5) has with certainty a stylar cusp in the C position, the conclusion was drawn that the ancestral “pediomyid” must have also lacked this stylar cusp. Fox (1987a) stated that the morphology seen in *P. elegans* implies the stylocone was suppressed before a cusp in the C position arose in the ancestral “pediomyid”, and this appears to be fully congruent with the results of this study. A stylar cusp in the C position was present at least as far back as the common ancestor for the PEDIOMYOIDEA (new rank). However, Fox (1987a) placed such emphasis on this cusp as to implicate an ancestry for *P. elegans* separate from the rest of the “pediomyids” simply based on the distribution of cusp C. It agrees much more with the data to evolve this cusp once in pediomyid (s.s.) ancestry (at some point before loss of the stylocone, which defines the PEDIOMYIDAE s.s.), keeping it in

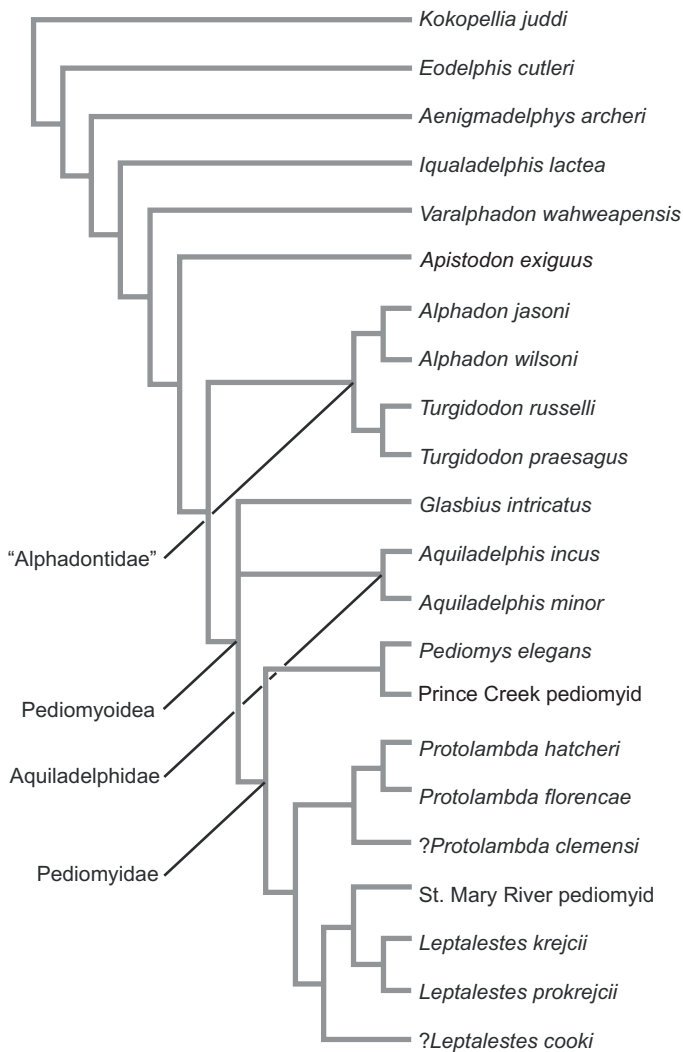


Fig. 24. Strict-consensus cladogram from Fig. 5, relabeled with revised taxonomy.

the lineage leading to *Pedimys* s.s. while losing it in the lineage leading to *Leptalestes* gen. nov. and *Protolambda*. An ancestor with an *Alphadon*-like arrangement of styler cusps indeed must have been present prior to the Campanian, but such a form would have independently given rise only to the principal members of the Pedimyioidea (*Pedimyidae* s.s., *Aquiladelphidae*, and *Glasbius*).

Pedimyidae are redefined based on a number of characters related to two important functional complexes. First, suppression of the anterolabial portion of the upper molar, together with expansion of the postmetacrista, implies a departure from prevallum/postvallid shear, which is prevalent in early boreosphenidan mammals (Crompton 1971; Crompton and Kielan-Jaworowska 1978). It is clear that the majority of the shearing function of pedimyid molars is accomplished by a postvallum/prevallid mechanism, though the molars of this group lack any degree of specialization that can be characterized as hypertrophied (seen in many carnivorous groups, such as the borhyaenids of South America). It is more likely that the

strong postmetacrista on the upper molars is all that is left after the reduction in function at the anterior end of the styler shelf. The basal expansion of the protocone, present in all pedimyoids, is likely related to the labial shift of the cristid obliqua and transverse expansion of the talonid basin (Clemens 1968; Fox 1972, 1975, 1980; Archer 1982; Kielan-Jaworowska and Nessov 1990). Improvement upon this grinding ability provided pedimyids with an advanced, multi-functional molar that likely assisted in their dominance of Late Cretaceous North American marsupial faunas.

It should also be noted that not all taxa commonly referred to the “Alphadontidae” nest in a monophyletic fashion (Fig. 5, node 6). *Aenigmadelphys* has been classified within the “Didelphidae” (see Johanson 1996a; McKenna and Bell 1997), though here it is treated as a primitive stem marsupial (following Muizon and Cifelli 2001). Additionally, *Varalphadon* has a similar place on the cladogram, despite its typical classification within the “Alphadontidae” (Johanson 1996a; Kielan-Jaworowska et al. 2004) or the “Didelphidae” (McKenna and Bell 1997). However, the two much better known genera *Alphadon* and *Turgidodon* are sister taxa, supporting the core composition of the “Alphadontidae”. Despite a fine work on the subject by Johanson (1996a), perhaps this suggests another look at “alphadontid” interrelationships in light of character polarity provided by taxa such as *Kokopellia*, and a thorough comparison to more Late Cretaceous marsupial outgroups.

Finally, Clemens (1966) spoke first of the potential generic-level diversity of pedimyid marsupials, based on his description of the mammalian fauna of the Lance Formation of Wyoming. In assigning several new species to “*Pedimys*”, he wrote: “Future discoveries, I judge, will not result in the merging of any of the species recognized here, but may justify placing some of them in pedimyid genera other than *Pedimys*. [...] This morphological diversity among Late Cretaceous species of *Pedimys* suggests they had long, independent phylogenetic histories.” (Clemens 1966: 54–55). Fox (1987a) arrived at a similar conclusion, though he went a step further, calling for a revision of the entire group. Both authors, it appears, were correct: Clemens (1966), in that the genus “*Pedimys*” contains sufficient diversity to warrant its split; Fox (1987a), in that both the genus “*Pedimys*” and the family “*Pedimyidae*” are polyphyletic. Two lineages are also composed approximately as Fox predicted: the two smaller species “*P.*” *krejci* and “*P.*” *prokrejci* are most closely related (*Leptalestes* gen. nov.), as are the two larger forms “*P.*” *hatcheri* and “*P.*” *florencae* (*Protolambda*). Fox (1987a) also proposed a third lineage, containing “*P.*” *cooki* and “*P.*” *clemensi*, but the data suggest that “*P.*” *cooki* is best referred to *Leptalestes* and “*P.*” *clemensi* to *Protolambda*. The removal of the small, poorly known Milk River taxon “*P.*” *exiguus* from *Pedimys* restores monophyly to the genus, as this taxon appears to be an enigmatic stem marsupial. It is placed in its own genus, *Apistodon* gen. nov., family *incertae sedis*. Redefining the family *Pedimyidae* s.s. to the exclusion of *Aquiladelphidae*, also from the Milk River Formation, securely establishes its monophyly, though the superfamily *Pedimyioidea* (new rank) is erected to

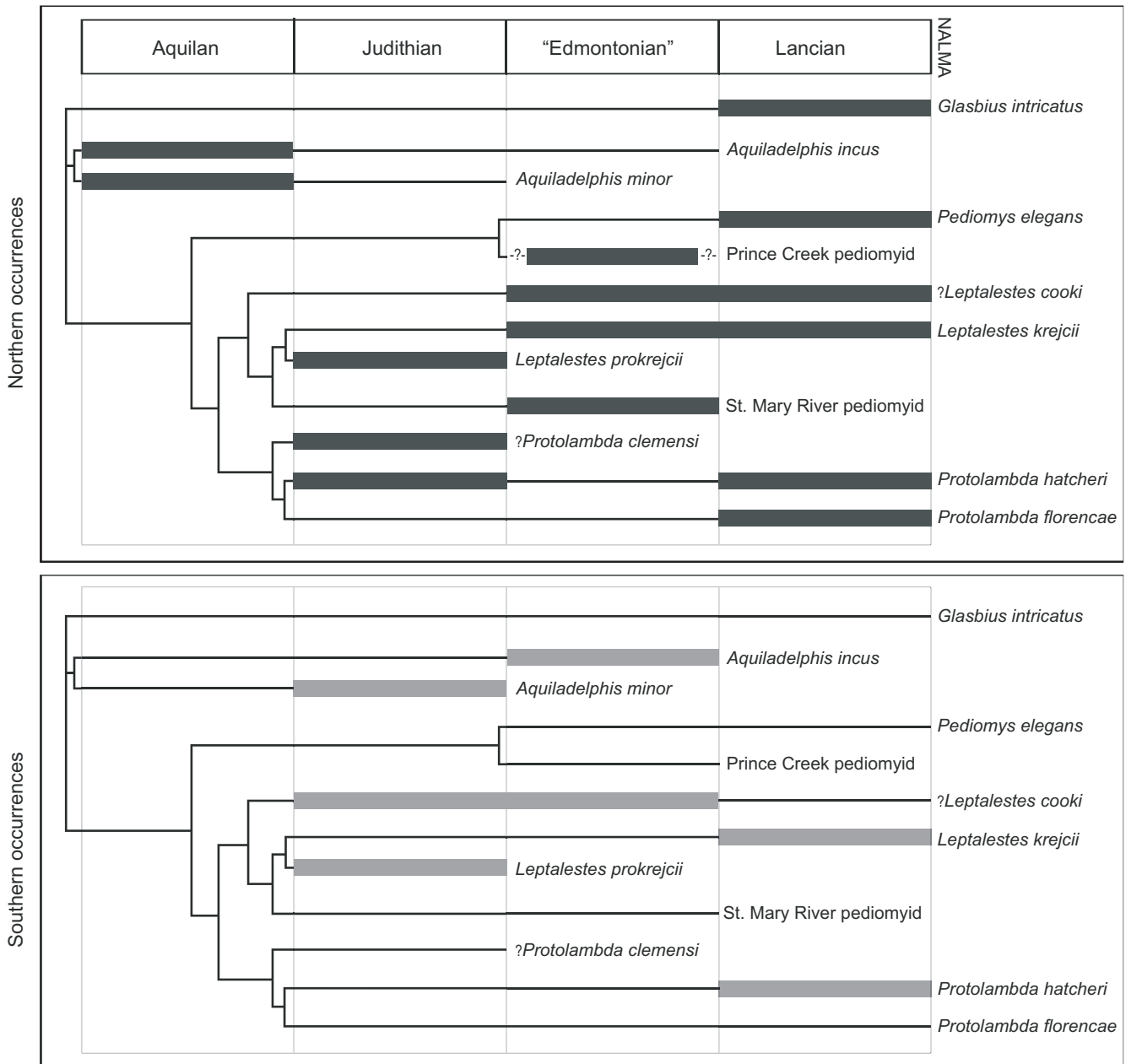


Fig. 25. Pediomysid phylogeny mapped across Late Cretaceous North American Land Mammal Ages (NALMAs), and northern and southern mammalian faunas. Solid bars indicate an occurrence during that particular NALMA. The uncertain age of the Prince Creek Formation and the poorly-defined boundaries of the “Edmontonian” NALMA are indicated by question marks for the distribution of the Prince Creek pediomysid. Definitions of northern and southern faunas follow Lehman (1997).

recognize the relationship that exists between pediomysids, *Aquiladelphis*, and *Glasbius* (see Fig. 24 and Table 1 for revised taxonomy).

This proposed relationship does not necessarily contradict several of the previous studies of relationships among South American marsupials (e.g., Aplin and Archer 1987; Marshall 1987; Marshall et al. 1990; Szalay 1994), some of which place pediomysids within the Microbiotheriidae and *Glasbius* within the Caroloameghiniinae; however, it is beyond the scope of this study to reevaluate endemic South American Paleocene genera. This leaves open the possibility that pediomysid marsupials (or some similar, related group)

played a significant role in a faunal exchange between the two American continents. For example, Case et al. (2004) suggested that some higher South American taxonomic groups are represented in collections from the Judith River and Lance formations, though only “alphadontid” specimens have been reassigned. Future discoveries of pediomysid or pediomysid-like taxa from rocks of the appropriate age (or descriptions of yet unpublished material; e.g., Fox 1987a: fig. 5) might shed additional light on pediomysid evolution during the important interval between the early diversification of marsupials in North America (Albian–Cenomanian) and the first undisputed pediomysids s.s. (late Campanian).

It should be reasonable to assume some biogeographical conclusions could be made given the broad geographical and temporal distribution of some pediomyoid taxa across the Late Cretaceous of North America (Fig. 25). However, the poor nature of the mammalian fossil record in the southern United States precludes much more than speculation. Based on available evidence, the Pediomyoidea likely originated in northern climes sometime during the Santonian (just prior to the Aquilan). This is, however, based only on the occurrence of taxa in the Milk River Formation of southern Alberta. The Cedar Canyon fauna, described by Eaton et al. (1999), is possibly of equivalent age (based on palynomorphs and the presence of *Iqualadelphis*) and contains a “pediomyid”-like taxon similar to an undescribed large taxon illustrated by Fox (1987a: fig. 5). However, pending full description and systematic analysis of this taxon, the absence of pediomyoids in the Wahweap Formation (Aquilan of Utah) implies a northern origin for the group.

It is interesting to note that the large pediomyoid *Aqualadelphis*, which likely evolved in the north, is restricted to rare, isolated occurrences in the south during the Judithian and “Edmontonian” before going extinct sometime prior to the Lancian. *Glasbius*, which according to these results must have split from the rest of the Pediomyoidea sometime during the Santonian, does not appear until the late Maastrichtian.

The Pediomyidae first occur in the Judithian, when approximately half of all described species appear. They are present in both northern and southern formations, though the conspicuous absence of pediomyids from the well-sampled Kaiparowits Formation of southern Utah restricts southern occurrences to the Fruitland-Kirtland formations alone (and even then, the two taxa present are represented by a combined three isolated teeth). Given the relative greater abundance of pediomyids in northern faunas, it is tempting to invoke a northern origin for this group as well. However, it is plausible that the various genera within the Pediomyidae differentiated in separate regions. Given that the only two pediomyids present in the south during the Judithian belong to the *Leptalestes* clade, it is possible that this genus evolved alone there. The *Protolambda* clade is present in Alberta and Montana during the Judithian, and it is likely that the *Pediomyis* clade was present in Alberta as well (based on a fragmentary upper molar, described by Fox 1979: fig. 2a, that belongs to a *Pediomyis elegans*-like taxon). Both these genera may well have evolved in the north. These patterns correspond with other conclusions on Judithian biogeography (Weil 1999), in that it is easier to recognize a distinct northern mammalian faunal province, due to the tremendous number of localities and specimens, than it is to structure the poorly known southern assemblages.

By the “Edmontonian”, both abundance and diversity balances begin to shift to the north. It is important to note that only one formation, the Williams Fork Formation in Colorado, is included in the “Edmontonian” of the south (this follows the conclusions on dinosaur biogeography of Lehman (1997)). The discrepancy between northern and southern occurrences is maintained during the Lancian, with only two

isolated teeth, belonging to *Leptalestes krejci* and *Protolambda hatcheri*, appearing in southern faunas (both in the North Horn Formation of central Utah). Pediomyids are very abundant and diverse in northern faunas, where they are often among the most abundant therian components. There is, however, a lack of well-sampled mammalian faunas in the southern United States from the Lancian, so it is difficult to draw many conclusions from this except that it is clear that pediomyids were extremely successful in northern faunas at the time. Cifelli et al. (2004) point out that pediomyids and stagodontids, both easily recognizable taxa, are absent in southern assemblages. However, the absence of *Pediomyis elegans* (ubiquitous in northern faunas) from southern faunas leaves open the possibility of some degree of faunal provincialism, though this is impossible to evaluate at this time given the paucity of southern Lancian assemblages.

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Addendum

Two notable studies were published shortly after the preparation of this manuscript and deserve comment, though they could not be incorporated into this project. Goin et al. (2006) published a cladogram that broadly sampled South American Tertiary marsupial taxa, but also included a number of North American Cretaceous forms. “*Pediomyis*”, along with other Late Cretaceous North American taxa, are nested within an otherwise Australasian marsupial radiation. The purpose of my study is to evaluate “*Pediomyis*” as a polytypic assemblage, rather than as a monotypic “taxon” as it appears in Goin et al. (2006) and other studies, in a hope to provide a better framework for the interpretation of marsupial evolutionary history during the Cretaceous.

Eaton (2006) published a mammalian fauna from the Late Cretaceous of southwestern Utah. One locality is from the uppermost Wahweap Formation (late Santonian), making it stratigraphically and temporally equivalent with the Milk River Formation of southern Alberta. Eaton (2006) described

specimens of three “pediomyid” taxa: a new species of *Aquiladelphis*, an upper molar closely resembling “*Pediomys*” *exiguus* (species moved to the new genus *Apistodon* in my study), and an indeterminate M1. In this last instance, I would agree with the original interpretation of the tooth as a deciduous upper premolar from an undetermined species of “*Pediomys*”, as described by Eaton et al. (1999). The presence of pediomyoid taxa in southwestern Utah during the late Santonian increases the known diversity and geographic range of the group as a whole, indicating that the group was well established across the Western Interior of North America by the Aquilan.

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Appendix 1

Characters and states.—The following is a comprehensive list of all morphological characters and their states used in the analysis, beginning with upper molar characters:

Stylar cusp A (parastyle)

1. Lingual placement relative to paracone: 0 – well-removed labial to paracone; 1 – somewhat lingually placed; 2 – extremely lingually placed so that it is directly anterior to paracone.

Stylar cusp B (stylocone)

2. Presence: 0 – present; 1 – absent.
3. Size: 0 – moderately developed; 1 – large; 2 – small; 3 – absent.
4. Height relative to paracone: 0 – B is shorter than the paracone; 1 – B is subequal in height; 2 – absent.

5. Position relative to paracone: 0 – positioned anterolabial to paracone; 1 – positioned more directly labial to paracone; 2 – absent.

Stylar cusp in the C position

6. Presence or absence: 0 – absent; 1 – present.
7. Presence of a “twinned” cusp anterior to cusp C: 0 – absent; 1 – variably present; 2 – consistently present.
8. Size: 0 – absent; 1 – small; 2 – well-developed; 3 – large.
9. Position relative to ectoflexus: 0 – absent; 1 – C positioned at deepest part of ectoflexus; 2 – positioned posterior to the deepest part of ectoflexus.

Stylar cusp D

10. Presence or absence: 0 – absent; 1 – present.
11. Size: 0 – absent; 1 – small to moderately developed; 2 – small or to absent only on M3.
12. Position relative to metacone: 0 – absent; 1 – positioned labial to metacone; 2 – positioned more anterolabially and closer to deepest part of ectoflexus.
13. Position relative to cusp C: 0 – cusp D absent; 1 – C and D are well-separated; 2 – C and D are closely approximated.
14. Shape at base: 0 – absent; 1 – broad and long at base; 2 – more conical at base.

Stylar shelf

15. Anterior reduction: 0 – anterior stylar shelf is not reduced; 1 – somewhat reduced; 2 – extremely reduced so that just a rim remains labial to paracone.

Preparacrista

16. Strength: 0 – well developed; 1 – weakly developed; 2 – nearly absent.
17. Orientation: 0 – runs to cusp B; 1 – runs to cusp A.
18. Presence of carnassial notch along preparacrista: 0 – carnassial notch is present; 1 – notch is absent.

Postmetacrista

19. Height (as judged by point of departure from the metacone): 0 – low (arising from the lower half of the metacone); 1 – tall (arising from the upper half of the metacone).
20. Presence of carnassial notch along postmetacrista: 0 – carnassial notch is present; 1 – notch is absent.

Ectoflexus

21. Depth on M3: 0 – very deep; 1 – moderately deep; 2 – shallow.
22. Depth across molar series: 0 – increases in depth posteriorly through molar series; 1 – little or no change through the series.

Paracone and metacone

23. Relative height: 0 – paracone is taller; 1 – two cusps are subequal; 2 – metacone is taller.
24. Relative sizes in labial view: 0 – paracone is broader than metacone; 1 – paracone and metacone are equally broad; 2 – metacone is broader than paracone.
25. Shape: 0 – the paracone and metacone are uninflated and unrounded; 1 – the paracone is inflated and rounded compared to the metacone.
26. Shape of labial faces: 0 – labial faces are nearly flat or concave; 1 – face of paracone is rounded while face of metacone is flat; 2 – both labial faces are rounded.
27. Relative separation at base: 0 – paracone and metacone share a portion of their bases; 1 – cusps are entirely separate.

Centrocrista

28. Strength: 0 – weakly developed; 1 – strongly developed.
29. Morphology (refers to location of the deepest point of the centrocrista relative to an imaginary line between the apices of the paracone and metacone): 0 – straight (equivalent to a U-shaped ectoloph); 1 – labially deflected (equivalent to a W-shaped ectoloph).

Conules

30. Size: 0 – paraconule and metaconule are small; 1 – large.
31. Position of conules relative to protocone and paracone/metacone: 0 – positioned relatively closer to protocone; 1 – positioned relatively closer to paracone/metacone.
32. Strength of the internal cristae: 0 – well-developed; 1 – weakly developed.

Protocone

33. Height relative to paracone/metacone (whichever is taller): 0 – protocone shorter than paracone/metacone; 1 – protocone subequal in height.
34. Transverse width: 0 – protocone is of moderate width; 1 – very wide.
35. Basal posterior expansion: 0 – basal posterior portion of protocone

is unexpanded; 1 – basal portion is significantly expanded so that part of the protocone is somewhat lobe-like.

36. Presence of protoconal cingula or rugosities: 0 – absent; 1 – present.

Trigon basin

37. Length: 0 – trigon basin is relatively short; 1 – basin is antero-posteriorly long.

Preprotocrista

38. Strength: 0 – weakly developed; 1 – strongly developed.

Postprotocrista

39. Labial extension past metaconule: 0 – absent; 1 – present.
40. Strength of labial extension: 0 – absent; 1 – weakly developed; 2 – strongly developed.
41. Length: 0 – terminates at metaconule; 1 – extends labially only to base of metacone; 2 – extends past metacone.

Trigonid

42. Relative transverse width of trigonid to talonid: 0 – talonid and trigonid are of approximately equal width; 1 – talonid is somewhat wider than trigonid; 2 – talonid is significantly wider.
43. Relative height of trigonid and talonid: 0 – talonid is much lower than trigonid; 1 – talonid is closer to trigonid in height.
44. Relative heights of paraconid and metaconid: 0 – two cusps are subequal in height; 1 – paraconid is taller than metaconid; 2 – metaconid is taller than paraconid.
45. Relative lengths of paraconid and metaconid in lingual view: 0 – two cusps are relatively equal in length; 1 – paraconid is longer than metaconid; 2 – metaconid is longer than paraconid.
46. Position of paraconid relative to metaconid: 0 – paraconid positioned labially relative to metaconid; 1 – paraconid positioned more lingually, such that the paraconid, metaconid and entoconid all line up anteroposteriorly.
47. Robustness of all cusps (includes talonid): 0 – not inflated or robust; 1 – inflated and robust
48. Angle of trigonid (measured from entoconid to protoconid, with metaconid as vertex): 0 – obtuse; 1 – approaching 90 degrees.

Talonid

49. Size of entoconid: 0 – entoconid is comparable in size to hypoconulid; 1 – entoconid is significantly larger than hypoconulid.
50. Degree of “twinning” between the hypoconulid and entoconid: 0 – not twinned or weak twinning; 1 – highly-developed twinning.
51. Presence of an accessory cusp adjacent to entoconid along entocristid: 0 – absent; 1 – present.
52. Presence of labial cingulids (as extensions of pre- and postcingulids): 0 – absent; 1 – present.
53. Ventral extent of talonid portion of crown (in labial view): 0 – talonid extends ventrally to level of trigonid; 1 – talonid extends slightly past trigonid (ventral margin of crown slopes gently posteriorly); 2 – talonid significantly expanded such that the ventral margin of crown slopes steeply posteriorly.
54. Labial height versus lingual height of talonid (as measured from apices of hypoconid and entoconid): 0 – talonid subequally high on both sides; 1 – lingual side of talonid slightly taller than labial side; 2 – lingual side significantly taller.

Cristid obliqua

55. Position at which the cristid obliqua meets the posterior trigonid wall: 0 – cristid obliqua meets posterior wall of trigonid at a point lingual or basal to the protocristid notch; 1 – labial to protocristid notch, at the midline of the protoconid; 2 – meets nearly at the labial margin of the trigonid.

Premolars

56. Inflation of p3: 0 – uninflated; 1 – somewhat inflated, so that the main cusp of p3 is wider than the trigonid of m1; 2 – markedly inflated.

General

57. Overall size of molars (as a rough indication of body size): 0 – molars are very small; 1 – large.

Appendix 2

Character state matrix.—Missing or indeterminate characters coded as “?”; polymorphic condition for character 57 coded as “A”, indicating states 0 and 1.

Kokopellia juddi Cifelli, 1993a

0000000000 0000000000 0000000000
0000000000 0000000000 00000000

Aenigmadelphys archeri Cifelli and Johanson, 1994

0000000001 11?1000011 0000000000
0101000011 1002000001 00100000

Varalphadon wahweapensis (Cifelli, 1990b)

0000100001 11?2010101 1101021001
1000000011 1012200011 00110?0

Alphadon jasoni Storer, 1991

0011110211 1112000001 0011001011
1010000011 1012200011 011000A

Alphadon wilsoni Lillegraven, 1969

0011110111 1112000001 0011001011
1010000011 1012210011 001000A

Turgidodon russelli (Fox, 1979)

0011110211 1112000011 0021001001
1010010011 2012210011 101001A

Turgidodon praesagus (Russell, 1952)

0011110211 1112000011 0022001001
1010010011 2012210011 0010011

Pediomys elegans Marsh, 1889

1132211121 1122211101 1021111001
1111110112 2212210111 102220A

“*Pediomys*” *cooki* Clemens, 1966

1132200001 21?1211111 1012010101
1010110112 2112210111 001210A

“*Pediomys*” *krejci* Clemens, 1966

1132200001 21?1211111 1022010000
0011100112 2012010101 0012100

“*Pediomys*” *prokrejci* Fox, 1979

1132200001 21?1211111 1011010000
0011100112 2012010101 1012100

“*Pediomys*” *clemensi* Sahni, 1972

1132200001 12?1211101 1010111001
1010110112 2112210111 001111A

“*Pediomys*” *hatcheri* (Osborn, 1898)

2132200001 11?1221111 1112111101
1010101112 2110011111 0011111

“*Pediomys*” *florenceae* Clemens, 1966

2132200001 11?1221111 1111111101
1010111112 2110011011 0011111

“*Pediomys*” *exiguus* Fox, 1971

0000110221 1122000101 0001021100
0000000111 2????????? ????A

Prince Creek “pediomyid”

1132211121 1122101?0? 00210?1000
1110110112 2212210111 0????1?0

St. Mary River “pediomyid”

1132200001 21??211?1? 1???010001
10?1000112 1????????? ????A

Aquiladelphus incus Fox, 1971

2020110321 1122100?00 2?011?1101
1110111011 ?012211011 0011121

Aquiladelphus minor Fox, 1971

2020110321 1122100?00 2?01111101
11101?1011 ?112211011 00111?1

Iqualadelphus lactea Fox, 1987b

1000000001 11?1100111 1?21000000
0010000112 2????????? ????A

Glasbius intricatus Clemens, 1966

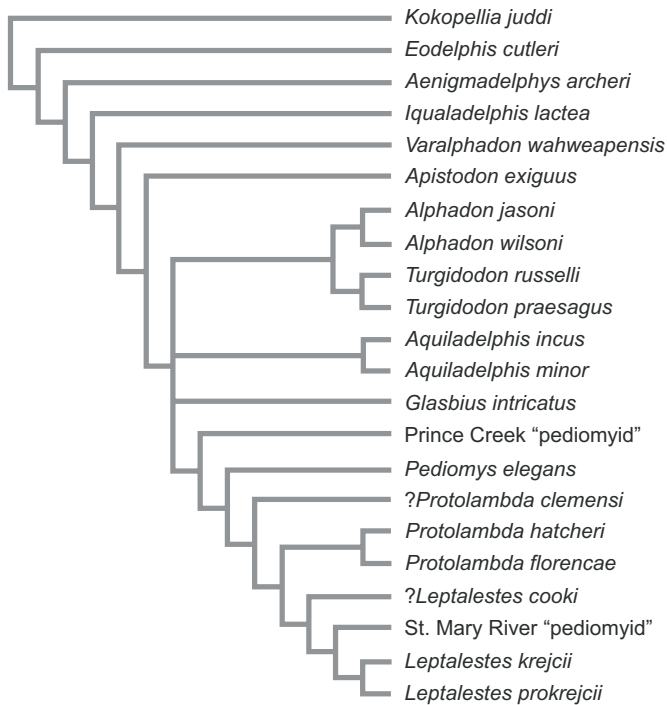
0011110121 1122001101 1121021001
1110111111 2112201011 0101100

Eodelphis cutleri (Woodward, 1916)

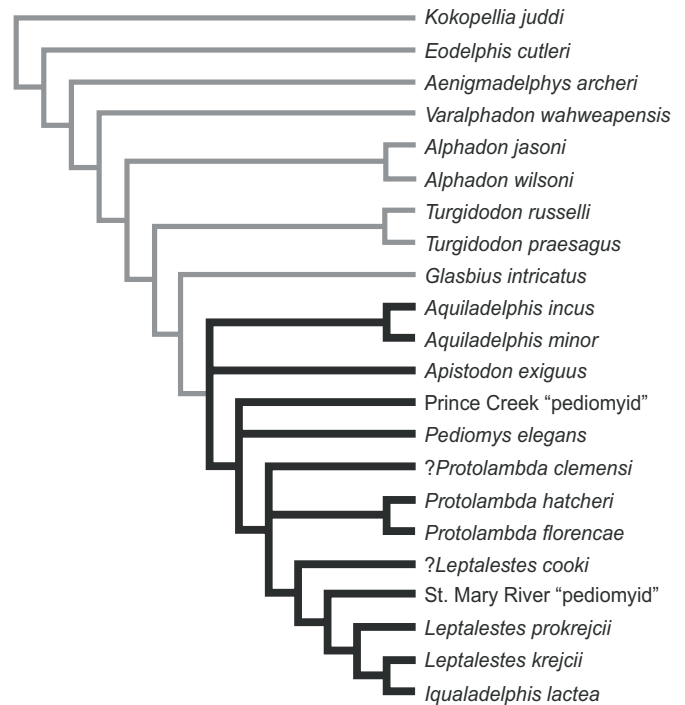
0010000000 0000000010 0022120101
1000000100 0011111001 0001121

Appendix 3

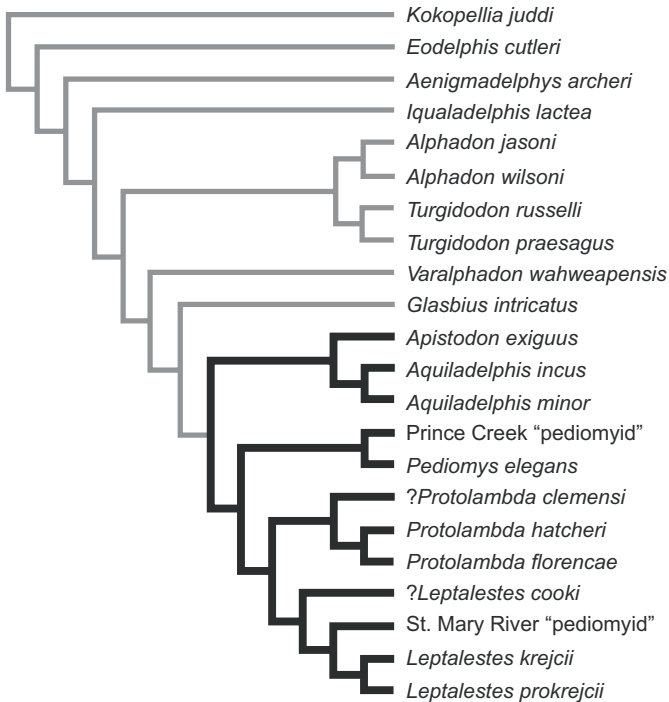
Additional cladograms.—The following cladograms are results of restrictions and constraints, as explained in the text:



Analysis restricted to upper molar characters only.



Analysis constrained to group members of the "Pediomyidae" (as classified by Kielan-Jaworowska et al. 2004) in a clade, but with the addition of *Iqualadelphis lactea* to the clade containing the "Pediomyidae". Heavy lines indicate constrained clade.



Analysis constrained to group members of the "Pediomyidae" (as classified by Kielan-Jaworowska et al. 2004) into a clade. Heavy lines indicate constrained clade.