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 stylar shelf, 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* (Aquilian) appears to be unrelated to the “pediomyid” radiation, and rests as a stem taxon near the base of the cladogram. The large Aquilian *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*, *Leptaleses* 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 stylar shelf 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
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 “stylolocus” 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

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

Class Mammalia Linnaeus, 1758
Infraclass Metatheria Huxley, 1880
Cohort Marsupialia Illiger, 1811
Order and family incertae sedis
Kokopellia juddi Cifelli, 1993a
Order “Didelphimorphia” Gill, 1872
Family incertae sedis
Iqualadelphis lactea Fox, 1987b
Aenigmadelphys archeri Cifelli and Johanson, 1994
Alphadon jasoni Storer, 1991
Alphodon wilsonei Lillegreven, 1969
Turgidodon praesagus (Russell, 1952)
Turgidodon russelli (Fox, 1979)
Varalphadon wahweapensis (Cifelli, 1990b)
Family “Pediomyidae” Simpson, 1927a
Alpidae incus Fox, 1971
Aquiladelphis minor Fox, 1971
“Pediomyid” elegans Marsh, 1889
“Pediomyid” clemensi Sahni, 1972
“Pediomyid” cooki Clemens, 1966
“Pediomyid” exigus Fox, 1971
“Pediomyid” fassetti Rigby and Wolberg, 1987
“Pediomyid” florenceae Clemens, 1966
“Pediomyid” hatcheri (Osborn, 1898)
“Pediomyid” krejci Clemens, 1966
“Pediomyid” prokrejci Fox, 1979
Family Stagodontidae Marsh, 1889
Aquiladelphis cutleri (Wolford, 1916)
Order Paucituberculata Ameghino, 1894
Family Gladiobiidae Clemens, 1966
Glasbius intricus Clemens, 1966
Historical background

The genus “Pediomys” 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 *Pediomys elegans*, after its tiny size relative to many other mammalian remains recovered from that formation. A second, much larger genus from the Lance Formation, *Proto- lambda hatcheri* Osborn, (1898), was moved to “Pediomys” 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 (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 “Pediomys” and added to the known diversity of the genus by describing three new species: “Pediomys” *cooki*, “P.” *krejci*, and “P.” *florencei*. Clemens (1966) demonstrated that the five known species of “Pediomys” 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 *Alphadon 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-
tation that the group was derived in its suppression of the anterior stylar shelf and stylocone. According to Clemens’ model, “Pediomys” evolved from a marsupial with an Alpha−don−like molar configuration, with upper molars bearing a wide stylar shelf and five stylar cusps, as suggested by the slightly less suppressed anterior stylar 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 Lillegren 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” exigus, 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 possesses 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.” exigus 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 stylar shelf and stylar cusps.
He also described a new species, “P.” prokrejcii, clearly named for its hypothesized ancestry to the Lancian “P.” krejcii (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.” prokrejcii (Judithian) and “P.” krejcii (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 “Pediomys” represent separate lineages, some of which never went through an Alphadon-like stage in which cusp C was present (Fox 1987a, b). *Pediomys*, 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.” krejcii–prokrejcii, “P.” cooki–clemensi, and “P.” hatcheri–florencae (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 “Pediomys” 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: “Pediomys” fassetti and *Aqui−ladelphis* paraminor. Neither is represented by a complete upper molar, though one can be reconstructed for “P.” fassetti 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 *Glaebius* 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 focus 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 “piedomyids”, 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 evolution. Previously, the suppression of the anterior stylar 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 stylar 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 Liscans 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 intricusatus 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; Aquiladephys paramior, known only by poorly preserved material, and “Pediomys” fassetti are synonymized with Aquiladephys minor and “Pediomys” prokrejci, 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 Liscans North American Land Mammal ages (Cifelli et al. 2004). The important Milk River “pediomyid”-like taxon Iqualadephys 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 Lillegren 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 “Pediomyiidae” 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 “Pediomyiidae” 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 “Pediomyiidae” 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 “Pediomyiidae” 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 “Pediomyiids” *krejcii-prokrejcii* 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 stylar shelf and some reduction in the size of the stylocone, since stylar cusp D 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 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) resinded his original assessment of “P.” *exiguus* as a “pediomyid”). “P.” *exiguus* not only retains a wide anterior stylar shelf 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 *Aqualadelphis*. *Aquiladelphis* was originally referred to the “Pediomyidae” s.l. (Fox 1971) based on its narrow anterior stylar 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 the 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 phyletogenetically disjunct groups (Fig. 5). Interestingly, this feature is also seen in South American peradectines and “didelphoids” (Muizon and Cifelli 1997; Cifelli 2004) clearly demonstrate the primitive dentition for all Late Cretaceous marsupials, possessing a well-developed stylocone but lacking all other stylar cusps. Stylar cusp D was likely added first, in ancestral stagodontids and basal “didel-phimorphians” such as *Aenigmadelphys*.

The topologic distribution of a stylar 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 stylar cusp C in marsupials). The results suggest a stylar cusp in the C position evolved only once in Late Cretaceous North American marsupials. However, it is important to note that small cusuples 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 stylar 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 styrar 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 Glassius—it is present in the type, G. intricatus, but absent in contemporaneous Glassius 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.” exigus, 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 Iqualadelphis, as well as all species therein). Interestingly, the contents and interrelationships of the Pediomyidae s.s. do not change. The Milk River “pediomyids” (Iqualadelphis and “P.” exigus) 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.” exigus. Regardless, even traditional “pediomyid” characters (such as suppression of the stylocone and anterior stylar 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”.

Systematic paleontology

Cohort Marsupialia Illiger, 1811

Remarks.—Following Kielan-Jaworowska et al. (2004), the cohort Marsupialia is defined as a stem-based taxon, containing the Family 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 Glasius, which is removed from the otherwise wholly South American Paucituberculata and placed in the “Didelphimorpha”. 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 “Didelphimorpha” 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” exigus, 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”, Iqualadelphis, is placed in its own monotypic family, the Aquiladelphidae fam. nov. However, a phylogenetic relationship is retained between Iqualadelphis and the Pediomyidae s.s., with the addition of
Glasbius, under the superfamly 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 exigus* (Fox, 1971); UALVP 5536 (holotype), Veregis 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 protocristal 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 molars (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-
delphis may superficially resemble some pediomyids (specifically species of Leptalestes gen. nov.), I herein exclude it from the Pediomysidae s.s. based on a number of features. It retains a somewhat broad stylar 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 Kielen-Jaworska 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

Holotype: UALVP 22823, a LM3.


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), Aquiladephidae 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 stylar 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 metacrista 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 in having upper molars characterized by strong suppression of the anterior portion of the stylar 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.—A relationship between Aquiladephis 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 superfam 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 Aquiladephis is more closely related to Glasbius than to the Pediomyidae s.s. Fox (1979) noted that the most important functional similarity between Aquiladephis and “Pediomyidae” 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 Aquiladephis, 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 Carolaomegabiriniinae (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 Kielen-Jaworska et al. 2004). Though it is lacking in one sampled species of Alphodon 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 Pediomys s.s.).

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

Family Pediomyidae Simpson, 1927a

Included genera.—Pediomys 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 stylar 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 protocristid, which is accomplished in pediomyids by a shift of the protoconid posteriorly so that the protocristid 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 stylar 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 stylar shelf and loss of the stylocone are synapomorphies, not homoplasies, for species assigned to “Pediomys” s.l. (minus “P.” exiguis), and the presence of stylar 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 stylocene on their reduced anterior stylar 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 paracoon, resulting in a large height difference between the paracoon and metacone; presence of an accessory cusp posterior to the stylar cusp C position but anterior to the deepest point of the ectoflexus; reduction in the height of the postmetacrista; metaconid significantly taller than paracoon; 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 paracoon, reduced postmetacrista, and a broadly expanded talonid. These features, along with well-developed comules, may suggest a departure from a shearing-based diet, though both taxa are very small. Both taxa also exhibit (though variably in P. elegans) a small accessory cusp anterior to the stylar cusp in the C position, just posterolobial to the paracoon. It is slightly larger in the Prince Creek form than in P. elegans, though it is unlikely that this cusp represents a vestigal stylocone (as suggested by Clemens 1966), since in no Late Cretaceous marsupial taxon is a stylocone located posterior to the paracoon. More plausibly, it is a de novo feature of limited (if any) functional significance. Twinned cusps are also present in Aquiladelphis, though their position labial relative to the paracoon, 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).


*Emended diagnosis.*—Distinctive from the Prince Creek form in larger size, stronger inflation of the paracoon, 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
important to our understanding of Late Cretaceous marsupial diversity. Though situated in the first lineage to branch within the Pediomyidae, *Pediomys elegans* exhibits many derived features that likely distance it from the morphology expected for an ancestral pediomyid (contrary to earlier ideas by Clemens 1966 and Fox 1987a). *P. elegans* is the only pediomyid to have potentially survived beyond the K/T boundary, with a possible occurrence in the lower Ravenscrag.
Formation (Puercan, Saskatchewan; Johnston and Fox 1984). Fox (1979: fig. 2a) figured a fragmentary upper molar from the Dinosaur Park Formation, described as *Pediomys 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 pediomyid 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).
Diagnosis.—Moderate to large pediomydids differing from all other pediomydids 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 pediomydids in general), as well as features that give their molars a relatively broad appearance. The ectoflexus retains 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 pediomydoid condition, where the metaconid is taller. Most notably, the taxon exhibits an inflated P3, though the ultimate premolar of the lower dentine is only slightly larger than in other taxa. This is significant in that it differs from the condition seen in stagodontids and Aquiladelphis, where both the upper and lower ultimate premolars are inflated (presumably, the P3 of Aquiladelphis would have been inflated, based on comparisons with stagodontids, though this tooth is unknown in Aquiladelphis). 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.
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).


**Emended diagnosis**.—Diffs 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. Diffs 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 (Hell Creek formations); Canada, Alberta (Scollard Formation).

Protolambda florencae (Clemens, 1966)
Figs. 11, 12.

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


**Distribution**.—Lancian: United States, Wyoming (Lance Formation); South Dakota, North Dakota, and Montana (Hell Creek Formation).
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 entocristid and protocristid (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.
Emended diagnosis.—Differs from Protolambda hatcheri and P. florencae in stylar cusp D positioned anteriolabiolabial relative to the metacone (autopomorphy), 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 krejcii (Clemens, 1966); UCMP 51390 (holotype), V-5711, Lancian: United States, Wyoming (Lance Formation).

Included species.—Type species; L. prokrejcii (Fox, 1979) (equal to or including “Pediomys” fassetti Rigby and Wulber, 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 pediomysids differing from all other pediomysids 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
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 *Pediomys* 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.
Leptalestes krejcii (Clemens, 1966)

Figs. 15, 16.

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


*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. 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.

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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 krejcii* are known only from the Lancian. However, a lower molar was described from the lower St. Mary River Formation by Sloan.
and Russell (1974) and referred to “Pediomys” cf. “P.” krejcii, 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 prokrejcii* (Fox, 1979)

Figs. 17, 18.

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


*Emended diagnosis.*—Diffs from other species of *Leptalestes* in frequent presence of an accessory cuspule along the entocristid. Diffs specifically from the St. Mary River form in having smaller conules that are placed close to the protocone. Diffs 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 krejcii*, leading Fox (1979; 1987a) to suggest a possible an-
cestral-descendent relationship between the two. “Pediomys” 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. prokrejcii 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 stylar cusp D. This description appears to be based primarily on a molar they designate...
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 stylar shelf of UNM B1738 is wider than that on the holotype, whereas the typical condition seen in pediomyids is for the stylar 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 as M1 is 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. prokrejcii* 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.

Emended diagnosis.—Resembles other species of *Leptalestes* in apomorphies characteristic of the genus, such as near complete reduction of stylar cusp D on M3, possession of a tall postmetacrista, and loss of a stylar 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 pemioyid, 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 pemioyoids 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).
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 “*Pediomyx*” s.l. in the “*Pediomyidae*” s.l. based on shared suppression of the anterior stylar 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

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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).
from other pediomyoids in the very large size of the stylar cusp in the C position. Similar to pediomyids in reduction of the anterior stylar 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, Colorado, 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.
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.


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” fassetii). 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 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, RP1–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 Caroloameghinini (Marshall 1987) or, more conservatively, the Paucituberculata (Kielan-Jaworowska et al. 2004). It appears that most of the similarities result from convergence to classify it among endemic South American groups, such as the Caroloameghinini (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 deltaethiodontids; depending on how Metatheria is defined, this group may also be included). An incomplete dentary described by Clemens (1966: fig.19, AMNH 87589) 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 Aquiladeltidae.

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; n2 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 stylo 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 Iquala-delphis and perhaps two still undescribed “pediomyids” resembling “P.” florenceae; 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
the lineage leading to Pediomys s.s. while losing it in the lineage leading to Leptalestes gen. nov. and Protolambda. An ancestor with an Alphadon-like arrangement of stylar 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 Pediomyoidea (Pediomyidae s.s., Aquiladelphis, and Glasbius).

Pediomyidae 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 Kielen-Jaworowska 1978). It is clear that the majority of the shearing function of pediomyid 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 stylar shelf. The basal expansion of the protocone, present in all pediomyoids, 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; Kielen-Jaworowska and Nessov 1990). Improvement upon this grinding ability provided pediomyids 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 as 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; Kielen-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 pediomyid marsupials, based on his description of the mammalian fauna of the Lance Formation of Wyoming. In assigning several new species to “Pediomys”, 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 pediomyid genera other than Pediomys. […] This morphological diversity among Late Cretaceous species of Pediomys 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 “Pediomys” contains sufficient diversity to warrant its split; Fox (1987a), in that both the genus “Pediomys” and the family “Pediomyidae” are polyphyletic. Two lineages are also composed approximately as Fox predicted: the two smaller species “P.” krejcii and “P.” prokrejcii 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.” exiguis from Pediomys restores monophyly to the genus, as this taxon appears to be an enigmatic stem marsupial. It is placed in its own genus, Api−stodon gen. nov., family incertae sedis. Redefining the family Pediomyidae s.s. to the exclusion of Aquiladelphis, also from the Milk River Formation, securely establishes its monophyly, though the superfamiliy Pediomyoidea (new rank) is erected to
recognize the relationship that exists between pediomyids, *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 pediomyids 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 pediomyid 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 pediomyid or pediomyid-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 pediomyid evolution during the important interval between the early diversification of marsupials in North America (Albian–Cenomanian) and the first undisputed pediomyids s.s. (late Campanian).

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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 Aquilian). 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 Igualadelphis) 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 (Aquilian of Utah) implies a northern origin for the group.

It is interesting to note that the large pediomyoid Aquiladelphis, 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 Leptaleses 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 Pediomys clade was present in Alberta as well (based on a fragmentary upper molar, described by Fox 1979: fig. 2a, that belongs to a Pediomys 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 Leptaleses krejcii 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 Pediomys 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. "Pediomys", along with other Late Cretaceous North American taxa, are nested within an otherwise Australasian marsupial radiation. The purpose of my study is to evaluate "Pediomys" 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 Aquilodelphis, an upper molar closely resembling “Pediomys” exigus (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 pediomyid 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 Aquilian.

References


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.
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 B (stylocone)**
2. Presence: 0 – present; 1 – absent.
3. Size: 0 – 5. 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.

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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 coni-
  cal 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 ab-
  sent.
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 un-
  rounded; 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 por-
  tion 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 – labi-
  ally deflected (equivalent to a W-shaped ectoloph).
Conules
30. Size: 0 – paracune and metacone 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 de-
  veloped.
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.
Trigon basin
36. Presence of protoconal cingula or rugosities: 0 – absent; 1 – present.
Trigonid
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.
Talonid
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 posi-
  tioned 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 hypo-
  conulid; 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 ento-
  cristid: 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 poste-
  riorly); 2 – talonid significantly expanded such that the ventral mar-
  gin 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 protocristid; 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 – mo-
  lars 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.

<table>
<thead>
<tr>
<th>Species</th>
<th>Character State Matrix</th>
</tr>
</thead>
<tbody>
<tr>
<td>Kokopellia juddi Cifelli, 1993a</td>
<td>11322000001 12?1211101 1010111001</td>
</tr>
<tr>
<td>Aenigmadelphys archeri Cifelli and Johanson, 1994</td>
<td>21322000001 11?1221111 1112111101</td>
</tr>
<tr>
<td>Varalphadon wahweapensis (Cifelli, 1990b)</td>
<td>21322000001 11?1221111 1112111101</td>
</tr>
<tr>
<td>Alphadon jasoni Storer, 1991</td>
<td>0011110211 1112000001 0011001011</td>
</tr>
<tr>
<td>Alphadon wilsoni Lillegraven, 1969</td>
<td>2112211001 0110000A</td>
</tr>
<tr>
<td>Turgidodon russelli (Fox, 1979)</td>
<td>0011110211 1112000001 0021001001</td>
</tr>
<tr>
<td>Pediomys elegans Marsh, 1889</td>
<td>11322111101 1122211101 102111001</td>
</tr>
<tr>
<td>“Pediomys” cooki Clemens, 1966</td>
<td>11322000001 21?1211111 1012010101</td>
</tr>
<tr>
<td>“Pediomys” krejcii Clemens, 1966</td>
<td>11322000001 21?1211111 1012010101</td>
</tr>
<tr>
<td>“Pediomys” prokrejcii Fox, 1979</td>
<td>11322000001 21?1211111 1011010000</td>
</tr>
</tbody>
</table>

"Pediomys" clemensi Sahni, 1972
11322000001 12?1211101 1010111001
1010111011 2132210111 0011111A

"Pediomys" hatcheri (Osborn, 1898)
21322000001 11?1221111 1112111101
1010101112 2110011111 00111111

"Pediomys" florencae Clemens, 1966
21322000001 11?1221111 1111111011
1010111112 2110011111 00111111

"Pediomys" exiguis Fox, 1971
0000110221 1122000001 0001021100
0000000111 2?????????? ??????0

"Pediomys" clemensi prokrejcii Sahni, 1972
11322200001 21?1211111 1112211101
1012211101 1112111101 00111111

"Aquiladelphis incus" Fox, 1971
20201110321 1122100001 1?2?211111111 1????00001
10?1000112 1?????????? ??????A

"Aquiladelphis" minor Fox, 1971
20201110321 1122100001 2?011111111 0????1111111
1110111111 0112221101 00111111

"Iqualadelphis lactea" Fox, 1987b
1000000001 2?1?1110001 1??21000000
0010000112 2?????????? ??????0

"Glasbius intricatus" Clemens, 1966
0011101001 1122000110 1120121001
1110111111 2112221011 01011000

"Eodelphis cutleri" (Woodward, 1916)
0010000000 0000000001 0022120101
1000001000 0011111001 0001121

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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) into 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) in a clade. Heavy lines indicate constrained clade.