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In memory of Lauretta Cohen, for her love, wisdom, and commitment to seeing me succeed.

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Table of Contents

Acknowledgements iv

List of Tables vii

List of Figures viii

Abstract ix

CHAPTER 1: INTRODUCTION TO THE EARLY LATE CRETACEOUS OF NORTH AMERICA 1

- Literature Cited 6

CHAPTER 2: THE EARLIEST EUTHERIAN MAMMALS FROM THE LATE CRETACEOUS OF NORTH AMERICA 13

- Abstract 13
- Introduction 14
- Materials and Methods 15
- Geologic Age and Setting 16
- Systematic Paleontology 18
- Discussion 29
- Literature Cited 36

CHAPTER 3: EARLIEST DIVERGENCE OF STAGODONTID (MAMMALIA: MARSUPIALIFORMES) FEEDING STRATEGIES FROM THE LATE CRETACEOUS (TURONIAN) OF NORTH AMERICA 51

- Abstract 51
- Literature Cited 80

CHAPTER 4: GEOLOGICALLY OLDEST PEDIOMYOIDEA (MAMMALIA: MARSUPIALIFORMES) FROM THE LATE CRETACEOUS OF NORTH AMERICA WITH IMPLICATIONS FOR TAXONOMY AND DIET OF EARLIEST LATE CRETACEOUS MAMMALS 95

Abstract 95

Introduction 96

Materials and Methods 98

Systematic Paleontology 99

Discussion 119

Literature Cited 124

CHAPTER 5: A TRANSITIONAL MAMMALIAN FAUNA FROM THE LATE CRETACEOUS (TURONIAN) OF NORTH AMERICA 136

Abstract 136

Introduction 137

Materials and Methods 138

Systematic Paleontology 140

Discussion 164

Literature Cited 168

List of Tables

Table 2.1 Dental measurements of *Gypsonictops lewisi* 48

Table 2.2 Dental measurements of *Paranyctoides* sp. 49

Table 2.3 Dental measurements of ?Zhelestidae..50

Table 3.1 Dental measurements of *Fumodelphodon pulveris*...93

Table 3.2 Dental measurements of *Hoodootherium praeceps*.......................................94

Table 4.1 Dental measurements of *Scalaria diversicuspis*..133

Table 4.2 Dental measurements of *Scalaria aquilana*...134

Table 4.3 Dental measurements of Pediomyoidea...135

Table 5.1. Dental measurements of *Varalphadon* sp. 182

Table 5.2 Dental measurements of *Eoalphadon lillegraveni*.......................................184

Table 5.3 Dental measurements of *Eoalphadon clemensi*..185

Table 5.4 Dental measurements of *Kokopellia musicus*...187

Table 5.5 Dental measurements of *Apidelphys minuscularia*......................................188

Table 5.6 Dental measurements of ?*Anchistodelphys delicatus*...................................189

Table 5.7 Mammals of the Smoky Hollow fauna...190

List of Figures

Figure 1.1. Cretaceous mammalian faunas of North America.......................................12

Figure 2.1 Geologic scale and rock units of Kaiparowits Plateau.................................45

Figure 2.2 Dental reconstructions of Smoky Hollow eutherians..................................46

Figure 2.3 Phylogeny of Cretaceous eutherians from Asia and North America............47

Figure 3.1 Cretaceous North American mammal faunas and map of localities.............88

Figure 3.2 *Fumodelphodon pulveris* gen. et sp. nov. 89

Figure 3.3 Stagodontid root structures..90

Figure 3.4 *Hoodootherium praeceps* gen. et sp. nov. 91

Figure 3.5 Phylogenetic analysis of stagodontids..92

Figure 4.1 Lower dentition of *Scalaria diversicuspis* gen. et sp. nov. 129

Figure 4.2 Upper dentition of *Scalaria diversicuspis* gen. et sp. nov. 130

Figure 4.3 *Scalaria aquilana* gen. et sp. nov. 131

Figure 4.4 Pediomyoidea..132

Figure 5.1 *Varalphadon* sp. 175

Figure 5.2 *Eoalphadon lillegraveni*...176

Figure 5.3 *Eoalphadon clemensi*...177

Figure 5.4 *Kokopellia musicus* sp. nov. 178

Figure 5.5 *Apidelphys minuscularia* gen. et sp. nov. 179

Figure 5.6 ?*Anchistodelphys delicatus*..180

Figure 5.7 Temporal distribution of tribosphenidans present in the Smoky Hollow....181

Abstract

Tribosphenic mammals from the medial Cretaceous (encompassing the Cenomanian to the Campanian (~98–80 Ma)) are rare elements of the fauna, typically recovered via bulk sampling and underwater screen washing. Southern Utah preserves nearly the entire Late Cretaceous rock record, resulting in decades of concerted effort in collecting samples from earlier units of the Cretaceous to compare with typical well-sampled Late Cretaceous rocks from the Campanian and Maastrichtian. Unfortunately, very few described faunas have yielded large samples of well-preserved specimens (with the exception of the early Cenomanian Mussentuchit Local Fauna), making comparisons difficult. Further complicating the problem of understanding mammalian faunal transitions from the Cenomanian to the Campanian are large gaps of time with very little specimens known. One such gap is the Turonian (~94–90 Ma), where very few terrestrial rock is exposed worldwide, due to a global marine transgression. Fortunately, over the past three decades, the late Turonian-aged Smoky Hollow Member of the Straight Cliffs Formation from southern Utah has yielded a large and diverse sample of terrestrial microvertebrates, including mammals. Herein, I describe the tribosphenic mammal fauna, breaking the chapters down taxonomically. In the first chapter, I describe the eutherians, which are rare elements of the fauna and were previously considered to have locally gone extinct in North America by the late Santonian (~82 Ma). At least three taxa are present, all of which are dentally advanced and known from later in the Cretaceous: *Gypsonictops lewisi*, *Paranyctoides* sp., and ?Zhelestidae. The presence of *Gypsonictops* is of particular interest because of its close phylogenetic proximity to Crown Group Placentalia, either just basal or nested within Afrotheria, giving support to the long-fuse hypothesis for placental origins. *Paranyctoides* sp. and ?Zhelestidae are both present in Asia at the same time, suggesting an immigration event may have occurred between North America and Asia by the late Turonian. The marsupialiform family Stagodontidae is described in the second chapter, including two new taxa: *Fumodelphodon pulveris* gen. et sp. nov. and *Hoodootherium praeceps* gen. et sp. nov. These genera represent a divergence in dietary specializations based upon premolar morphology. These dietary specializations include a more sectorial premolar (*Hoodootherium praeceps*) and a crushing premolar (*Fumodelphodon pulveris*). The specializations are reminiscent of the later Cretaceous stagodontids *Eodelphis* (sectorial) and *Didelphodon* (crushing), highlighting that this divergence occurred much earlier than previously thought. In the third chapter, I describe specimens referable to the superfamily Pediomyoidea, a family well known from the Campanian and Maastrichtian, and without clear antecedents from the medial Cretaceous. Two new taxa are described from the Smoky Hollow fauna, *Scalaria diversicuspis* gen. et sp. nov. and *Scalaria aquilana* sp. nov., representing basal members of the pediomyoid family Aquiladelphidae. Specimens from the Campanian and Maastrichtian previously referred to Aquiladelphidae are reviewed, with *Aquiladelphis laurae* confirmed as a member of the family, and a new taxon, *Aquiladelphis analetris* sp. nov. from the Judith River Formation is described and included. A specimen previously referred to Aquiladelphidae is formally described and placed with the pediomyoid family Glasbiidae, as a new species, *Glasbius piceanus* sp. nov. The final chapter finishes the alpha-level taxonomy of the Smoky Hollow fauna, describing the "alphadontid"

marsupialiforms, including *Varalphadon* sp., *Eoalphadon lillegraveni*, *Eoalphadon clemensi*, *Kokopellia musicus* sp. nov., *Apidelphys minuscularia* gen. et sp. nov., and ?*Anchistodelphys delicatus*. The new occurrences from the Smoky Hollow fauna demonstrate a transitional mammalian fauna with elements from the earlier Cenomanian and the later Campanian faunas.

CHAPTER 1: INTRODUCTION TO THE EARLY LATE CRETACEOUS OF NORTH AMERICA

Mesozoic mammals of North America have been known since the late 1800s, and included the first descriptions of the dryolestids, docodons, and multituberculates from the Morrison Formation Jurassic aged rocks and multituberculates, metatherians, and eutherians (although not recognized as such at that time) from latest Cretaceous aged rocks (Marsh, 1878, 1879, 1880, 1887, 1889a, 1889b, 1892). The majority of the specimens from these original descriptions are based off of very few specimens (although many of the Jurassic specimens are known from near-complete jaws), which resulted in a number of taxonomic splitting based upon different tooth loci (i.e., lower molars were often identified as a separate species from upper molars) (Marsh 1889a). Due to the taxonomic splitting, subsequent students of Mesozoic mammals have revised the taxonomic status of these mammals based on additional collections (Simpson, 1927a, 1927b; Clemens, 1963, 1966, 1973). The rich history of collecting mammals from the latest Cretaceous of North America has resulted in large sample sizes and relatively complete fossils, including dentulous jaw fragments and skull fragments (Clemens, 1963, 1966, 1973; Wilson et al., 2016). Since this time, work has been done to fill in the gaps between the Jurassic and the latest Cretaceous faunas in order to better understand the faunal dynamics through the Cretaceous, leading up to the end-Cretaceous extinction and the mammalian radiation during the Cenozoic (Cifelli, 1990a, 1990b, 1990c, 1990d, 1994, 1999, 2004; Cifelli and Davis, 2015; Eaton, 1993, 1995, 2006a, 2006b, 2009, 2013; Fox, 1971; 1976, 1979a, 1979b, 1979c, 1981; Montellano, 1988, 1992). These studies indicate that the faunal turnovers and diversification within these lineages occurred before the end-Cretaceous extinction, earlier than previously thought (Fox, 1971; Kielan-Jaworowska et al., 2004). These transitions include the turnover from domination by archaic lineages (i.e. symmetrodonts and triconodonts) to domination by tribosphenic lineages (metatherians and eutherians) (Grossnickle and Polly, 2013). These findings have led to multiple meta-analyses investigating these trends within Cretaceous mammals leading up to and crossing the end-Cretaceous extinction event (Ahrens et al., 2014; Grossnickle and Newham, 2016; Grossnickle and Polly, 2013; Wilson, 2013; Wilson et al., 2012).

A common finding from these meta-analyses is that mammals increased in diversity within multituberculate and tribosphenic mammals before the end-Cretaceous extinction, indicating potential invasion into new dietary niche space created by the radiation and diversification of angiosperms during this time (Grossnickle and Newham, 2016; Grossnickle and Polly, 2013; Wilson, 2013; Wilson et al., 2012). Angiosperms began to radiate and diversify by the end of the Early Cretaceous, and represent new rich food resources (i.e. fruits, nectar, and pollen) that were available for exploitation and maybe have been one of the driving forces behind the diversification of mammals prior to the end-Cretaceous extinction (Ahrens et al., 2014). However, one drawback to these meta-analyses is the patchiness and incompleteness of the fossil record, especially earlier in the Cretaceous. While the latter half of the Late Cretaceous has been well sampled, earlier time bins have not been so fortunate, resulting in uneven sample sizes between time bins for these meta-analyses. The uneven sampling becomes readily apparent during the early Late Cretaceous, as these analyses appear to point to a decrease in diversity and disparity during the Turonian–Coniacian (Grossnickle and

Newham, 2016; Wilson et al., 2012). However, this decrease in disparity and diversity during the Turonian–Coniacian is most likely due to a sampling bias, as these time bins have the smallest samples available. These studies indicate a need to increase sampling during these time zones to determine if the decrease in diversity and disparity is a real phenomenon or merely an artifact of the sample size, or perhaps the diversification occurred even earlier during the Cretaceous.

A closer look at the sampling efforts into the Late Cretaceous also indicates a smaller sample available for the early Late Cretaceous. The smaller sample size is evident in the North America Land Mammal Ages (NALMAs), erected only for the latter half of the Late Cretaceous from the late Santonian to the Maastrichtian (Fig. 1.1). No NALMAs have been assigned for faunas earlier than the late Santonian for three main reasons: (1) lower sample sizes, (2) limited geographic distribution (nearly all are from the state of Utah), and (3) a discontinuous record through time (Cifelli et al., 2004). In order to achieve the status of a new NALMA, the faunal elements should be biogeographically widespread, rather than known from a single fauna. As sampling increases for these earlier time bins, it may become possible to erect additional NALMAs through the early Late Cretaceous.

Pre-NALMA faunas can be separated into local faunas from specific formations and time bins from the Cenomanian (~98 Ma) to the late Santonian (~85) Ma. The Cenomanian (~98–94 Ma) from North America is probably the best sampled time period from the early Late Cretaceous, with two described faunas, the Mussentuchit Local Fauna of the Cedar Mountain Formation (~98 Ma), and from the Naturita Formation (~95 Ma), both of Utah (Cifelli, 2004; Cifelli et al., 2016; Eaton, 1993, 1995). Following these faunas, the Turonian (~92 Ma) Smoky Hollow Member of the Straight Cliffs Formation of Utah is currently poorly described, with only preliminary descriptions of the fauna available (Cifelli, 1990c; Eaton, 1995). A handful of samples are known from the Coniacian–middle Santonian John Henry Member of the Straight Cliffs Formation (~89–85 Ma), but the available samples are small (Eaton, 2006a, 2006b, 2013; Eaton and Cifelli, 2013). All of these faunas are from formations found in Utah, so may not represent the continent as a whole. It is interesting to note that of all of the described faunas, the Mussentuchit Local Fauna (the best sampled fauna from the early Late Cretaceous) is the only fauna with a similar diversity in mammalian taxa (up to 22 distinct taxa) to the latest Cretaceous Lancian NALMA (from 23–33 taxa) (Cifelli et al., 2016). This suggests that the earliest Late Cretaceous Mussentuchit Local Fauna from the Cenomanian is well sampled, and that the records between the Mussentuchit Local Fauna and the late Santonian require additional sampling and description (assuming the drop in diversity and disparity is due to a sampling bias). One major difference between the Mussentuchit Local Fauna and the latest Cretaceous Lancian NALMA is the preservational quality of the fossils. While extraordinary specimens have been recovered from the Mussentuchit Local Fauna (such as *Kokopellia juddi* Cifelli, 1993) the majority of specimens are known from fragmentary remains (Cifelli, 2004).

Further complicating the fossil record between the Mussentuchit Local Fauna and the late Santonian Aquilan NALMA is the fact that a number of taxa within these faunas have not been identified past the genus, making faunal comparisons and diversity analyses difficult (Eaton and Cifelli, 2013). The poor resolution in taxonomy of these time bins is due to the lower available samples and poorer preservation of specimens, resulting in low confidence in identification to species due to unknown intraspecific variation within these taxa. If larger samples are available, intraspecific variation can be assessed and taxonomic resolution of these faunas can be increased.

In the following chapters, I will investigate a large sample within this critical time period from the middle Turonian Smoky Hollow Member of the Straight Cliffs Formation. In completing the description of the tribosphenic mammals of the fauna, I hope to shed light on the emergence and relationships of the latest Cretaceous mammals. The middle Turonian (~92 Ma) is situated nearly at the halfway point between the Mussentuchit Local Fauna (~98 Ma) and the late Santonian (~84 Ma), making it an ideal fauna to investigate whether the previously identified drop in diversity and disparity during the Turonian is real or simply due to a sampling bias (Grossnickle and Newham, 2016; Wilson et al., 2012). A complete description coupled with comparisons to both older and younger faunas also serves to clarify evolutionary relationships and the origins of the latest Cretaceous mammalian faunas.

The specimens are a result of a long-term collection effort led by Dr. Richard Cifelli, curator of the Sam Noble Oklahoma Museum of Natural History (OMNH), investigating faunal turnovers and evolution of mammalian lineages leading up to and during the Late Cretaceous. The collection effort has resulted in over 1300 catalogued specimens referable to Mammalia at the OMNH available for study, similar to the sample size for the Mussentuchit Local Fauna (~1600 specimens referable to Mammalia) (Cifelli et al., 2016). Adding a well-sampled unit from the early Late Cretaceous medial in time between the Mussentuchit Local Fauna and the late

Santonian Aquilan NALMA should help to resolve the taxonomic status of some of these mammals during the early Late Cretaceous and clarify potential diversity patterns occurring during the early Late Cretaceous.

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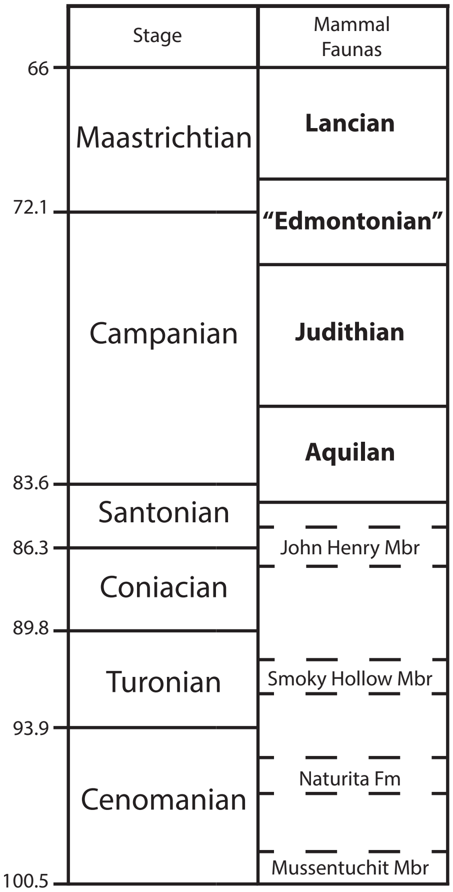
Figure 1.1. Cretaceous mammalian faunas of North America. North American Land Mammal Ages (NALMA) in bold.



CHAPTER 2: THE EARLIEST EUTHERIAN MAMMALS FROM THE LATE CRETACEOUS OF NORTH AMERICA

Abstract

Putative eutherians have been described from the late Early Cretaceous (Albian, about 105 Ma) of North America, but relationships of included taxa remain unclear; undoubted eutherians belonging to recognized clades do not appear until the Santonian–Campanian, 20 or more Ma later, despite major improvements in the fossil record. Herein we document the first occurrence of definitive eutherians from the Turonian of North America, represented by isolated teeth from the Smoky Hollow Member of the Straight Cliffs Formation, southern Utah. We recognize at least three groups of eutherians, including *Gypsonictops lewisi*, *Paranyctoides* sp., and one or more unidentified form(s). *Gypsonictops* specimens are all morphologically indistinguishable from the later Judithian species, *G. lewisi*. *Paranyctoides* sp., known by less complete material, is identical in known respects to *Paranyctoides*, until now the only pre-Campanian definitive eutherian from North America. Four large specimens are comparable in size to large zhelestids (e.g., *Eoungulatum*, *Parazhelestes*). Most informative of these is a lower deciduous premolar, which is low-crowned and bears a broad talonid, closely resembling deciduous premolars of the much smaller Asian *Aspanlestes aptap* and European *Lainodon* spp. The Smoky Hollow eutherians are significant in their temporal occurrence, near the middle of a 20 Ma eutherian hiatus in the North American record (eutherians thrive in Asia during this North American hiatus). Furthermore, each of the three (or more) occurrences represents a group or

taxon typical of later North American assemblages, showing that most of the North American Late Cretaceous faunal composition (all except cimolestids) was established by or during the Turonian. Each also plausibly represents an Asian clade (*Paranyctoides*, recognized from both landmasses, is known from the Turonian of Uzbekistan), suggesting the possibility of intercontinental migration by the early Late Cretaceous.

Introduction

The evolution of early eutherians is poorly understood, with the first potential eutherian, *Juramaia*, known from the Late Jurassic of China, ~160 Ma (Luo et al., 2011). Geologically younger early eutherians hailing from the Early Cretaceous of North America (*Montanalestes*, ~104–109 Ma) and China (*Eomaia*, ~125 Ma) have expanded our knowledge of basal eutherians, and indicate that a biogeographical context is required to fully understand early eutherian evolution (Cifelli, 1999; Ji et al., 2002; Cifelli and Davis, 2015). After the end of the Early Cretaceous, eutherians are conspicuously absent in the fossil record of North America until their re-emergence near the end of the Santonian, roughly 20 Ma later (Fox, 1984; Cifelli, 2001; Cifelli and Davis, 2003, 2015; Cifelli et al., 2016). During the North American eutherian hiatus, eutherians dominate the mammalian tribosphenic faunas in Asia, in both sheer numbers and diversity (Archibald and Averianov, 2005; Averianov and Lopatin, 2014; Kielan-Jaworowska, 1977, 1978).

Negative evidence must be interpreted cautiously, but the mounting evidence favors the interpretation of a local eutherian extinction in North America (Cifelli and Davis, 2015; Cifelli et al., 2016). Previously, the earliest Late Cretaceous North American eutherian was *Paranyctoides*, from the Milk River Formation of Alberta and Eagle Formation of Montana, both of which are late Santonian in age (~83.5 Ma) (Fox, 1984; Payenberg et al., 2002; Davis et al., 2016). The sudden reappearance of eutherians in North America has prompted the suggestion that the North American Late Cretaceous eutherian fauna migrated to North America from Asia, potentially as early as the middle Turonian (Lillegraven, 1969; Averianov and Archibald, 2013). Here we report the discovery of the first Turonian (~92 Ma) eutherians from North America situated near the halfway point of the eutherian hiatus, extending their Late Cretaceous record in North America back by some eight million years. Whereas Early Cretaceous representatives such as *Montanalestes* are basal eutherians (e.g., Wible et al., 2009), these Turonian mammals represent three advanced, possibly Asiatic clades known from later faunas in North America.

Materials and Methods

Specimens for this study were collected from OMNH localities V1404 and V4, both located on federal land within the Grand Staircase-Escalante National Monument; the Utah State Office of the Bureau of Land Management is the official repository for precise locality data. All specimens described were obtained through underwater screen–washing and bulk sampling techniques following Cifelli et al. (1996). Scanning electron micrographs were taken at the OMNH using a Denton Vacuum Desk II sputter coater (Denton Vacuum LLC, 1259 North Church Street Building 3, Moorestown, New Jersey 08057, USA) and a LEO 1450VP SEM (Carl Zeiss NTS LLC, One Corporation Way, Peabody, Massachusetts 01960, USA). Measurements were taken using a Reflex Microscope (see MacLarnon, 1989, Consultantnet Ltd, 94 High Street, Linton, Cambridge, CB21 4JT, UK), as defined by Lillegraven and McKenna (1986).

Measurement abbreviations. — ANW, anterior (mesial) width (trigonid width of lower molars); AP, anteroposterior (mesiodistal) length; POW, posterior (distal) width (talonid width of lower molars).

Institutional Abbreviations.— CCMGE, Chernyshev's Central Museum of Geological Exploration, Saint Petersburg, Russia; L1AT, Museo de Ciencias Naturales de Álva, Vitoria-Gasteiz, Spain; MNA, Museum of Northern Arizona, Flagstaff, Arizona, USA; OMNH, Oklahoma Museum of Natural History, Norman, Oklahoma, USA; UALVP, University of Alberta Laboratory of Paleontology, Edmonton, Alberta, Canada; URBAC, Uzbek/Russian/British/American/Canadian Joint Palaeontological Expedition (specimens currently housed at San Diego State University, San Diego, California, USA).

Geologic Age and Setting

The Straight Cliffs Formation is a geologic unit on the Kaiparowits plateau (Fig. 2.1), located in south-central Utah. The Straight Cliffs Formation is subdivided into four distinct members: the Tibbet Canyon Member situated at the base, followed up-section by the Smoky Hollow Member, the John Henry Member, and the Drip Tank Member capping the formation (Peterson, 1969a, b; Eaton, 1991). The Tibbet Canyon Member is mostly composed of nearshore marine sandstones and is regressive, representing the withdrawal of the Greenhorn Sea (Eaton, 1991). Marine invertebrates have been recovered from the Tibbet Canyon Member, allowing for the use of index fossils to age the member (Peterson, 1969a; Eaton, 1991). The Smoky Hollow Member is a sequence of terrestrial sandstones, mudstones, and coals, that has been subdivided into three informal units: the Calico bed at the top of the member, a barren zone in the middle of the unit, and a coal zone at its base, giving the unit its name (Peterson, 1969a; Eaton, 1991). Vertebrate fossils have all been recovered from the barren middle unit. The overlying John Henry Member consists of interbedded sandstones, mudstones, carbonaceous mudstones, and coals. The member sits unconformably on top of the Smoky Hollow Member and intertongues with the overlying Drip Tank Member. The marine and terrestrial portions of the John Henry Member are separated geographically, with the marine portions predominately to the northeast and the terrestrial portions to the southwest (Peterson, 1969a; Eaton, 1991). Marine and terrestrial fossils have been recovered from the John Henry Member (Peterson, 1969a; Eaton, 1991, 2006). The Drip Tank Member is terrestrial and primarily consists of cliff-forming sandstones (Peterson, 1969a; Eaton, 1991). The only fossils that have been recovered from the Drip Tank Member are gar scales and turtle shells from the upper part of the member

(Eaton, 1991). Overlying the Drip Tank Member is the early-mid Campanian Wahweap Formation (Eaton, 1991; Eaton and Cifelli, 2013).

The marine invertebrates from the Tibbet Canyon and John Henry members have been useful for biostratigraphically aging those members, as well as constraining the ages of the Smoky Hollow and Drip Tank members (Peterson, 1969a; Eaton, 1991). The Tibbet Canyon Member contains marine invertebrates consistent with a middle Turonian age (Peterson, 1969a) and the lowest part of the John Henry Member contains marine fossils from the early Coniacian, restricting the age of the Smoky Hollow Member to a middle-late Turonian age (Eaton, 1991). The Smoky Hollow Member was recently directly dated using an ash bed in the upper part of the member, resulting in an age of ~91.86 – 91.88 Ma (Titus et al., 2013). This date confirms a middle Turonian age for the Smoky Hollow Member.

Systematic Paleontology

Eutheria Gill, 1872

Leptictida McKenna, 1975

Gypsonictopidae Van Valen, 1967

Gypsonictops Simpson, 1927

Gypsonictops lewisi Sahni, 1972

Fig. 2.2A; Table 2.1

Included material. — OMNH 68786, right M1, missing the tip of the paracone; 68787, right maxilla fragment with P4; 68788, left p5, missing the labial half of the protoconid and hypoconid; and 69424, eroded right dp5, missing lingual half of the talonid.

Description. — OMNH 68786 is a right upper first molar and is similar to previously described upper molars of *Gypsonictops* (Lillegraven, 1969; Clemens, 1973; Sahni, 1972). As preserved, the paracone and metacone are subequal in height; were the tip of the paracone present, the paracone would have been the taller cusp (Fig. 2.2A_3). The paracone and metacone are well separated and the base of the paracone is slightly wider than the base of the metacone. A postmetacrista is present running distolabially from the tip of the metacone to a swelling on the posterolabial corner and at the termination of the postmetaconular crista. Apical wear is seen on the tips of the protocone and metacone. The protocone is anteriorly recumbent with a precingulum and postcingulum. The cingula are separate and do not wrap around the lingual side of the protocone. The postcingulum is larger than the precingulum and may have an incipient hypocone. The protoconal cingula are less robust than those typically seen in *Gypsonictops hypoconus* and *Gypsonictops illuminatus*, which suggest affinities to *Gypsonictops lewisi* (Fox, 1979), although this could be attributable to intraspecific variation in *G. hypoconus*. A paraconule and metaconule are both present and located near the base of the paracone and metacone, respectively. The internal crista is sharp on the metaconule, while the paraconule and trigon basin are covered by sediment, so cannot be observed.

OMNH 68787 is a right maxilla fragment with a complete P4. The metacone on the P4 is much shorter than and is well joined to the paracone. A parastyle is present directly anterior to and in line with the paracone and metacone. A stylar shelf is present, manifesting as a continuous ridge along the labial margin of the tooth. The stylar shelf is at its widest posteriorly, directly labial to the metacone. In comparison to *G. hypoconus* and *G. illuminatus*, the stylar shelf is wider in OMNH 68787. A protocone is present with a postcingulum; a precingulum is lacking. The preprotocrista and postprotocrista are sharp and run all the way to the base of the paracone and metacone, respectively. No metaconule is present, but an incipient paraconule may be present where the preprotocrista runs along the base of the paracone.

OMNH 68788, a left p5, is similar to previously described *Gypsonictops* specimens (Fox, 1979; Sahni, 1972), with the protoconid and metaconid well joined, and a very low, paraconid (Fig. 2.2A_1), the latter being one of the hallmark characteristics of *Gypsonictops*. The protoconid is taller and anteroposteriorly wider than the metaconid, while the metaconid is more conical. A groove separates the anterior faces of the protoconid and metaconid, and runs down the anterior side of the trigonid. A preprotocristid is present, starting from the apex of the protoconid and ending at an anterior cingulid, where the incipient paraconid is located (Fig. 2.2A_2). The talonid has all three cusps present, with the hypoconid being the tallest cusp and the entoconid being the shortest. The entoconid is reduced and appressed against the hypoconulid, resulting in an open talonid on the lingual side. The talonid basin slopes anterolingually toward a notch between the entoconid and the metaconid, as seen in *G. hypoconus, G. lewisi*, and some specimens of *G. illuminatus* (Clemens, 1973; Lillegraven, 1969). The cristid obliqua extends mesiolingually from the hypoconid and meets the posterior wall of the trigonid below the notch formed at the junction of the metaconid and protoconid and is continuous with a distal metacristid.

OMNH 69424 is a badly eroded dp5, preserving most of the crown, missing the lingual half of the talonid. Due to the erosion of the tooth, fine details cannot be observed, only general anatomical positions of the major cusps. The protoconid and metaconid are subequal in height and share their bases, while the paraconid is low and anteriorly placed. The talonid is a shelf-like projection, but all detail is lost from the eroded surface of the tooth.

Comments. — The specimens from the Smoky Hollow Member of the Straight Cliffs Formation are nearly identical to specimens of *Gypsonictops* from the Campanian and Maastrichtian. All of the teeth are within the size range of both *G. hypoconus* and *G. lewisi* (see Table 2.1; Fox, 1979: table 1). The identified penultimate premolar (AMNH 77442) described by Sahni (1972) is most likely a P2 in light of the new evidence from OMNH 68787. Most notably, the presence of a metacone separated from the paracone in OMNH 68787 compared to the P3 described by Sahni (lacking any differentiation of a metacone) suggests the P3 described by Sahni is actually a P2. The evidence for inclusion of the Turonian specimens into *G. lewisi* comes from two sources: the relative robustness of the protoconal cingula on the upper molar and the relative width of the stylar shelf on the upper molariform premolars. Fox (1979) noted the increased robustness of the protoconal cingula of *G. hypoconus* and *G. illuminatus* in comparison to *G. lewisi,* with OMNH 68786 sharing the weaker protoconal cingula. However, Fox (1979) suggested that the robustness of the protoconal cingula could be attributed to intraspecific variation (especially in light of the great diversity seen in *G. hypoconus* [Clemens, 1973]), and with the limited sample size available from the Smoky Hollow it cannot be disregarded. The relative width of the stylar shelf on the ultimate upper premolar has been shown to be a diagnostic character to differentiate *G. lewisi* from *G. hypoconus,* with *G. lewisi* having the wider stylar shelf (Fox, 1979). Unfortunately, no ultimate upper premolars have been recovered as of yet, but penultimate upper premolars were compared to see if the trend for a wider stylar shelf in the older species can be observed. The width of the stylar shelf on the penultimate upper premolar appears to follow the trend; OMNH 68787 has a wider stylar shelf when compared to specimens of both *G. hypoconus* and *G. illuminatus,* but again with the currently available sample size, intraspecific variation cannot be ruled out.

Incertae sedis

Paranyctoides Fox, 1979

Paranyctoides sp.

Fig. 2.2C; Table 2.2

Included material. — MNA V5638, left m3; OMNH 68862, talonid of left m3; 20021, talonid of left m3; and 25498, left p5 missing the anterior half of the protoconid.

Description. — MNA V5638 preserves a nearly complete lower molar, with only slight damage to the buccal margin of the tooth. All of the cusps are slightly inflated, giving them a rounded appearance (Fig. 2.2C_1–C_2). The paraconid is the lowest cusp on the trigonid, and is positioned further buccally than the metaconid. The paraconid leans slightly anteriorly, and is not appressed to the metaconid, resulting in a slightly open trigonid. The protoconid is taller than the metaconid and leans slightly posteriorly. The talonid is nearly identical in width with the trigonid, although the enamel on the buccal margin on both the trigonid and talonid is missing, so the widths for the trigonid and talonid should be regarded as minimum estimates. The talonid is preserved on all three molars, so the following descriptions are based on these specimens, unless otherwise specified. The entoconid and hypoconid are the tallest cusps on the talonid and are subequal in height, with the exception of OMNH 20021, where the hypoconid is damaged. The hypoconulid is finger-like and points straight back on all three specimens, suggesting that all three specimens are from the ultimate molar. The hypoconulid is closer to the entoconid, but not twinned, as seen in other species of *Paranyctoides* (Montellano-Ballesteros et al., 2013). A labial postcingulid is present on MNA V5638 and OMNH 20021, but OMNH 68862 is damaged where it would be present, so its presence cannot be determined. Strong wear facets are present on the cristid obliqua and the postcristid, with apical wear on the hypoconid and hypoconulid. A strong crest is present, connecting the entoconid to the hypoconulid, and exhibits a wear facet on OMNH 20021.

The ultimate lower premolar is known from a single, fragmentary specimen, OMNH 25498 (Fig. 2.2C_1, C_2), missing the anterior half of the protoconid. The presence of a paraconid cannot be determined due to breakage. No metaconid is developed, although a slight swelling on the buccal side of the protoconid is present. The posterior face of the protoconid has a sharp crest with a strong wear facet that is continuous from the apex of the protoconid, down to the talonid, and terminating at the apex of the hypoconid. The hypoconid is the tallest cusp of the talonid. A crest defines the lingual border of the talonid, and is continuous with the hypoconulid at its posterior terminus. An entoconid is expressed as a small cusp situated on the lingual crest.

Comments. — Overall, the Smoky Hollow *Paranyctoides* is similar to previously identified specimens from North America, with the presence of a buccal postcingulid on the last lower molars, a low, buccally shifted paraconid, and relatively wide talonid. The lower ultimate premolar shares many similarities with *P. maleficus* and *P. sternbergi*, with no metaconid and a well-developed, bicuspid talonid. The Smoky Hollow *Paranyctoides* is slightly larger than the two named species from North America, *P. maleficus* and *P. sternbergi* (see Table 2.2; Fox, 1984: table 1; and Fox, 1979: table 1) and the unnamed *Paranyctoides* species from the Kaiparowits and Wahweap formations (Cifelli, 1990: table 2) (although see Averianov and Archibald, 2013b for an alternate hypothesis proposing only a single *Paranyctoides* species in North America). Morphologically, the Smoky Hollow *Paranyctoides* have a more vertically oriented hypoconid on the lower molars, a higher degree of inflation in the cusps, and a larger talonid on the ultimate premolar than the younger taxa. The higher degree of inflation of the cusps in the Smoky Hollow *Paranyctoides* is reminiscent of the Asian *Paranyctoides* specimens, and a point of departure with specimens from North America (Montellano-Ballesteros et al., 2013). The higher degree of cusp inflation from the Smoky Hollow *Paranyctoides* specimens follows the trend seen within North America, where *Paranyctoides* species appear to decrease cusp robustness through time, as the Smoky Hollow *Paranyctoides* specimens are the oldest with the greatest amount of inflation (Fox, 1984; Montellano-Ballesteros et al., 2013). The decrease in cusp inflation also agrees with the hypothesis that *Paranyctoides* originated in Asia and subsequently migrated to North America, because the Asian *Paranyctoides* specimens are more inflated than the North American *Paranyctoides*. The Smoky Hollow *Paranyctoides* appears to be an appropriate intermediate between the Asian *Paranyctoides* and the later North American *Paranyctoides*, with more rounded and inflated cusps similar to the Asian *Paranyctoides*, but shares a bicuspid talonid on the ultimate lower premolar, a deep hypoflexid notch, and an anteroposteriorly elongate talonid, with the North American *Paranyctoides*. The Smoky Hollow *Paranyctoides* is distinct from any previously named species, but with the Kaiparowits and Wahweap species and specimens for *P. sternbergi* and *P. maleficus* difficult to differentiate (see Averianov and Archibald, 2013b and Cifelli, 1990b for further discussion), it is appropriate to leave the Smoky Hollow *Paranyctoides* in open nomenclature at this time.

?Zhelestidae Nessov, 1985

Fig. 2.2B; Table 2.3

Included material. — OMNH 68785, right dp5.

Tentatively-referred material. — OMNH 68789, left M3, missing paracone and anterolabial corner of tooth; 68861, left Mx, protocone only; and 25501, right dp5?.

Description. — OMNH 68785 is a complete, well-preserved deciduous premolar with low, rounded cusps (Fig. 2.2B_1, B_2). The talonid is wider than the trigonid with a shallow basin. The entoconid and hypoconid are subequal in height, with the hypoconulid being the shortest cusp. The hypoconulid is closer to the entoconid than the hypoconid, but is not twinned, as seen in other zhelestids (Archibald and Averianov, 2012). The talonid cusps are bulbous and connected by sharp ridges. The cristid obliqua is slightly labially shifted and connects with a distal metacristid, which runs to the protocristid notch. A small wear facet can be seen on the postcristid just posterior to the entoconid apex. The trigonid is open, with the paraconid positioned mesially, a character seen in deciduous premolars. The paraconid is also the shortest cusp of the trigonid and leans mesially. The precingulid is composed of cusps e and f, which are located directly buccal to the paraconid. The protoconid is the tallest cusp, and is about twice as tall as the metaconid. The trigonid is buccolingually compressed, with the metaconid appressed against the protoconid. Apical wear can be seen on all three main cusps of the trigonid. Overall, the deciduous premolar is low-crowned with bulbous, robust cusps and a broad talonid.

OMNH 68789 and 68861 are tentatively referred to the same taxon as 68785 due to their large size and eutherian affinities (Fig. 2.2B$_3$). With additional specimens, it may be prudent to separate these specimens into different taxa. OMNH 68789 is a large last molar preserving the protocone and metacone. The protocone is tall, robust, and leans slightly mesial. No protoconal cingula are present. Heavy apical wear is present, as well as wear facets on the preprotocrista and postprotcrista, extending from the apex of the protocone to the paraconule and metaconule, respectively. The paraconule is broken and poorly preserved, but appears to have had a postparaconular crista. The metaconule is separated from the metacone by a deep notch, with the mesial and distal border defined by a premetaconular crista and a postmetaconular crista, both of which form sharp crests. The premetaconular crista runs up the anterolingual face of the metacone before it terminates about halfway up, while the postmetaconular crista runs along the posterior margin of the base of the metacone and terminates at a cuspule at the posterobuccal corner of the tooth. The metacone is conular and leans posteriorly and lingually. Heavy apical wear and a wear facet along the premetacrista are present. A hint of a stylar shelf can be seen at the buccal side of the metacone, but the extent of the stylar shelf anteriorly cannot be said, as it is broken.

OMNH 68861 is a poorly preserved protocone, with a paraconule and a metaconule. No protoconal cingula can be observed, but heavy wear facets are present along the preprotocrista and postprotocrista.

Comments. — The deciduous premolar OMNH 68785 makes the most compelling case for the presence of a large zhelestid from the Turonian of Utah, but whether the specimen belongs to the same species (or group), as OMNH 68789 and 68861 is still in question. OMNH 68785 and 68789 are within a plausible size range and are currently the largest eutherians known from the Smoky Hollow Member, but more specimens are needed to determine the validity of this association.

OMNH 25501 is similar to 68785 in size (Table 2.3), in having a wider talonid than trigonid, and bulbous cusps, so may belong to the same tooth locus. However, OMNH 25501 exhibits extreme wear on the trigonid to the point where all cusp morphology is gone, suggesting the possibility that 25501 may not be a deciduous premolar, but rather a first molar. High degree of wear tends to be seen in the adult dentition rather than in deciduous teeth, due to the extended length of time required to wear a tooth down (Montellano-Ballesteros and Fox, 2015). If OMNH 25501 is a deciduous premolar, this taxon may have had a diet that incorporated a higher degree of abrasive materials, which can have a similar effect on wear over a shorter amount of time.

Zhelestid dp5s are known from *Aspanlestes aptap* from the Turonian of Uzbekistan (Archibald and Averianov, 2012, figure 10C) and *Lainodon ragei* from the late Campanian–early Maastrichtian of Spain (Gheerbrant and Astibia, 2012; figures 4 and 5). OMNH 68785 is generally similar to dp5s of *Aspanlestes aptap* (URBAC 97–8) and *Lainodon ragei* (L1AT 5, 15), in that the cusps are low, bulbous, and robust; the talonid is wider than the trigonid, and the trigonid is open (i.e. the paraconid is shifted mesially). The general robust construction has been identified as characteristic of zhelestids and is the main basis for the inclusion of OMNH 68785 within Zhelestidae (Gheerbrant and Astibia, 1999, 2012). OMNH 68785 compares more favorably with known dp5s from *Lainodon ragei* than *Aspanlestes aptap*. The paraconid on both OMNH 68785 and L1AT 5 are positioned further mesial and buccal than the condition seen in *Aspanlestes*, resulting in a wider, more open trigonid. The metaconid is much lower than the protoconid on OMNH 68785 and *Lainodon*, in contrast to *Aspanlestes*. The morphology of the talonid is similar between OMNH 68785, *Lainodon*, and *Aspanlestes*, but the greater width of the talonid compared to the trigonid in *Lainodon* and *Aspanlestes* is not as exaggerated in OMNH 68785.

The ultimate upper molar OMNH 68789 is within the size range of large zhelestids, such as *Parazhelestes robustus* (M3 POW range 2.54 – 3.91 mm) (Archibald and Averianov, 2012, appendix 2), but it is unknown whether the Smoky Hollow ?zhelestid exhibits a size reduction in the ultimate molar, a character seen in advanced zhelestids (Nessov et al., 1998). If the Smoky Hollow ?zhelestid lacks the reduction of the ultimate molar in the molar series, the Smoky Hollow ?zhelestid may be larger than *Parazhelestes robustus*. Regardless of its relative size to *Parazhelestes robustus*, the Smoky Hollow ?zhelestid represents the largest eutherian in North America before the emergence of cimolestids during the Lancian North American Land Mammal Age (NALMA).

The majority of zhelestids exhibit protoconal cingula, with the exception of the basal zhelestid *Sheikhdzheilia rezvyii* and the endemic European zhelestids *Lainodon* spp. (Averianov and Archibald, 2005; Gheerbrant and Astibia, 2012). The absence of protoconal cingula in *Sheikhdzheilia rezvyii* and *Lainodon* spp. has been interpreted as the plesiomorphic condition for Zhelestidae (Averianov and Archibald, 2005; Archibald and Averianov, 2012). No protoconal cingula are present on OMNH 69789, suggesting that if the Smoky Hollow ?zhelestid were to be confirmed as a member of Zhelestidae, it would most likely be a basal member of the clade.

Discussion

Previously, the Smoky Hollow fauna was known from only a few species (see Cifelli, 1990a and Eaton, 1995) but with the addition of new specimens, rare elements of the fauna have come to light. Out of the 1253 mammal specimens from the fauna catalogued in the OMNH database, only 12 specimens from three (or more) species are referable to Eutheria. All three taxa are extraordinary in their similarities to Late Cretaceous North American eutherians (Cifelli, 1990b, 1994; Clemens, 1973; Fox, 1979, 1989; Lillegraven, 1976; Zhang, 2009). These taxa represent the first appearance of three iconic groups of eutherians in the Late Cretaceous of North America: Gypsonictopidae, *Paranyctoides*, and Zhelestidae, pushing back the first appearance date of these groups seven million years (in the case of *Paranyctoides*) and more (Fig. 2.3). The Smoky Hollow eutherians bridge a nearly 20 Ma hiatus in the North American eutherian record, from putative, basal eutherians in the Albian, to the emergence of *Paranyctoides* in the late Santonian (Cifelli and Davis, 2015; Fox, 1984; Davis et al., 2016).

The temporal distribution of *Gypsonictops* was previously restricted to the age span Campanian to the Maastrichtian, but the addition of the Smoky Hollow specimens increase its range by nearly 15 Ma, for a first appearance date of ~92 Ma (Cifelli et al., 2004; Kielan-Jaworowska et al., 2004; Titus et al., 2013). Despite the range extension, the specimens referred to *Gypsonictops* from the Smoky Hollow fauna are indistinguishable from the Campanian species, *Gypsonictops lewisi*, warranting referral of the much older Turonian specimens to the same species, based upon the morphological species concept. *Gypsonictops* is characterized by having a highly advanced dentition, and the new range extension doubles the temporal range of the genus; this suggests that its dental morphology was very successful during the Late Cretaceous and did not warrant further modifications.

Gypsonictops, from its first conception, was recognized as closely related to leptictids (Simpson, 1927), and is considered today as the oldest member of Order

Leptictida (Averianov and Lopatin, 2014; Clemens, 2015). The placement of Leptictida, however, has been variably considered as belonging to crown group Placentalia or just outside of crown group Placentalia (see O'Leary et al., 2013 and Wible et al., 2007, 2009 for contrasting placement of Leptictida). However, the vast dataset amassed by O'Leary et al. (2013) has been criticized for excluding the majority of Cretaceous mammals, resulting in some misleading conclusions about the timing of placental mammals (Averianov and Lopatin, 2014; Clemens, 2015). O'Leary et al. (2013, supplementary materials) preferentially excluded species known only from dental material, thereby eliminating the vast majority of Cretaceous eutherians from the analysis. In the case of Order Leptictida, the representative genus used in the analysis was *Leptictis*, known from the Paleocene and Eocene, and was recovered nested within Afrotheria, sister group to Macroscelidea, while the first appearance of Lepticitida was reported as *Prodiacodon crustulum*, a Paleocene species, rather than *Gypsonictops lewisi* (O'Leary et al., 2013, supplementary material). The relationship between *Gypsonictops* and Leptictida was briefly mentioned in the supplementary material but the authors regarded the relationship as poorly understood due to the incomplete morphology representing *Gypsonictops*: known only from isolated teeth, mandibles, and maxillae fragments. Numerous studies, however, have all independently placed *Gypsonictops* as the basal member within Leptictida. Therefore, if Leptictida were to be regarded as part of crown group Placentalia, *Gypsonictops* would represent the earliest placental mammal, dating back to ~92 Ma (Gunnell et al., 2008; Hooker and Russell, 2012; Novacek, 1986; Wible et al., 2007, 2009).

Regardless of where subsequent analyses place Leptictida, the timing of the Turonian fossils has broad implications for the emergence of crown group placentals. The range extension into the middle Cretaceous supplies potential evidence for the emergence of crown group Placentalia as far back as ~92 Ma, a date within molecular clock estimates, which range from 100 Ma to 80 Ma (Meredith et al., 2011; Kitazoe et al., 2007, and references therein). The timing of crown group placentals is a major point of contention between morphological and molecular datasets. The fossil record, through necessity, relies upon morphological data, and to date, no Cretaceous mammal has been confidently assigned to any modern placental Order (but see Archibald et al., 2011 and Kelly, 2014 for potential placentals). With the lack of any confidently assigned placentals present in the Cretaceous, using paleontological data, the origin of crown group Placentalia tends to be placed after the Cretaceous–Paleogene extinction, because that is when the first fossil species can confidently be assigned to the crown group (O'Leary et al., 2013). In contrast, molecular clock models not restricted by the fossil record suggests modern placental Orders first began to diverge by the early Late Cretaceous. The placement of Order Leptictida has far reaching implications, whether it ends up being placed as the sister group to Placentalia or within crown group Placentalia, as Leptictida emerged by the early Late Cretaceous of North America, consistent with molecular clock estimates for the emergence of crown group Placentalia.

The arrival of *Gypsonictops* in North America remains enigmatic, as there are no clear antecedents known in North America or elsewhere. The closest Cretaceous relatives to *Gypsonictops* are the Zalambdalestidae, a small, endemic group of eutherians that first emerged during the Turonian of Asia (Archibald and Averianov, 2003). *Gypsonictops* represents a clade endemic to North America, so the exact relationship to contemporary groups in Asia or other continents is uncertain. However, the sudden appearance of advanced eutherians in North America suggests a migration event, especially since earlier well-sampled faunas aged from the Cenomanian such as the Mussentuchit Local Fauna from the Cedar Mountain Formation are devoid of eutherians (Cifelli and Davis, 2015; Cifelli et al., 2016). In contrast, Cretaceous mammalian faunas of the Campanian and Maastrichtian show an increased diversity of eutherians with the emergence and radiation of cimolestids and zhelestids (Lillegraven, 1969, 1976; Clemens, 1973; Fox 1989; Cifelli, 1994). However, it should be noted that Cretaceous eutherian phylogenies routinely place these groups basal to *Gypsonictops* (Wible et al., 2009; Averianov and Archibald, 2012). Furthermore, no other potential placental mammals have been identified in the fossil record until the latest Cretaceous of North America with the emergence of *Protungulatum coombsi* and *Protungulatum mcgilli*, the former of which has been suggested to be an immigrant (Archibald et al., 2011; Kelly, 2014).

Paranyctoides is the only Cretaceous eutherian genus that has been reported from both Asia and North America (Fox, 1979, 1984; Nessov, 1993; Archibald and Averianov, 2001). Recent work has called into question the close relationship between the North American and Asian *Paranyctoides* spp. and expressed doubts as to whether the Asian *Paranyctoides* should be considered the same genus as the North American *Paranyctoides* (Montellano-Ballesteros and Fox, 2013, but see Averianov and Archibald, 2013a, 2013b, for a contrasting opinion). Regardless of whether the Asian

Paranyctoides should be considered a separate genus or not, it is more closely related to the North American *Paranyctoides* than to any Asian zhelestids, based on published phylogenies (Wible, 2007, 2009; Averianov and Archibald, 2013b, 2016).

The Asian *Paranyctoides* has been reported from the middle – late Turonian Bissekty Formation and the late Turonian – early Coniacian Aitym Formation of the Central Kyzylkum Desert of Uzbekistan (Averianov and Archibald, 2013b). *Paranyctoides* in North America has previously been reported from the Late Santonian – Late Maastrichtian (Fox, 1979, 1984; Cifelli, 1990b; Zhang, 2009), but with the addition of the Smoky Hollow *Paranyctoides*, the earliest record of *Paranyctoides* is now middle Turonian. The similar temporal distribution of *Paranyctoides* in both Asia and North America strongly implies a migration event between these two continents by the middle Turonian. The direction of eutherian migration is presumed to be from Asia to North America because of the eutherian hiatus in North America.

Zhelestidae first arose in Central Asia in the Cenomanian, where it quickly diversified and grew in abundance by the Turonian (Averianov and Archibald, 2005; Archibald and Averianov, 2012). Representatives of Zhelestidae have been found in the Late Cretaceous of North America and Europe, but never reached the same level of diversification as their relatives in Central Asia. Previously in North America, zhelestids were known from the Campanian to Maastrichtian, but were never abundant or diverse, with their total diversity comprising three genera and four species. The Campanian species include *Avitotherium utahensis* from the Kaiparowits Formation of Utah (Cifelli, 1990b), *Gallolestes pachymandibularis* from the El Gallo Formation of Baja California (Lillegraven, 1976), and *Gallolestes agujaensis* from the Aguja

Formation of Texas (Cifelli, 1994), with the Maastrichtian species restricted to *Alostera saskatchewanensis* from the Frenchman Formation of Saskatchewan (Fox, 1989). In Archibald and Averianov's (2012) revision of Zhelestidae, they did not consider *Alostera* to be a member of Zhelestidae because it appeared to share traits with archaic ungulates instead of zhelestids, such as: lacking a parastylar groove, lacking an ectoflexus, and having a metacingulum formed by the postmetaconular crista continuing onto the metastylar lobe. However, when *Alostera* was included in the phylogenetic analysis, it was recovered within Zhelestidae, rather than within archaic ungulates (Archibald and Averianov, 2012, figure 29D).

Zhelestidae and *Paranyctoides* are known from North America and Asia, with *Paranyctoides* representing the only Cretaceous eutherian genus reported from both continents. In Asia, Zhelestidae appears to have originated by the Cenomanian (Averianov and Archibald, 2005), with *Paranyctoides* originating by at least the middle Turonian (Nessov, 1993; Archibald and Averianov, 2001, 2005). These groups subsequently emerged in North America by the middle Turonian, suggesting eutherians participated in a faunal exchange between Asia and North America (Archibald and Averianov, 2001; Averianov and Archibald, 2003; Sues and Averianov, 2009). These new specimens provide strong evidence for a Turonian faunal interchange between Asia and North America, establishing, in part, the eutherian fauna of the Late Cretaceous of North America. In addition, the earliest record of *Gypsonictops* potentially brings back the origin of crown group Placentalia to ~92 Ma, dependent on the phylogenetic position of Order Leptictida.

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FIGURE 2.1. Geologic scale and rock units of the Kaiparowits Plateau of southern Utah. Rock units with metatherians and eutherians identified with a kangaroo symbol and elephant symbol, respectively, and a map of approximate locations of all Late Cretaceous eutherian localities in Asia and North America, color-coded following the geologic time scale.

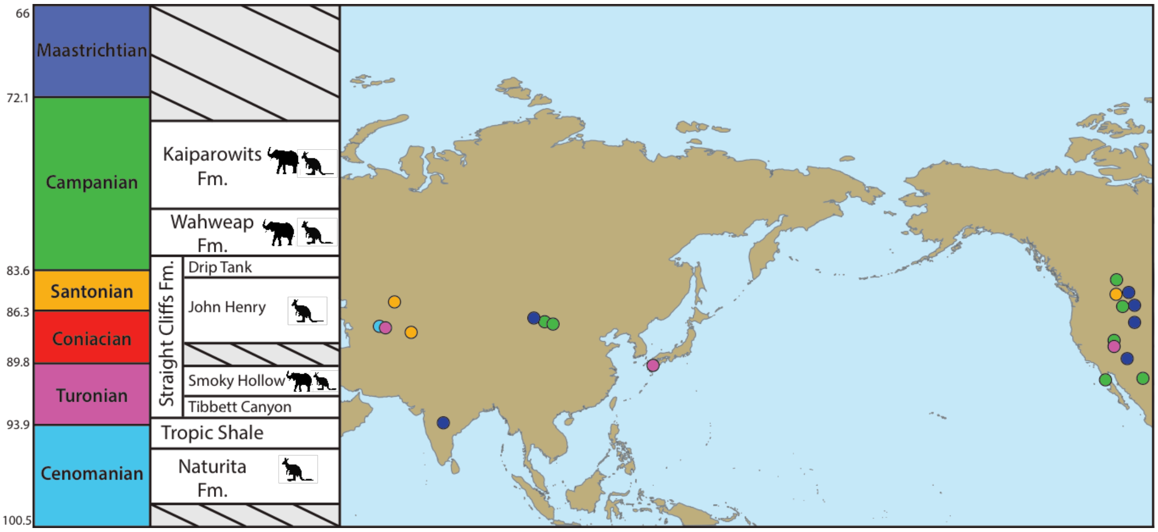

FIGURE 2.2. Smoky Hollow eutherians with dentition reconstruction line drawings based on closely related taxa. A, *Gypsonictops lewisi* with reconstruction based on *Gypsonictops illuminatus* (UALVP 3373 and 2447), with OMNH 68788, left p5 (inverted), OMNH 68787, right P4 (inverted), and OMNH 68786, right M1 (inverted), in lingual (A_1), and occlusal (A_2, A_3) views. B, ?Zhelestidae with reconstruction based on *Aspanlestes aptap* (CCMGE 4/12176 [only m1–2 shown], CCMGE 69/12176 [m3 shown and inverted], CCMGE 1/12455, and URBAC 03–179), with OMNH 68785, right dp5 and OMNH 68789, left M3, in lingual (B_1) and occlusal (B_2, B_3) views. C, *Paranyctoides* sp. with reconstruction based on *Paranyctoides maleficus* and *Paranyctoides sternbergi* (UALVP 6998 [inverted], UALVP 14822 [only p5 shown], and UALVP 16176 [inverted]), with OMNH 25498, left p5 (inverted) and MNA V5638, left m3 (inverted), in lingual (C_1) and occlusal (C_2) views.

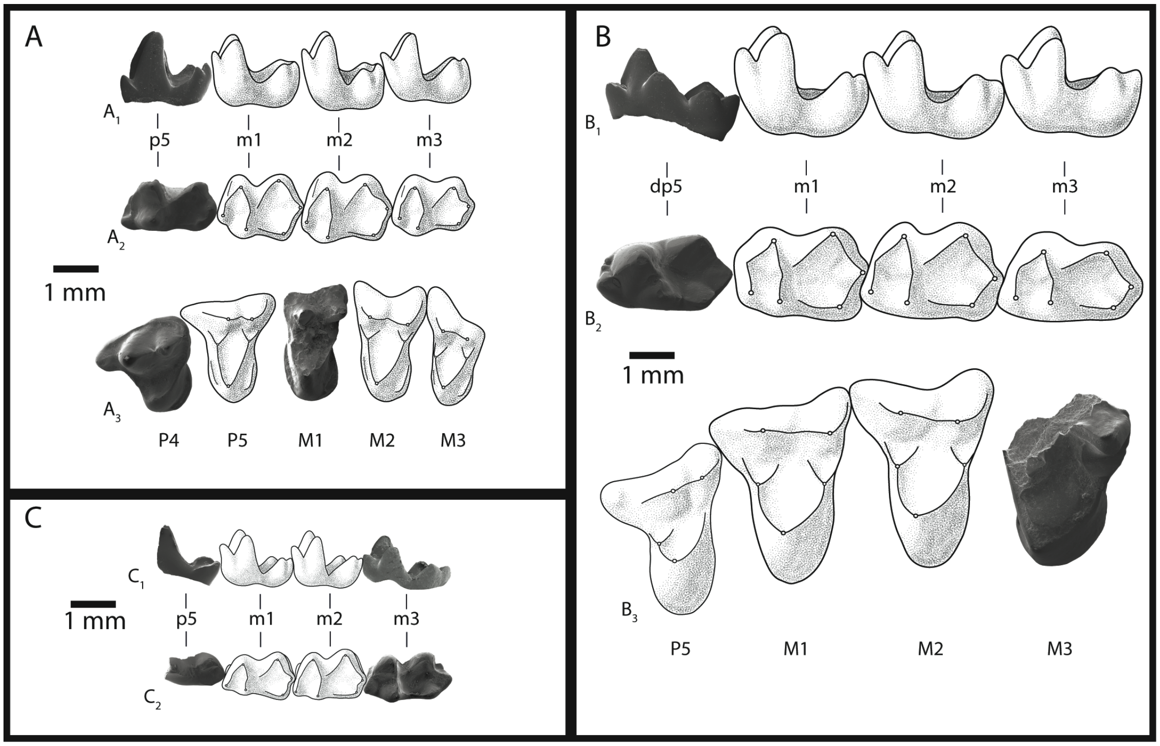

FIGURE 2.3. Phylogeny of Cretaceous eutherian mammals from Asia and North America with range extensions inferred by the Smoky Hollow eutherians. Modified after Wible et al., 2009.

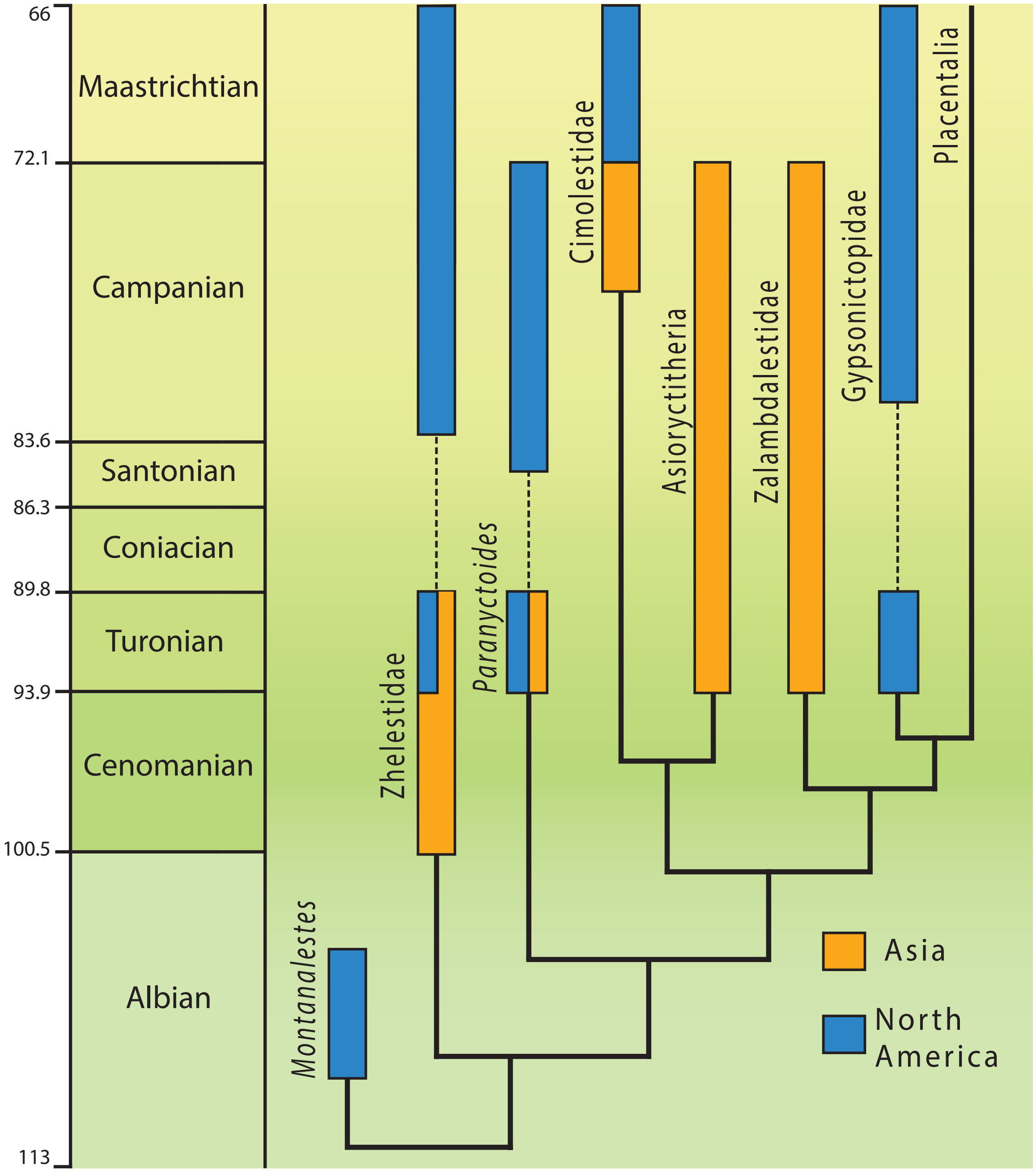

Table 2.1. Dental measurements (in mm) of *Gypsonictops lewisi*. ANW = anterior width, POW = posterior width, AP = anteroposterior length.

Specimen	**Tooth**	**ANW**	**POW**	**AP**
OMNH 69424	dp5	0.88	0.67	2.04
OMNH 68788	p5	1.16	1.18	2.18
OMNH 68787	P4	2.17	2.26	2.29
OMNH 68786	M2	2.78	2.91	1.59

Table 2.2. Dental measurements (in mm) of *Paranyctoides* sp.

Specimen	Tooth	ANW	POW	AP
OMNH 25498	p5	0.79	0.84	—
MNA V5638	m3	1.01	1.03	1.99
OMNH 68862	mx	—	1.10	—
OMNH 20021	mx	—	—	—

Table 2.3. Dental measurements (in mm) of ?Zhelestidae.

Specimen	Tooth	ANW	POW	AP
OMNH 68785	dp5	1.50	1.80	2.90
OMNH 25501	dp5?	1.41	1.66	2.71
OMNH 68789	M3	—	3.86	—

CHAPTER 3: EARLIEST DIVERGENCE OF STAGODONTID (MAMMALIA: MARSUPIALIFORMES) FEEDING STRATEGIES FROM THE LATE CRETACEOUS (TURONIAN) OF NORTH AMERICA

Abstract

Two new unequivocal stagodontids, *Fumodelphodon pulveris*, gen. et. sp. nov., and *Hoodootherium praeceps,* gen. et. sp. nov., are described from the Turonian (~92 Ma) Smoky Hollow Member of the Straight Cliffs Formation, of southern Utah, USA. Mammals from this time period are poorly represented; the recovery of these two large stagodontids demonstrates the early emergence of faunal elements mostly associated with the later Cretaceous. These taxa represent the earliest stagodontids with crushing premolars (*Fumodelphodon*) and sectorial premolars (*Hoodootherium*), morphologically similar to the well-known stagodontids *Didelphodon* and *Eodelphis*, respectively. The similar morphologies suggest that these two new genera may be early members of later Cretaceous stagodontid clades, implying a ~7 Ma ghost lineage leading to *Eodelphis* and a ~15 Ma ghost lineage to *Didelphodon*. A reexamination of stagodontid characters suggests a basal placement of *Pariadens* within Stagodontidae, contrary to some recent studies. The discovery of two new stagodontids bearing lower molars morphologically similar to, but premolars distinct from, *Eodelphis* highlights the importance of the specialized premolar morphology for resolving the relationships between genera within Stagodontidae.

Introduction

Stagodontidae comprise a family of marsupialiforms with two generally accepted genera, *Didelphodon* and *Eodelphis*. The group did not survive the end-Cretaceous extinction (Clemens, 1966; Fox and Naylor, 2006; Wilson, 2013). Members of the Stagodontidae typically represent the largest mammals from their respective faunas in North America (Clemens, 1966; Fox, 1971), with the earliest definitive record, that of *Eodelphis* sp., from the late Santonian Milk River Formation (Fox, 1971). The first occurrence of *Didelphodon,* however, is from the Campanian of Canada (Fox and Naylor, 2006). Stagodontids are characterized by having lower molars with a blade-like paracristid, a reduced metaconid, and a mesiodistally compressed trigonid, while upper molars have a short paracone, robust metacone with a tall postmetacrista, and well-developed conules positioned close to the bases of the paracone and metacone (Fox and Naylor, 2006). *Eodelphis* and *Didelphodon* represent two clades with distinct dietary specializations, characterized by contrasting premolar morphology: *Eodelphis* is considered more carnivorous, with premolars specialized for shearing; and *Didelphodon* is considered durophagous or molluscivorous, with low-crowned and bulbous premolars specialized for crushing (Clemens, 1966, 1968; Fox and Naylor, 1986, 2006; Scott and Fox, 2015). These two genera were contemporaries during the Campanian, but only *Didelphodon* survived into the Maastrichtian (Scott and Fox, 2015) (but see Kelly [2014] for a possible extension of *Eodelphis* in the Maastrichtian).

Two putative stagodontids have been described from the Cenomanian of Utah: *Pariadens mckennai* from the Mussentuchit Member of the Cedar Mountain Formation, and *Pariadens kirklandi* from the Naturita Formation (previously considered the Dakota Formation) (Young, 1960; Cifelli and Eaton, 1987; Cifelli, 2004; Cifelli et al., 2016). Cifelli and Eaton (1987) tentatively referred *Pariadens* to Stagodontidae because of its overall dental similarities to *Eodelphis* and *Didelphodon*. It is also different from all other known Cretaceous metatherians, with a large body size, a larger paraconid than metaconid, and a posteriorly increasing size of molars, suggesting that *Pariadens* may represent a morphological antecedent to later Cretaceous genera. Fox and Naylor (2006), however, removed *Pariadens* from Stagodontidae because the genus "lacks crucial stagodontid features, including the high blade-like paracristid containing a large, keyhole-like carnassial notch, mesiodistal compression of the lower molar trigonids, and a labial position of the cristid obliqua on all of the lower molars" (Fox and Naylor, 2006: 14).

The only other potential stagodontid fossils older than Aquilan (North American Land Mammal Age, or NALMA, see Fig. 3.1A) include a fragmentary lower molar from the Santonian part of the John Henry Member and a lower premolar from the Smoky Hollow Member, both of the Straight Cliffs Formation, Utah (Cifelli, 1990a; Eaton, 2006). The lower molar fragment from the John Henry Member, dated to the middle Santonian, is morphologically similar to lower molars of *Eodelphis* but significantly smaller (Eaton, 2006). Cifelli (1990a) reported the occurrence of a potential stagodontid from the Smoky Hollow Member (Turonian), based on the presence of a single inflated premolar. The discovery of additional specimens, including lower molars, upper premolars, and an upper molar (this study), confirms the presence of at least two new taxa of definitive stagodontids, herein regarded as representatives of different genera, from the Smoky Hollow Member of the Straight Cliffs Formation. These fossils, dated to the middle Turonian, represent the geologically oldest occurrences of unequivocal stagodontid marsupialiforms, and demonstrate that significant morphologic diversification had already occurred within the clade.

Methods and Terminology

Specimens for this study were collected from OMNH localities V60, V843 (=MNA 995), and V1404 (Fig. 3.1B and C)**.** All sites are in Grand Staircase-Escalante National Monument, and exact locality data are maintained by the Bureau of Land Management. All specimens described were obtained through underwater screen-washing and bulk sampling techniques following Cifelli (1996). Scanning electron micrographs were taken at the OMNH using a Denton Vacuum Desk II sputter coater (Denton Vacuum LLC, 1259 North Church Street Building 3, Moorestown, New Jersey 08057, USA) and a LEO 1450VP SEM (Carl Zeiss NTS LLC, One Corporation Way, Peabody, Massachusetts 01960, USA). Measurements were taken using a Reflex Microscope (see MacLarnon 1989, Consultantnet Ltd, 94 High Street, Linton, Cambridge, CB21 4JT, UK), as defined by Lillegraven and McKenna (1986). Dental terminology follows Kielan-Jaworowska et al. (2004).

Measurement abbreviations. — ANW, anterior width (trigonid width of lower molars); AP, anteroposterior (mesiodistal) length; POW, posterior width (talonid width of lower molars).

Institutional Abbreviations. — MNA, Museum of Northern Arizona, Flagstaff, Arizona, USA; OMNH, Oklahoma Museum of Natural History, Norman, Oklahoma, USA; UCM, University of Colorado Museum, Boulder, Colorado, USA.

Geologic Setting and Age

The localities are situated within the Smoky Hollow Member of the Straight Cliffs Formation, in Kane County, Utah. The Smoky Hollow Member has been suggested to be late Turonian in age, as it is well constrained between the underlying Tibbet Canyon Member and the overlying John Henry Member, both of which contain marine invertebrates (Peterson, 1969; Cifelli, 1990a; Eaton, 1987, 1991; Eaton and Cifelli, 2013). The Tibbet Canyon Member has been dated to the middle Turonian and the lower section of the John Henry Member has been dated to the early Coniacian, based on marine index fossils (Peterson, 1969; Eaton, 1991). An unconformity exists between the Smoky Hollow Member and the John Henry Member, suggesting the Smoky Hollow Member is restricted to a middle-late Turonian age (Eaton, 1991). Recently, the discovery of an ash bed in the upper part of the Smoky Hollow Member has made it possible to directly date the member for the first time, resulting in an age of ~91.86–91.88 Ma (Titus et al., 2013).

Systematic Paleontology

Marsupialiformes Vullo et al., 2009

Stagodontidae Marsh, 1889

Fumodelphodon, gen. nov.

Type species. — *Fumodelphodon pulveris,* sp. nov., monotypic.

Etymology. — Fumo-, Latin, smoke, for the Smoky Hollow Member of the Straight Cliffs Formation; and -delphodon, in allusion to the hypothesized relationship with *Didelphodon*.

Distribution. — As for the type and only species.

Diagnosis. — As for the type and only species.

Fumodelphodon pulveris, gen. et sp. nov.

Fig. 3.2; Table 3.1

Etymology. — Pulveris, from pulverize, in allusion to the premolars with a proposed crushing function.

Holotype. — MNA V7340, left P3.

Type locality. — OMNH locality V843, Garfield County, Utah, USA. Smoky Hollow Member of the Straight Cliffs Formation, middle Turonian.

Referred material. — OMNH 68761, trigonid of left mx; 69319, trigonid of left m1; 29480, occlusal margin of left mx; 69321, talonid of right mx; 29466, left p3; 69323, right p3; 69324, left p3; 28048, left p2; 29075, left DP3.

Diagnosis. — Lower molars are similar in size and known morphology to *Eodelphis*, with the exception of having a taller protoconid than paraconid (subequal in *Eodelphis*). Premolars are generally large and bulbous. Upper P3 has three roots, a protocone with a trigon basin, lacks a preparacrista, and has a weakly developed postparacrista. Lower premolars are inflated, but not lobate as in *Didelphodon*; differs from *Eodelphis* in lacking strong crests on the mesial and distal faces and has a basined heel.

Description. — Lower p3s are large, with a robust, bulbous appearance. The preserved lower premolars are mostly complete but most exhibit heavy apical wear. The paraconid is tall and rounded, lacking any crest on the mesial slope, but has a faint crest (Fig. 3.2D) on the distal slope on OMNH 69323 and 69324. A small heel, present on all specimens, consists of a shallow basin with a single small cusp positioned directly distal to the paraconid. A weakly-developed crest defines the labial margin of the basin. All available premolars lack basal cingulids. OMNH 28048 is generally similar to the other premolars assigned to *Fumodelphodon*, but is smaller, so is provisionally identified as p2 rather than p3. OMNH 28048 lacks a crest on the distal slope of the protoconid; this is generally present on p3, although it is absent in one specimen (OMNH 29466). Lower premolars are two-rooted, with the roots for p3 being subcircular in cross section. The roots are oriented mesiodistally, and the distal root is the larger of the two.

The best-preserved lower molar, OMNH 68761, is a trigonid, which has a well-developed carnassial notch in the paracristid (Fig. 3.2F), as well as a lesser-developed carnassial notch in the protocristid. The paraconid is taller than the metaconid and is nearly subequal in height with the protoconid (the protoconid is slightly taller). The metaconid is mesially placed such that it is in line with the protoconid, giving the trigonid a mesiodistally compressed appearance. The paracristid is prominent and forms a blade-like crest. The trigonid is largely unworn, with only slight apical wear on all three cusps. A precingulid is present, which forms a continuous shelf from the mesiolingual corner to the mesiolabial corner. The cristid obliqua meets the distal trigonid wall labial to the protocristid notch. OMNH 69319, another trigonid, is identified as belonging to m1, owing to the mesially placed paraconid relative to the protoconid and metaconid, giving the trigonid an open appearance. The m1 provides addition information on occlusion and wear. The metaconid is nearly obliterated by a large, oval-shaped wear facet along the entire back of the trigonid. A contact facet for the preceding p3 is present on the mesial face of the paraconid, where it has obliterated the precingulid at that point. The remaining portion of the precingulid exhibits a well-developed wear facet, derived from occlusion with the upper ultimate premolar. A slight wear facet is preserved on the entire preserved length of the paracristid.

The talonid is known from a single specimen, OMNH 69321, and is associated with the trigonids based on size and predicted morphology. The hypoconid is worn away, making it impossible to say which cusp on the talonid would have been the tallest. A wear facet extends lingually from the hypoconid onto the labial edge of the hypoconulid (Fig. 3.2C); however, enough of the hypoconulid remains to observe that the entoconid was the taller of the two. The entoconid and hypoconulid are closely approximated and twinned, with a postcingulid running labially from the hypoconulid along the distal margin of the tooth. From what remains of the base of the trigonid, the talonid would have been subequal in width. The entocristid lacks a carnassial notch, unlike what is seen in the majority of specimens assigned to *Eodelphis* and *Didelphodon*. It is impossible to determine where the cristid obliqua would have intersected the trigonid due to breakage on OMNH 69321.

The holotype (MNA V7340) is a large P3 (compared to most mammalian teeth known from pre-Santonian faunas of North America), greatly inflated, and lobate in general appearance (Fig. 3.2A). A lingual swelling, interpreted here as a protocone, is separated from the principal cusp (or lobe), the paracone, by a developed trigon basin. No other cusps or cusp-like structures are present on the premolar. The paracone dominates the tooth and is much taller than the protocone. Both cusps bear heavy apical wear and appear to lack any vertical wear facets, suggesting an emphasis on horizontal wear. A small, slightly crenulated postparacrista is present distal to the paracone, where it terminates at the distal margin of the tooth. The trigon basin is shallow, with the distal margin defined by a postprotocrista running from the tip of the protocone to the posterolingual base of the paracone. The mesial margin of the trigon basin is open and lacks a preprotocrista. On the mesial edge of the tooth, a projection from the base of the paracone extends anterolabially. The projection is broken at its most mesial portion. The tooth is three-rooted (see Fig. 3.3B), and only the bases of the roots remain. The roots are placed in the mesial, distal, and lingual positions. The lingual root is circular in cross section and supports the protocone, appearing to have extended straight dorsally. The mesial and distal roots diverge, with the distal root oriented somewhat posteriorly and the mesial root oriented anteriorly. The cross-section of the mesial root is circular; that of the distal root is oval. The long axis of the distal root is oriented transversely across the tooth, stretching from the distolabial corner of the tooth toward the lingual root. The root canal for the distal root is also elongated lingually.

OMNH 29075 is a complete DP3 and resembles the corresponding tooth of other Late Cretaceous marsupialiforms (see Cifelli et al. [2016] and Clemens [1966] for examples of Late Cretaceous marsupialiform DP3 morphology) in having a reduced anterior stylar shelf and a well-developed, mesiodistally broad (but labiolingually narrow) protocone (Fig. 3.2B). Stylar cusps C and D are present and are subequal in height, with cusp C situated distal to a very shallow ectoflexus. Two small cuspules are present on the anterior stylar shelf and are attached to the mesial slope of stylar cusp C. The labial margin of the parastyle is crenulated with small cuspules, but cusps A and B are not definitively present. The paracone and metacone are subequal in height and taller than the protocone. The preprotocrista extends past the paracone ending at the parastyle, while the postprotocrista terminates at the base of the metacone. A paraconule and metaconule are present, with short internal cristae. The paraconule has been almost completely worn away. Overall, the tooth exhibits heavy wear, much of it situated on the mesial half of the tooth. Apical wear is evident on all three main cusps, as well as on stylar cusps C and D, with the paracone exhibiting the most wear. The pre- and postprotocrista are worn, with the mesial crest showing the most wear. A wear facet is observed on the labial half of the postmetacrista.

Comments. — Overall, the known specimens assigned to *Fumodelphodon* are reminiscent of the Late Cretaceous stagodontids *Eodelphis* and *Didelphodon*. While lower molars of *Fumodelphodon* are fragmentary, they share important morphological characters that identify them as belonging to the family Stagodontidae. For example, they share diagnostic features indicated by Fox and Naylor (2006), such as an enlarged, blade-like paracristid with a carnassial notch, attachment of the cristid obliqua labial to the protocristid notch, a reduced metaconid, and a paraconid subequal in height with the protoconid. Lower molar measurements of *Fumodelphodon* fall within the size range and are morphologically similar to those of *Eodelphis* (see Table 3.1 and Fox, 1981: tables 1–4), unlike those of *Didelphodon*, with their advanced molar construction highlighted by a widely-basined talonid, acutely-angled trigonid, and enlarged, mesially projecting precingulid.

By contrast, the single upper premolar of *Fumodelphodon* shares more in common with *Didelphodon* than with *Eodelphis*, primarily in the presence of a lingual lobe (interpreted as a protocone on *Fumodelphodon*) and lack of strong crests running down the mesial and distal faces. Upper premolars of *Eodelphis cutleri* tend to have a small lingual swelling, but not to the extent seen in either *Didelphodon* or *Fumodelphodon*. Upper premolars known from *Eodelphis* (see Scott and Fox, 2015) are laterally compressed and less robust when compared with those known from *Fumodelphodon* and *Didelphodon*. As with *Eodelphis* and *Didelphodon*, the apex of P3 in *Fumodelphodon* is heavily worn down, indicating an emphasis on horizontal wear and a possible crushing function. The P3 of *Fumodelphodon* differs from both *Eodelphis* and *Didelphodon* in its possession of three distinct roots.

Lower premolars assigned to *Fumodelphodon pulveris* appear more generalized when compared to *Eodelphis* and *Didelphodon*, which have highly specialized lower premolars suitable for either a sectorial or crushing function, respectively (Scott and Fox, 2015). Lower premolars for *Eodelphis* bear sharp crests running down the mesial and distal faces of the main cusp. The distal crest runs down to the heel at the back of the tooth, which is dominated by a tall, sharp cusp, identified as a hypoconulid by Scott and Fox (2015). A separate sharp crest descends down the mesial face of the hypoconulid giving the heel a notched appearance (see Scott and Fox, 2015: figs. 4M–R, 6J–L). The sharp crests are suitable for cutting vertebrate flesh, and thus they have been hypothesized to correspond to a highly carnivorous diet in *Eodelphis* (Scott and Fox, 2015). In contrast, p3s of *Didelphodon* appear highly derived for crushing, being large, low-crowned, lobate, and lacking sharp crests. Crests, when present, tend to be thick and crenulated, giving them a rounded appearance (see Lillegraven, 1969: fig. 25, 3D). When comparing lower p3s, the heel on the lower premolar of *Fumodelphodon pulveris* appears more similar to that of basal marsupialiforms, such as *Kokopellia juddi*, as it is shallowly basined with a small, generalized cusp, and lacks basal cingulids. The lower premolars, however, also have more typical stagodontid features, such as large size, and robust, bulbous cusps with heavy apical wear.

The deciduous premolar is assigned to *Fumodelphodon pulveris* based on its size (it is, by a considerable margin, the largest DP3 from the Smoky Hollow fauna [see Table 3.1]) and its morphological similarity to known DP3s of *Didelphodon vorax* (described in Clemens, 1966). OMNH 29075 differs from *Didelphodon vorax*, particularly with the presence of a large stylar cusp C that is subequal in size to cusp D.

In *Didelphodon*, stylar cusp D is by far the largest cusp on the stylar shelf and is greatly expanded labially, with cusp C either small or variably present (Clemens, 1966). However, cusp D of *Fumodelphodon* is not greatly expanded labially, but does appear to be slightly swollen beyond the labial margin. As evidenced from the heavy wear facets along the preprotocrista and the mesial face of the paracone and a much smaller wear facet on the postmetacrista, prevallum/postvallid shear was also important on the DP3, indicating that a crushing function may have been present for juveniles as well.

Hoodootherium, gen. nov.

Type species. — *Hoodootherium praeceps,* gen. et sp. nov., monotypic.

Etymology. — Hoodoo-, for the geologic features that are common throughout southern Utah, and -therium, a common suffix for Mesozoic mammals.

Distribution. — As for the type and only species.

Diagnosis. — As for the type and only species.

Hoodootherium praeceps, gen. et sp. nov.

Fig. 3.4; Table 3.2

Etymology. — Praeceps, Latin for a steep place or cliff, in allusion to the Straight Cliffs Formation.

Holotype. — OMNH 68804, left P3.

Type locality. — OMNH locality V1404, Kane County, Utah, USA. Smoky Hollow Member of the Straight Cliffs Formation, middle Turonian.

Referred material. — OMNH 68760, a left m4?; 69320, left mx missing the talonid; 69351, right M4; and MNA V5652, ?left ?p3.

Tentatively referred specimens. — OMNH 69328, incomplete p3?; 69322, left mx with occlusal surface of trigonid; 69329, mx with paraconid and metaconid only; and 24632, right mx trigonid.

Diagnosis. — Similar to *Eodelphis*, but significantly smaller. P3 differs from that of *Eodelphis* in the lack of a definitive basal cingulum and preparacrista, and the presence of a distinct keyhole-shaped pit on the lingual side. Lower molars differ from *Eodelphis* in having a shorter paraconid than protoconid and lack of carnassial notch on the entocristid. Lower p3 differs from *Eodelphis* in lacking sharp keels on the mesial and distal faces, and the heel on the back of the tooth lacks a prominent cusp.

Description. — Lower molars are represented by OMNH 68760, a complete m4? (Fig. 3.4A), and 69320, a trigonid. Two other trigonid fragments are tentatively referred to the species based on overall size and morphological similarity, but are too fragmentary to be definitively assigned. OMNH 68760 has heavy apical wear on all of its cusps. The trigonid is slightly wider than the talonid, and the protoconid and paraconid are subequal, with the protoconid being slightly taller. The metaconid is mesially placed to the point that it is nearly transversely in line with the protoconid, shorter than the paraconid and protoconid, and exhibits the most apical wear on the trigonid. The placement of the metaconid in relation to the protoconid and paraconid gives the trigonid a compressed look, similar to that seen in *Didelphodon*. A strong wear facet is present along the entirety of the protocristid and is widest on the distal half of the apex of the protoconid and metaconid. The distal half of the metaconid is nearly obliterated by this wear facet. A contact facet for the preceding molar is present on the mesial face of the paraconid directly below the apex. A worn paracristid is present with a well-developed wear surface and the remnants of a carnassial notch. A heavily worn precingulid is present as a narrow, shelf-like structure, extending from the lingual to the labial side of the mesial face of the trigonid. The talonid appears to be that of the last molar as the hypoconulid points distally. It is impossible to ascertain which talonid cusp would have been the tallest. They are all heavily worn to the same level (almost to the level of the talonid basin), making the talonid a flat surface. Based on the size of the wear surfaces, however, the entoconid may have been the tallest cusp, as it has the largest wear surface. A strong, shelf-like postcingulid is present labial to the hypoconulid. The hypoconulid is closer to the entoconid than it is to the hypoconid, but the extent to which the hypoconulid and entoconid were twinned is difficult to say due to the amount of wear. The bases of the hypoconulid and entoconid were separate, as evidenced by a thin, unworn groove separating the cusps. The cristid obliqua attaches to the distal face of the trigonid labial to the protocristid notch. OMNH 69320 is fragmentary but unworn, so it adds important morphological detail to the trigonid, specifically highlighting a blade-like paracristid with a well-developed carnassial notch.

A lower premolar (MNA V5652) was briefly described by Cifelli (1990a) and is referred here to *Hoodootherium praeceps* based on its appropriate size (smaller than p2 and p3 referred to *Fumodelphodon pulveris*, and within the plausible size range of OMNH 68760, based on comparison with *Eodelphis*, which is represented by associated premolars and molars). MNA V5652 bears a heavily worn paraconid. It is moderately inflated and has a small heel situated at the back of the tooth. A faint postparacristid is present on the distal face of the premolar, extending to the small heel. OMNH 69328, a p3? provisionally referred to *Hoodootherium*, preserves only the apex of the paraconid. OMNH 69328 is wider mesially than MNA V5652, but the extent of this difference is unclear because the former specimen is incomplete.

The holotype, OMNH 68804, is a left P3 (see Fig. 3.4C) that is oval in occlusal view with a bulbous appearance and a slight lingual swelling. The apex of the paracone is sharp (see Fig. 3.4D), with only slight apical wear, and is connected to a postparacrista, extending down to the base of the crown where it bends labially before terminating. The labial edge of the postparacrista drops off sharply, leaving a distinct edge, where a slight wear facet is preserved. No preparacrista is present, but at the base of the mesial face, a faint crenulation is observed, possibly an incipient mesial basal cingulum. No distal basal cingulum is present on the tooth. The lingual swelling is situated along the distal half of the tooth. Directly distal to the lingual swelling is a large, keyhole-shaped pit in the lingual side of the tooth (see Fig. 3.4D). The long axis of the pit is oriented toward the cusp tip, where it becomes a faint sulcus for the majority of the height of the tooth. The premolar is two-rooted, with the distal root circular in cross section and larger than the mesial root. The distal root supports the lingual swelling as well as the distal half of the tooth.

The single upper molar known is a complete M4, and is morphologically appropriate for the taxon. The protocone is transversely wide and mesiodistally narrow, resulting in a transversely long trigon basin. The trigon basin is bordered by well-developed pre- and post-protocristae, but conules are poorly developed. The preprotocrista extends past the paracone and terminates at the mesiolabial corner of the stylar shelf, with wear facets developed along its entire length. A slight mound is present where a paraconule would have been present with the faintest hint of an internal crista, while the metaconule is slightly more distinct, forming a notch with the metacone, but lacks an internal crista. The paracone, despite advanced apical wear, is taller than the protocone, with the metacone being the shortest cusp. The labial face of the paracone is rounded and convex. The preparacrista extends towards the mesiolabial corner of the tooth, but terminates well before. The stylar shelf is of note as the parastylar lobe is labially expanded, while the metastylar lobe is reduced, as is expected from a last upper molar. The margin of the expanded region of the stylar shelf is crenulated between the A and B positions, with a distinct B cusp present. A cusp in the C position is present directly labial to the notch in the centrocrista, and is conical in shape. A very shallow ectoflexus is situated mesial to the cusp in the C position. The paracone and protocone exhibit heavy apical wear that runs down the centrocrista on the paracone, and terminates before the centrocrista notch. Slight apical wear is present on the expanded crenulated margin of the stylar shelf.

Comments. — Despite its poor preservation, the lower premolar (OMNH 69328) is associated with the holotype primarily based on its size. It is smaller than the p2 from *Fumodelphodon pulveris* (OMNH 28048) but within the appropriate size range when compared to the lower molars for *Hoodootherium praeceps*. If OMNH 69328 belongs to *Hoodootherium*, it is probably an ultimate premolar. OMNH 69328 resembles stagodontids in its rounded, bulbous appearance, especially when compared with basal marsupialiforms such as *Kokopellia juddi* (Cifelli, 1993).

The upper premolar is associated with the lower molars because of their size and overall resemblance to teeth of stagodontid taxa. The premolar is inflated, suggestive of stagodontid affinities, yet bears sharp crests. OMNH 68804 is best compared with P3s known from *Eodelphis*, rather than *Didelphodon*, because of the presence of the sharp postparacrista. The P3 is functionally similar to that of *Eodelphis*, with an emphasis on shearing rather than crushing, indicated by the well-developed postparacrista. A diagnostic feature shared by *Hoodootherium* and *Eodelphis* is the presence of a shallow sulcus running toward the cusp apex on the posterolingual corner of the tooth, seen on figured upper premolars of both species of *Eodelphis* (Scott and Fox, 2015). However, this sulcus originates from a keyhole-shaped pit in *Hoodootherium*, unlike in *Eodelphis*. *Hoodootherium* has more in common with *Eodelphis cutleri* than it has with *Eodelphis browni* as there is a distinct lingual swelling making the tooth wider distally than it is mesially, a distal root that is much larger than the mesial root, a reduced preparacrista (absent in *Hoodootherium* and better developed in *Eodelphis browni*), and greater inflation of the tooth. OMNH 68804 differs from both species of *Eodelphis* in its incipient development of a mesial basal cingulum and complete lack of distal basal cingulum.

The upper molar resembles those known for both *Didelphodon* and *Eodelphis*, with the labially expanded parastylar lobe, transversely long trigon basin, robust protocone, and presence of stylar cusp C (indicated by a swelling in that position for *Eodelphis*) (Clemens, 1966; Fox, 1981). OMNH 69351 differs from *Didelphodon* and

Eodelphis by lacking a large, mesially projecting parastylar lobe, a greatly reduced metacone, and poorly developed conules (Clemens, 1966; Fox, 1981). The reduction of the metacone in *Hoodootherium* is most likely a plesiomorphic feature, as *Didelphodon* and *Eodelphis* tend to have a subequal paracone and metacone on the last upper molar. The wear patterns exhibit both horizontal and vertical shear surfaces, with the apices of the paracone and protocone worn flat, and the preprotocrista with well-developed vertical wear facets. This differential wear pattern most likely indicates a highly variable diet, where both shear and crushing is important.

Discussion

The Smoky Hollow fauna is poorly known, with only a few specimens described for tribosphenic mammals (Cifelli, 1990a). The inclusion of advanced stagodontids to the fauna highlights a changing mammal biota from the Early to Late Cretaceous. During the earliest part of the Late Cretaceous, the North American mammalian fauna is more similar to the Early Cretaceous faunas, when tribosphenic mammals account for only a small portion of the fauna and archaic lineages (i.e., symmetrodonts and triconodonts) dominated (Cifelli and Davis, 2015; Cifelli et al., 2016). By the late Santonian, tribosphenic mammals had diversified into a large variety of morphological groups and body sizes, while archaic lineages subsequently declined (Fox, 1968, 1971, 1972, 1984; Davis et al,. 2016). With new specimens from the Smoky Hollow, the emergence of well-known elements typical of the Late Cretaceous mammalian fauna appears to have occurred earlier than previously thought. *Fumodelphodon* and

Hoodootherium represent the earliest divergence of Stagodontidae with respect to their premolar morphology. *Fumodelphodon* is most similar to *Didelphodon* with large, low-crowned and lobate ultimate premolars with reduced crests, while premolars of *Hoodootherium* are high-crowned with prominent, sharp crests similar to premolars of *Eodelphis*.

Dietary Inferences

Unlike any other Cretaceous mammal from North America, stagodontid premolars have been shown to be of the utmost importance for interpretation of dietary specializations, as well as identification to species (Clemens, 1966; Fox, 1971; Fox and Naylor, 1986, 2006; Scott and Fox, 2015). The crown morphology of P3s from *Didelphodon* and *Fumodelphodon* suggests an enhanced crushing function, which may be indicative of a durophagous diet (*Didelphodon* premolars have been hypothesized to be used for crushing mineralized tissue, whether mollusk shells or vertebrate bones to get at the rich nutrients inside [Clemens, 1966, 1968, 1973, 1979; Lillegraven, 1969; Fox and Naylor, 1986, 2006; Lofgren, 1992; Scott and Fox, 2015; Wilson et al., 2016]). In contrast, premolars from *Eodelphis* and *Hoodootherium* are less bulbous than *Didelphodon* and *Fumodelphodon* and bear sharper crests, suggesting an emphasis for vertical shear, rather than crushing, indicative of a more carnivorous trophic role.

Premolars of *Didelphodon vorax* have been favorably compared with those of living sea otters (*Enhydra lutris*), resulting in the interpretation of *Didelphodon* as a hard-object feeder (Clemens, 1966). However, low-crowned and bulbous cusps are characteristic of the entire postcanine tooth series for *Enhydra lutris*, indicative of an obligate durophage (Constantino et al., 2011 and references therein). In *Didelphodon*, only the premolars have been extensively modified for a durophagous diet, leaving the molar series capable of shearing. If *Didelphodon* were an obligate durophage, one would expect an entire dentition of low-crowned, bulbous teeth, instead of only characterizing the premolar series. With the presence of a molar series specialized for postvallum/prevallid shear (characterized by a tall, blade-like postmetacrista/paracristid), a high occurrence of premortem tooth breakage would be expected (Van Valkenburgh, 1988, 2009). While molars of *Didelphodon* may be found broken or incomplete, this breakage can be attributed to postmortem damage (although see Wilson et al. [2016] for evidence to the contrary).

Another potential indicator of durophagy is root size. Roots are an important feature in the mammalian dentition, as they help anchor the teeth in the jaw and dissipate the bite force exerted on the crown (Kovacs, 1971; Kupczik and Stynder, 2012). Kupczik and Stynder (2012) showed for the first time a significant positive correlation between the root surface area with bite force and a durophagous diet in Order Carnivora. The study found that the larger the bite force and/or increased durophagous diet, the larger the roots in order to hold the tooth in place and dissipate the necessary forces to avoid cracking the crown. Marsupialiforms primitively have two-rooted premolars, wherein the roots are subequal in size and positioned mesiodistally (Clemens, 1966; Cifelli, 1993). Interpreted in this light, the premolar root configuration in stagodontids may well be correlated with hard-object feeding, with the development of an additional root or an increase in root size in *Fumodelphodon* and

Didelphodon, respectively. The additional root surface area would have helped to dissipate the great forces subjected to the crown while feeding on hard objects. The P3 of *Fumodelphodon* has three roots, with the additional root supporting the protocone, thereby increasing the surface area of the roots on the premolar. The P3s of *Eodelphis*, *Hoodootherium*, and *Didelphodon*, however, have only two roots, but the construction of those roots differs dramatically. The roots of P3 for *Eodelphis* and *Hoodootherium* are subcircular in cross section and oriented mesiodistally, with the distal root generally larger than the mesial root (Scott and Fox, 2015). In *Didelphodon*, the mesial root is subcircular in cross section, similar to those seen in all other marsupialiform premolars, but the distal root is expanded transversely to support the lingual lobe and the entire distal edge of the tooth (Lillegraven, 1969: fig. 25, 3D; and Fig. 3.3A, this paper). The distal root pulp cavity for *Didelphodon* P3s is constricted in the middle but continuous, suggesting that the distal root may have begun as two separate roots: one situated underneath the lingual lobe and the other situated in the distolabial corner, that later fused into a single root during development. In some preserved roots of upper premolars of *Didelphodon*, a distinct sulcus is developed on the distal root, and some specimens have two root tips, each with a distinct root canal (Cifelli, personal communication 2016). Taken together, the development of a lingual root and the transverse development of the distal root in *Fumodelphodon* provide a similar function as the single, expanded distal root in *Didelphodon*, supporting the entire distal side of the tooth, including the lingual lobe (Fig. 3.3). The more extensive root support, together with the distal root sulcus and variable occurrence of two tips on the distal root in *Didelphodon*, suggests the working hypothesis that the three-rooted condition in *Fumodelphodon* is morphologically and functionally antecedent to that of *Didelphodon*.

Molars of stagodontids, as with all molars in basal tribosphenic mammals, are dual functional: they have both shearing and grinding regions, which correspond—in the lower molars—to the trigonid and talonid, respectively (Kielan-Jaworowska et al., 2004). When compared with other Late Cretaceous mammals, stagodontids appear to have emphasized both functions. The development of a hypertrophied paracristid on the trigonid is useful for processing vertebrate and invertebrate flesh (Evans and Sanson, 2003; and references therein), and a broad, low-crowned talonid, prone to heavy wear, is useful for a durophagous diet. The wear patterns observed for stagodontids also reflects the dual functionality of the molar series, with the main cusps of the talonid becoming almost completely obliterated by wear, thereby creating a flat surface for the corresponding protocone on the upper molar to crush food upon, while the trigonid retains sharp cusps longer, with wear along the crests, rather than situated solely upon the apices (see Fig. 3.2C and 3.4A). This differential wear can also be observed in the upper molar of *Hoodootherium*, OMNH 69351, with vertical wear facets present along the preprotocrista, while the protocone and paracone are worn flat. The presence of postvallum/prevallid shear is associated with carnivory and the processing of vertebrate prey, and prevallum/postvallid shear and near-obliteration of the metaconid (while the protoconid and paraconid remain relatively less worn) is associated with crushing. Both wear features can be observed in OMNH 68760, indicating that with the retention of a fully tribosphenic molar, stagodontids were suitably equipped for a generalist diet, as they were capable of processing almost any food type. Wear and morphology of the premolars, however, indicate an additional specialization for either carnivory or durophagy. The large, bulbous premolars of *Didelphodon* and *Fumodelphodon* only exhibit horizontal wear, and taking the morphology and wear facets together, the premolars are more useful for processing hard food items. On the other hand, *Eodelphis* and *Hoodootherium* are hypothesized to have had a more carnivorous diet, as they have upper premolars with increased vertical shear facets and crests. Although the retention of tribosphenic molars and the presence of some *Eodelphis* specimens that are known to have lower premolars and molars heavily worn in the horizontal plane, indicates a generalized diet, where these animals were capable of eating almost any food (see Scott and Fox, 2015 for examples).

The differential functions seen in the premolar and molar series hints at different selective forces acting upon these distinct tooth types. The mammalian dentition has been shown to be modular in its development and evolution, suggesting different evolutionary forces can impact morphological diversity between premolars and molars (Rizk et al., 2013; Grieco et al., 2013). Stagodontids appear to exhibit this modularity, with the increased specialization of the premolars and retention of the more generalized molars, potentially allowing for a greater diversity of food resources to be utilized. Large, crushing premolars of *Didelphodon* and *Fumodelphodon* potentially allowed for the additional processing of hard objects (bone or shell), while the more sectorial premolars of *Eodelphis* and *Hoodootherium* may have permitted an increased specialization toward processing the flesh of larger-bodied vertebrates, all the while, retaining tribosphenic molars, allowing for a generalist diet. A modern analogue occurs in *Crocuta crocuta* (Spotted Hyena), where the premolars are large and rounded, specialized for crushing and breaking bone, while the carnassials remain specialized for vertical shear ideal for processing flesh (Ewer, 1954). This modular dentition allows *Crocuta crocuta* to process entire carcasses of large ungulate prey efficiently, including both muscle and bone tissue (Trinkel, 2010; Kupczik and Stynder, 2012). With the available evidence at hand, stagodontids with crushing premolars may have been suitable as an opportunistic scavenger of relatively large-bodied vertebrates. These additional lines of evidence agree with a recent analysis of dietary preferences of *Didelphodon vorax* based upon a well-preserved skull (Wilson et al., 2016).

Stagodontidae Character Evolution

Identified synapomorphies of Stagodontidae lower molars include large size, subequal paraconid and protoconid heights, a tall, blade-like paracristid with a carnassial notch, labial placement of the termination of the cristid obliqua on the distal wall of the trigonid, and a mesiodistally compressed trigonid (Fox and Naylor, 2006). Fox and Naylor (2006) reviewed taxa referred to Stagodontidae and concluded that the two species of *Pariadens* fall outside of the family. They suggested that the more basal species, *Pariadens mckennai*, should be considered a basal therian of tribosphenic grade, and not referable to Marsupialia because the entoconid and hypoconulid are not closely apposed (“twinned”; see discussion below). However, Cifelli and Eaton (1987) did observe the presence of carnassial notches in the paracristid and protocristid of *Pariadens kirklandi* (the geologically younger of the two species assigned to *Pariadens*) but suggested that the carnassial notches may have been only weakly developed (the holotype, UCM 54155, exhibits heavy wear on all molars). When erecting the genus, Cifelli and Eaton (1987) acknowledged the differences between *Pariadens kirklandi* and the advanced stagodontids *Eodelphis* and *Didelphodon*, but they considered *Pariadens* a suitable ancestral morphotype for these later Cretaceous animals. Eaton (1993) described additional specimens of *Pariadens kirklandi* from the Naturita Formation and revised the diagnosis to include well-developed notches within the paracristid and protocristid (herein regarded as carnassial notches).

The apparent absence of a carnassial notch in illustrated specimens of *Pariadens* was one of the reasons Fox and Naylor (2006) placed *Pariadens* outside of Stagodontidae. Based on the available morphological data, *Pariadens kirklandi*, at least (*Pariadens mckennai* is known only from three lower molars, two of which are incomplete), may be closer allied to stagodontids than any other family of Cretaceous metatherians. This conclusion is based on its shared and presumably derived features including large size (largest tribosphenic mammal in its respective faunas), taller paraconid than metaconid (subequal in some specimens), presence of a carnassial notch in the paracristid, and posteriorly increasing size of the molar series (Cifelli and Eaton, 1987; Eaton, 1993). However, *Pariadens kirklandi* lacks other apomorphies of *Eodelphis* and *Didelphodon*, including trigonids that are mesiodistally compressed, attachment of the cristid obliqua labial to the protoconid notch, and a tall, blade-like paracristid with paraconid and protoconid subequal in height.

In relegating *Pariadens mckennai* to a basal position among Tribosphenida, Fox and Naylor (2006) emphasized the lack of twinning between hypoconulid and entoconid, a widespread feature of marsupialiforms (Clemens, 1966) (although not as clearly developed in some basal taxa such as *Kokopellia*; Cifelli, 1993). It is relevant to note that of the three lower molars known for *P. mckennai*, only one (OMNH 33072, the holotype) preserves this region of the tooth. This specimen, however, is almost certainly a last lower molar, wherein the talonid is markedly narrow; the hypoconulid tends to project distally and is not closely twinned with the entoconid as on preceding teeth, even in presumably advanced taxa such as *Alphadon* (e.g., Cifelli, 1990b: fig. 9R) and *Eodelphis* (Scott and Fox, 2015: fig. 8C). Hence, the significance of this character as it relates to *Pariadens mckennai* is uncertain. On the other hand, this species exhibits other traits of *Pariadens kirklandi*, such as large size (largest tribosphenic mammal in the fauna), paraconid taller than metaconid (subequal in anterior molars), and presence of well-developed carnassial notches (Cifelli, 2004; Cifelli et al., 2016). Because so little is known for *Pariadens mckennai*, key characteristics such as proportions of the molar series and morphology of the premolars cannot be evaluated. The little that can be said at present is that available data are insufficient to falsify (or strongly corroborate) a potential relationship with Stagodontidae.

Phylogenetic Analysis

The proposed relationships within Stagodontidae and the placement of *Fumodelphodon* and *Hoodootherium* were tested using a Late Cretaceous character matrix based on Rougier et al. (1998, 2004, 2015). The character matrix was modified with a few corrected states for *Didelphodon* and *Eodelphis* and new character data added to *Didelphodon* based on the recent description of a well-preserved skull (Wilson et al., 2016). Deleted taxa followed Rougier et al. (2015) with the addition of *Picopsis*, following the interpretation of *Picopsis* as nomen dubium (Cifelli et al. 2016). A heuristic search was conducted using the program PAUP v4.0a150, with character state types following Rougier et al. (2015 supplemental data). The analysis yielded five equally parsimonious trees of 565 steps, with a CI of 0.372 and an RI of 0.671. A strict consensus was computed, resulting in a topology similar to Rougier et al. (2015) (Fig. 3.5). The main difference in topology is with the placement of Marsupialia within Cretaceous North American marsupialiformes, a similar relationship recovered by Wilson et al. (2016). Further differences result in a polytomy at the base of the metatherian-eutherian split, with the relationships between *Holoclemensia*, *Pappotherium*, deltatheroidans, metatherians, and eutherians unresolved. Stagodontids are well resolved with *Hoodootherium*, *Fumodelphodon*, and *Pariadens* all forming a single clade with *Didelphodon* and *Eodelphis*. *Fumodelphodon* was recovered as sister taxon to *Didelphodon* with *Pariadens* as the basal member in the family.

The two new genera of stagodontids from the Smoky Hollow Member of the Straight Cliffs Formation differ from their later Cretaceous counterparts in having more plesiomorphic conditions. *Hoodootherium* lacks sharp pre- and postparacristae and mesial and distal basal cingula on the P3, and also lacks a sharp paracristid and protocristid and the strongly developed hypoconulid as seen in lower molars of *Eodelphis*. Similarly, *Fumodelphodon* differs from *Didelphodon* in the P3 with a definitive protocone (*Didelphodon* has been variably considered as having a definitive protocone, but see Fox and Naylor [2006: appendix 1] for the contrary) and three roots, lower premolars that are not lobate, and subequal C and D cusps on DP3. In these features, the Turonian taxa are morphologically antecedent to the later Cretaceous genera, *Didelphodon* and *Eodelphis*. Fossils described herein show clear differentiation of the two distinct stagodontid premolar morphologies (seen in *Didelphodon* and *Eodelphis*, respectively) by the Turonian. This is contrary to the hypothesis put forth by Fox and Naylor (1986, 2006), who posited that *Didelphodon* evolved as an offshoot from *Eodelphis cutleri*. If *Fumodelphodon* is a proximal relative of *Didelphodon*, then a 15-Ma ghost lineage exists, from the middle Turonian (~92 Ma) to the Judithian (~77 Ma [Scott and Fox, 2015]). Similarly, if *Hoodootherium* is sister-taxon to *Eodelphis*, a ~7-Ma ghost lineage is recognized, because of the earliest definitive occurrence of *Eodelphis* in the Milk River Formation (Fox, 1981). However, the time interval between the Smoky Hollow Member and the next well-sampled unit (Milk River Formation) remains poorly studied. The Coniacian and early Santonian are almost unrepresented, with only a handful of mammal specimens known from North America (Eaton, 2006, 2009). In fact, Eaton (2009) described an undetermined stagodontid from the middle Santonian of the John Henry Member of the Straight Cliffs Formation, but because it is only known from an incomplete lower molar, assigning this taxon to clade is impossible.

The proposed ghost lineage between *Fumodelphodon* and *Didelphodon* remains problematic, as *Didelphodon* is primarily known from the latest Cretaceous Lancian faunas, although a fragmentary edentulous jaw has recently been reported from the Judithian of Alberta (Scott and Fox, 2015). No evidence from earlier faunas has been reported to suggest the occurrence of a large, *Didelphodon*-like mammal with crushing premolars, but again, these faunas are poorly known with the exception of the Aquilan

(Fox, 1968, 1971, 1976; Davis et al., 2016). As illustrated by the example of *Eodelphis*, molar anatomy does not resolve species identification; instead, identification to the species level is based on the more specialized premolars (Fox, 1981; Fox and Naylor, 2006; Scott and Fox, 2015). The similarity of size and morphology in lower molars of *Fumodelphodon* and *Eodelphis* would be sufficient to indicate close relationship or referral of Turonian *Fumodelphodon pulveris* to *Eodelphis*, but because the premolars of the former differ dramatically, *Fumodelphodon* can confidently be assigned to a distinct genus, one that is morphologically closer to *Didelphodon*. The use of associated premolars, therefore, becomes imperative for identification of stagodontids and interpretation of their diet, because lower molars by themselves cannot be conclusively identified with either functional dietary group.

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FIGURE 3.1. A, Cretaceous North American mammal faunas (NALMAs in bold) with gray box denoting mammals described in this study. B, Map of Utah with Garfield and Kane counties in gray. C, Garfield and Kane counties with approximate location of Smoky Hollow localities.

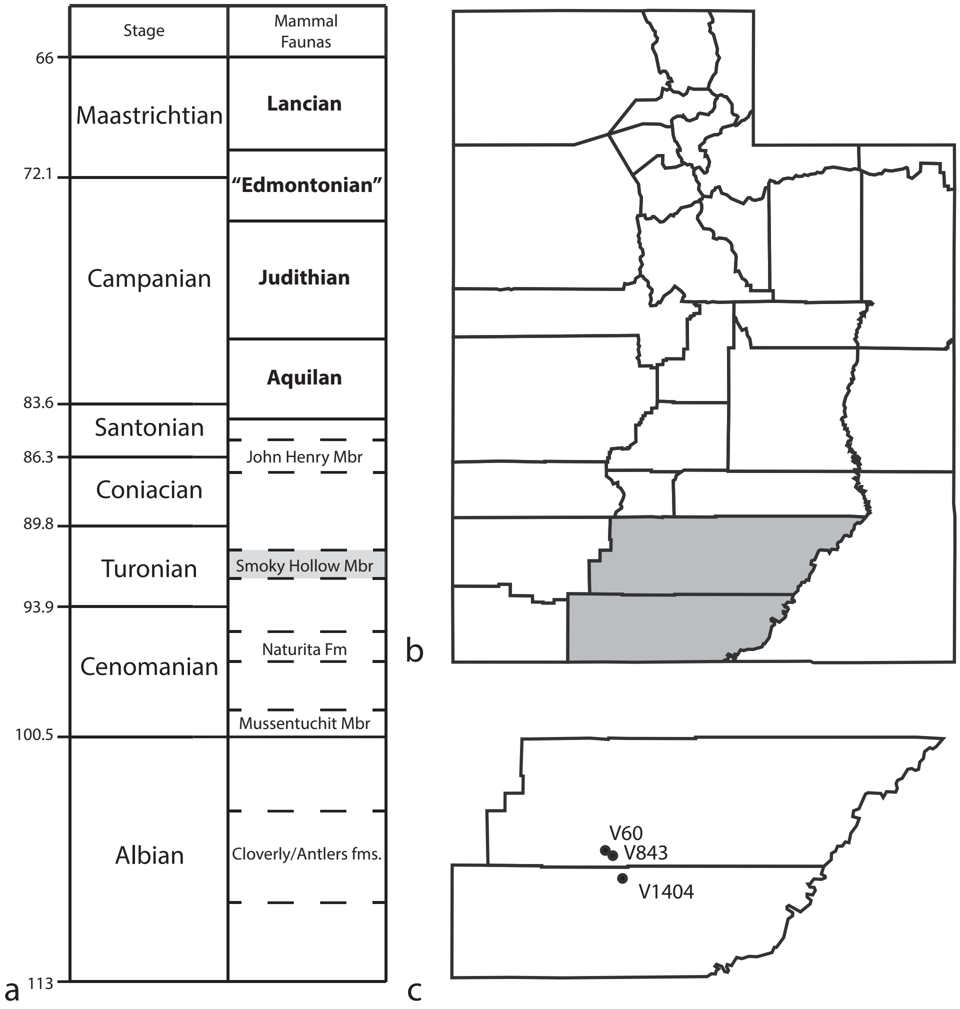

FIGURE 3.2. ***Fumodelphodon pulveris*** **gen. et. sp. nov. A, MNA V7340, holotype, left P3 occlusal stereopair.B, OMNH 29075, left DP3 occlusal stereopair. C, OMNH 69321, right talonid of mx occlusal stereopair, D–E, OMNH 69323, right p3 in occlusal stereopair (D) and lingual (E) views. F–G, OMNH 68761, left trigonid of mx in occlusal stereopair (F) and lingual (G) views.**

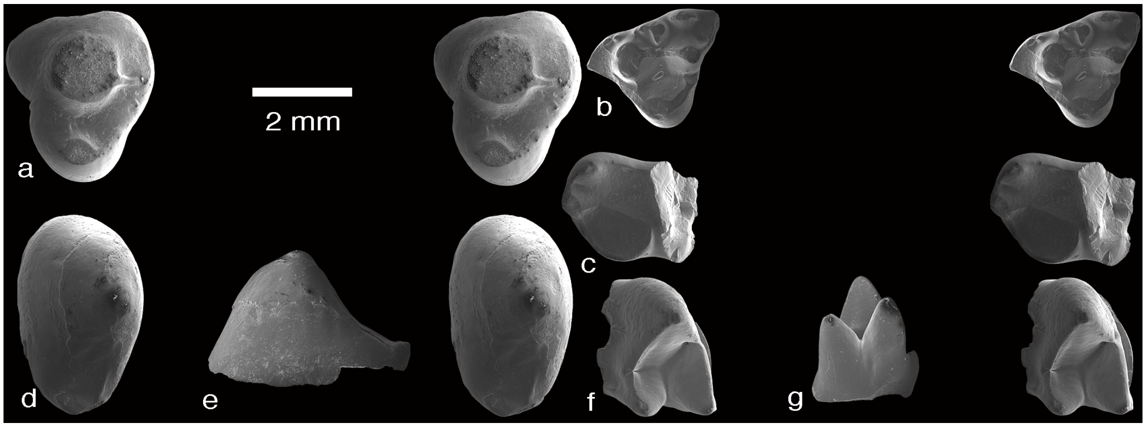

FIGURE 3.3. Camera lucida drawings of root structures. A, *Didelphodon vorax* (based on Lillegraven [1969: figure 25, 3D], inverted for the sake of comparison). B, *Fumodelphodon pulveris*, MNA V7340, not to scale.

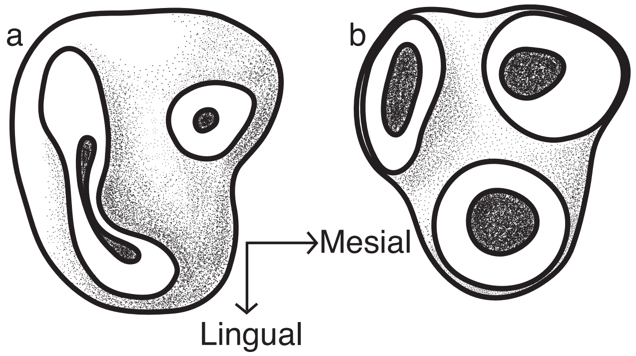

FIGURE 3.4. ***Hoodootherium praeceps* gen. et. sp. nov. A–B, OMNH 68760, left m4? in occlusal stereopair (A) and lingual (B) views. C–D, OMNH 68804, holotype, left P3 in occlusal stereopair (C) and lingual (D) views. E, OMNH 69351, right M4 in occlusal stereopair.**

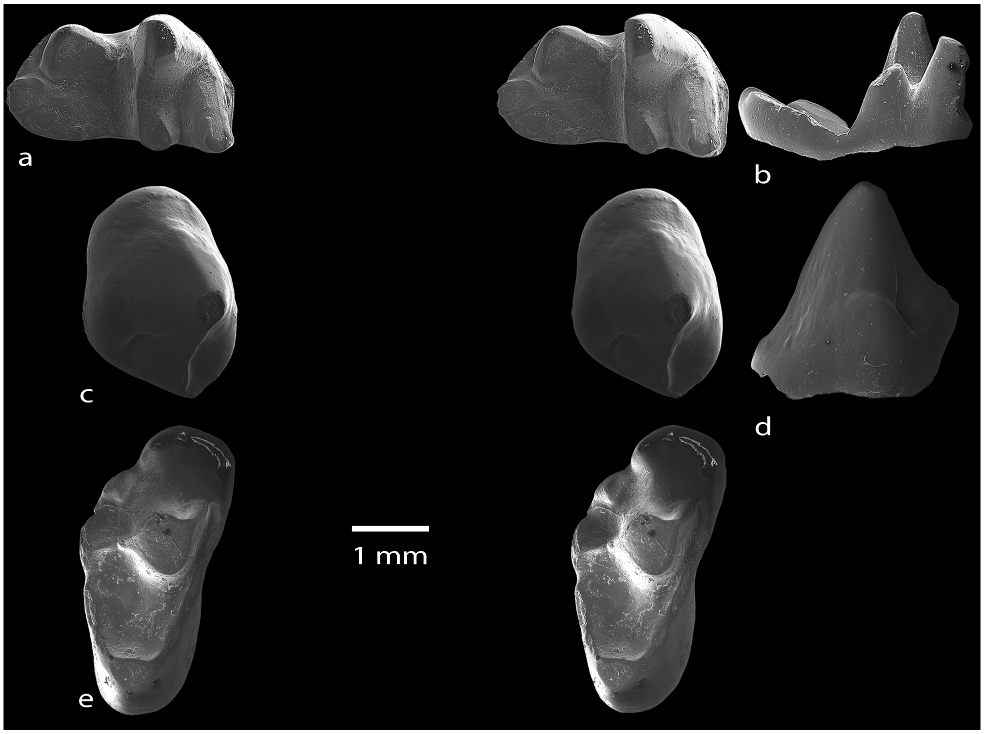

FIGURE 3.5. Phylogenetic analysis based on character matrix from Rougier et al. (2015); strict consensus of five equally parsimonious trees from 156 characters across 47 taxa, with a tree length of 565, a CI of 0.372, and an RI of 0.671.

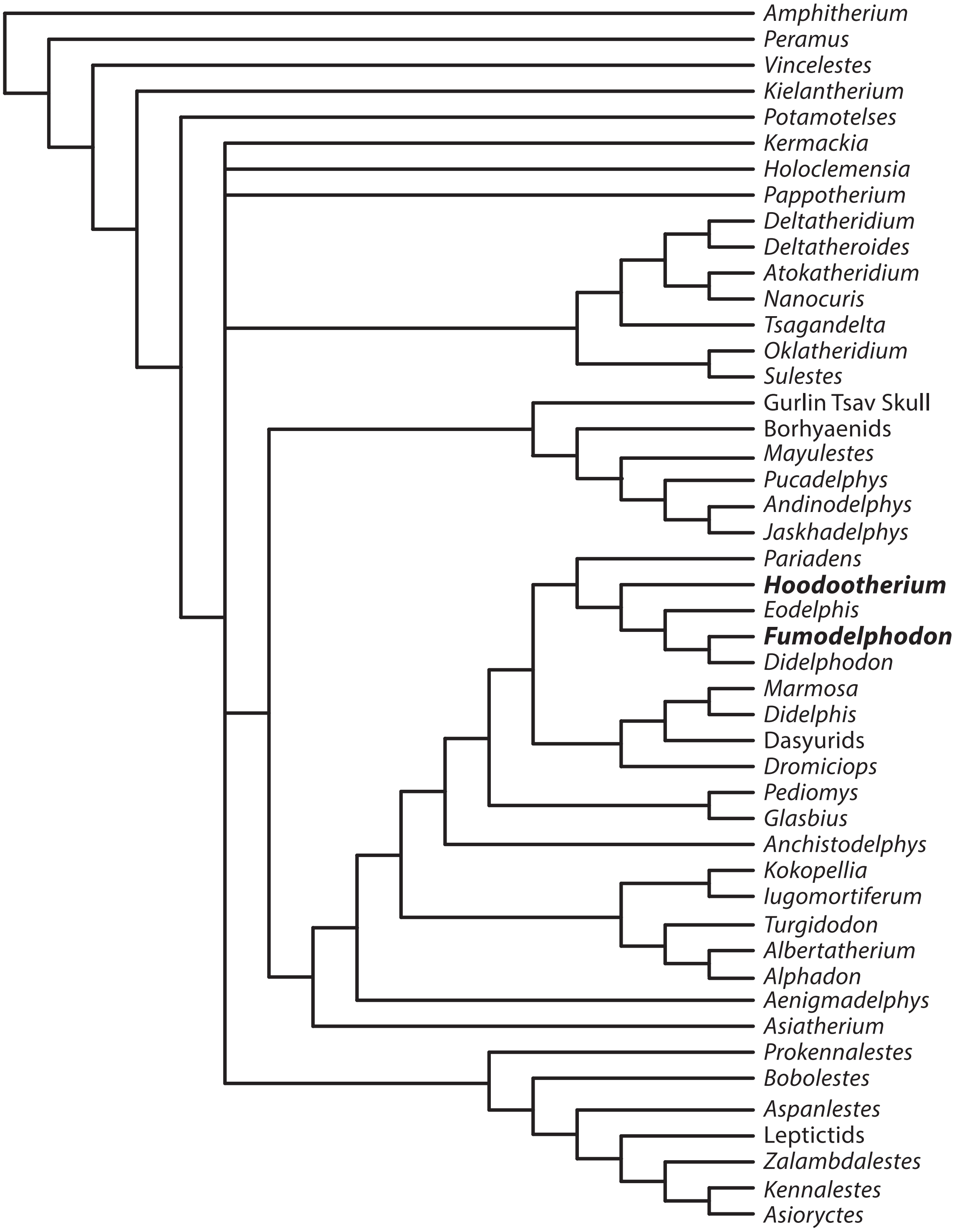

Table 3.1. Dental measurements (in mm) of *Fumodelphodon pulveris* gen. et sp. nov. ANW = anterior width, POW = posterior width, AP = anteroposterior length.

Specimen	Tooth	ANW	POW	AP
OMNH 68761	mx	3.09	—	—
OMNH 69319	m1	2.74	—	—
OMNH 69321	mx	—	2.58	—
OMNH 29480	mx	2.72	2.63	4.24
OMNH 29075	dP3	2.22	2.69	3.21
MNA V7340*	P3	4.17	—	3.62
OMNH 69324	p3	2.70	—	4.97
OMNH 29466	p3	2.69	—	4.44
OMNH 69323	p3	2.82	—	4.60
OMNH 28048	p2	2.28	—	3.71

* denotes holotype

Table 3.2. Dental measurements (in mm) of *Hoodootherium praeceps* gen. et. sp. nov.

Specimen	Tooth	ANW	POW	AP
OMNH 69320	mx	1.93	—	—
OMNH 68760	m4?	1.93	1.69	3.41
OMNH 68804*	P3	2.35	—	3.18
OMNH 69351	M4	4.30	3.44	2.47

* denotes holotype

CHAPTER 4: GEOLOGICALLY OLDEST PEDIOMYOIDEA (MAMMALIA: MARSUPIALIFORMES) FROM THE LATE CRETACEOUS OF NORTH AMERICA WITH IMPLICATIONS FOR TAXONOMY AND DIET OF EARLIEST LATE CRETACEOUS MAMMALS

Abstract

Terrestrial faunas of Turonian age are poorly known due to the paucity of the fossil record in North America and globally. The Smoky Hollow Member of the Straight Cliffs Formation of southern Utah has yielded a rich assemblage of terrestrial vertebrates and here we recognize the geologically oldest definitive members of Pediomyoidea. Pediomyoidea consist of two major groups, the Aquiladelphidae and the Pediomyidae, both of which are present in the Smoky Hollow Fauna. Two new species, *Scalaria diversicuspis,* gen. et sp. nov. and *Scalaria aquilana*, gen. et sp. nov., are recognized as members of Aquiladelphidae based upon shared characteristics with the family, including a subdivided B cusp, rounded and inflated main cusps, and an anteroposteriorly expanded protocone. A fragmentary specimen, identified as *Leptalestes* sp., is recognized as clearly belonging to Pediomyidae, with a strong reduction in the anterior stylar shelf and loss of the stylar cusp B. The occurrence of these two distinctive groups in the Turonian prompted a re-evaluation of possible antecedents from earlier in the Cretaceous, and a review of specimens referred to Aquiladelphidae. A possible antecedent is the Cenomanian *Dakotadens*, which shares a number of characters with the family. Of specimens referred to Aquiladelphidae, we recognize *Aquiladelphis laurae* as a valid member of the family and genus, but the

"Edmontonian" Williams Fork specimen is sufficiently different from both *Scalaria* gen. nov. and *Aquiladelphis* to be placed outside of the family, belonging within the pediomyoid family Glasbiidae, and is described as a new species, *Glasbius piceanus* sp. nov. Additionally, a new species from the Judith River Formation of Montana is described, *Aquiladelphis analetris* sp. nov. The presence of dentally derived metatherians in the Turonian suggests that the ecological drivers credited with dietary specializations among later Cretaceous taxa, such as proliferation of angiosperms and pollinating insects, were at work earlier than previously thought.

Introduction

Late Cretaceous marsupialiforms from North America were a diverse group, comprising three major clades: Stagodontidae, Alphadontidae, and Pediomyoidea (Wilson et al., 2016). The origins of Stagodontidae and Alphadontidae have been traced back to the early part of the Late Cretaceous (Cohen, 2017; Eaton, 1993), but the origins of Pediomyoidea remain poorly understood (Davis, 2007; Davis et al, 2016; Fox, 1971). Additionally, many elements of the marsupialiform fauna from the earliest Late Cretaceous of North America remain poorly resolved, with little knowledge of the higher taxonomic standing of these animals (Cifelli et al., 2016). Pediomyoidea make up a highly diverse clade that is best known from later Cretaceous faunas, such as the Judithian and Lancian North America Land Mammal Ages (NALMAs), but it first appears in the late Santonian (Clemens, 1966; Davis, 2007; Fox, 1971; Montellano, 1986). Pediomyoids share a number of characters, including a shallow ectoflexus with a stylar cusp in a posteriorly-located C position (posterior to the deepest part of the ectoflexus) on the upper molars, a lingually placed attachment of the cristid obliqua, and a wider talonid than trigonid on the lower molars (Davis, 2007). Pediomyoidea are a diverse superfamily and comprises three families: Aquiladelphidae, Pediomyidae, and Glasbiidae (Davis, 2007). The earliest members of Pediomyoidea are all members of the Aquiladelphidae, from the late Santonian Milk River and Eagle formations, although fragmentary remains from the late Santonian John Henry Member of the Straight Cliffs Formation have been referred to Pediomyidae (Davis et al., 2016; Eaton, 2013; Fox, 1971). Glasbiidae, on the other hand, is restricted to a single highly distinctive genus from the latest Cretaceous Lancian NALMA, with no clear antecedents (Clemens, 1966).

Aquiladelphidae include three species placed in the single genus *Aquiladelphis* (Eaton, 2013; Fox, 1971). Aquiladelphidae are best known from the late Santonian Milk River and Eagle formations, but additional specimens from the Campanian ?Wahweap Formation of Utah, the Kirtland Shale of New Mexico, and the Maastrichtian Williams Fork Formation of Colorado have been referred to the genus, giving Aquiladelphidae a large latitudinal distribution, from Alberta, Canada, to New Mexico, USA (Davis, 2007; Davis et al., 2016; Diem, 1999; Eaton, 2013; Fox, 1971; Rigby and Wolberg, 1987). While lower in taxonomic diversity than other Late Cretaceous marsupialiform families, Aquiladelphidae are typically large and distinctive, with heavily built cusps hypothesized for a crushing function, a large cusp in the C position, and an extra cuspule on the stylar shelf situated between the B and C positions (Davis, 2007; Eaton, 2009).

Pediomyidae, on the other hand, comprise a diverse family, reaching peak diversity by the end of the Cretaceous (Clemens, 1966; Davis, 2007). Pediomyids are characterized by having extreme reduction in the anterior stylar shelf and loss of stylar cusp B in upper molars, with a labially oriented protocristid and a lower height of the hypoconid relative to the entoconid in lower molars (Davis, 2007). Pediomyidae are currently recognized as including three genera with seven named species, ranging from the Judithian NALMA to the end of the Cretaceous. Earlier specimens referred to Pediomyidae come in the form of isolated tooth fragments of uncertain affinities (Davis et al., 2016; Eaton, 2013).

Pediomyoidea represents a group of Cretaceous tribosphenic mammals that have been hypothesized to incorporate higher amounts of plant material in their diets (Wilson, 2013). The hypothesized increase in plants in the diets of pediomyoids comes during the Cretaceous Terrestrial Revolution, when angiosperms became the dominant flora worldwide for the first time in history (Benton, 2010). Angiosperms represent new food resources for Cretaceous mammals, with evidence for multituberculates responding to the new floral environment (Wilson et al., 2012). Herein, we report new specimens referable to Pediomyoidea from the middle Turonian Smoky Hollow Member of the Straight Cliffs Formation, Utah. These specimens bring to light an early divergence of Pediomyoidea much earlier than previously expected, with supposed adaptations for increased frugivory and granivory.

Materials and Methods

Specimens from the Smoky Hollow Member of the Straight Cliffs Formation were collected from federal land managed by the Bureau of Land Management on what is now part of Grand Staircase-Escalante National Monument from southern Utah through bulk sampling techniques following Cifelli et al. (1996). Standard measurements were taken using a Reflex Microscope (see MacLarnon, 1989, Consultantnet Ltd, 94 High Street, Linton, Cambridge, CB21 4JT, UK), accurate to 0.01 mm, following Lillegraven and McKenna (1986). Scanning electron micrographs were taken using a Denton Vacuum Desk II sputter coater (Denton Vacuum LLC, 1259 North Church Street Building 3, Moorestown, New Jersey 08057, USA) and a LEO 1450VP SEM (Carl Zeiss NTS LLC, One Corporation Way, Peabody, Massachusetts 01960, USA).

Measurement abbreviations. — ANW, anterior width (trigonid width of lower molars); AP, anteroposterior length; POW, posterior width (talonid width of lower molars).

Institutional abbreviations. — MNA, Museum of Northern Arizona, Flagstaff, AZ, USA; OMNH, Sam Noble Oklahoma Museum of Natural History, Norman, OK, USA; UCM, University of Colorado Museum of Natural History, Boulder, CO, USA; UCMP, University of California Museum of Paleontology, Berkeley, CA, USA; UMNH, Natural History Museum of Utah, Salt Lake City, UT, USA.

Systematic Paleontology

Marsupialiformes Vullo et al., 2009

Pediomyoidea Simpson, 1927

Aquiladelphidae Davis, 2007

Type genus. — *Aquiladelphis* Fox, 1971

Included genera. — The type and *Scalaria*, gen. nov.

Distribution. — Middle Turonian–late Campanian, from the Smoky Hollow Member of the Straight Cliffs Formation, Utah; Moreno Hill Formation, New Mexico; Milk River Formation, Alberta; Eagle Formation, Montana; ?Waheap Formation, Utah; and Kirtland Formation, New Mexico.

Emended diagnosis. — Moderate to large marsupialiforms differing from most Late Cretaceous taxa, except Stagodontidae and *Glasbius*, with cusps rounded and inflated, and broadly basined upper and lower molars. Differs from Stagodontidae with an anteroposteriorly broader protocone and variable presence of carnassial notches within the paracristid and protocristid. Similar to Pediomyidae with reduction of the anterior stylar shelf (although not to the same extent), and differs with the retention of stylar cusp B. Stylar cusp B is variable in size, but typically has an additional cusp present posteriorly, often referred to as either a subdivided B cusp or two B cusps. Differs from other pediomyoids in having a large C cusp.

Scalaria, gen. nov.

Type species. — *Scalaria diversicuspis*, gen. et sp. nov.

Included species. — The type, and *Scalaria aquilana*, gen. et sp. nov.

Etymology. — Scalaria, Latin, resembling stairs, named after Grand Staircase-Escalante National Monument.

Distribution. — Middle Turonian Smoky Hollow Member of the Straight Cliffs Formation, Utah; and Moreno Hill Formation, New Mexico.

Diagnosis. — Differs from *Aquiladelphis* in smaller size, stylar cusp B is larger than in *Aquiladelphis*. Stylar cusps B, C, and D are subequal in size, and protoconal cingula are absent. Differs from *Dakotadens* in larger size, higher degree of inflation in all cusps, and greater reduction in the anterior stylar shelf.

Scalaria diversicuspis, gen. et sp. nov.

Fig. 4.1, 4.2; Table 4.1

Etymology. — A combination of diverse and cusp, in allusion to the diverse morphology and size of the stylar cusps seen on all the specimens.

Holotype. — OMNH 68766, left dentary fragment preserving parts of dp3–m2.

Type Locality. — OMNH locality V1404, Smoky Hollow Member of the Straight Cliffs Formation, Kane County, Utah, USA

Distribution. — Middle Turonian Smoky Hollow Member of the Straight Cliffs Formation, Utah, and Moreno Hill Formation, New Mexico.

Included material. — MNA V7556, right M3; MNA V6945, left M1?; OMNH 24635, right Mx; OMNH 69354, right M1?, lacking the protocone; MNA V6363, right m1;

OMNH 68778, right m2 or m3; OMNH 68767, talonid of left mx; OMNH 69364, talonid of right mx; OMNH 69398, right p3; and OMNH 25505, left dp3.

Tentatively-referred material. — OMNH 23001, right DP3, lacking the metacone and metastyle.

Diagnosis. — Differs from *Esclantelestes aquilana* in smaller size, in preparacrista connecting to the stylocone, and a relatively stronger postmetacrista. Differs from *Aquiladelphis* and *Scalaria aquilana* with stylar cusps variable in relative size.

Description. — The holotype, OMNH 68766, is a dentary fragment, preserving portions of dp3–m2 (Fig. 4.1A_1). Meckel's groove is present on the medial side of the dentary as a shallow trough, extending at least as far anteriorly as the dp3. Meckel's groove appears to be wider further posteriorly under the second molar, but is difficult to determine due to breakage. The most anterior tooth preserves most of the talonid, including the basin, the hypoconid, and part of the postcingulid, and is identified as a deciduous premolar due to its diminutive size when compared with the remaining molars (see Table 4.1). The m1 is the most complete molar of the specimen, only missing the entoconid and hypoconulid on the talonid, with the m2 missing the metaconid and portions of the paraconid, as well as the entoconid and hypoconulid. Overall, the cusps are inflated, giving them a rounded appearance. The talonid basin for known specimens is wider than the trigonid (although most measured specimens are referable to the first molar which tend to have a wider talonid). The tallest cusp on the trigonid is the protoconid, with the metaconid being the shortest. In lingual view, the paraconid leans anteriorly. A cusp-like precingulid is present on the anterior face of the trigonid. The paracristid has a poorly developed carnassial notch, but no carnassial notch is present on the protocristid. The cristid obliqua terminates slightly labial to the protocristid notch. The only specimen to preserve a complete and unworn talonid is MNA V6363 (Fig. 4.1D). The tallest cusp on the talonid is the hypoconid. The entoconid and hypoconulid are subequal in size and are twinned. A postcingulid runs labially from the hypoconulid, and is composed of a variable number of small cuspules.

A single lower ultimate premolar is referred to *Scalaria diversicuspis*, based on size and morphology. OMNH 69398 (Fig. 4.1C) is robust and inflated, with a labial expansion, giving the tooth a rounded appearance in occlusal view. The crown was most likely tall (uncertain due to wear), anteroposteriorly compressed, and lacks a talonid basin. A worn postprotocristid is present running down the crown, ending at a posterior basal cingulid that runs lingually from the base of the postprotocristid to the lingual face of the crown. The apex of the crown is heavily worn, and the wear facet extends onto the labial face of the crown.

OMNH 25505 (Fig. 4.1B), a dp3, is referred to *Scalaria diversicuspis* based on the similar size to the holotype (Table 4.1); it is also worth noting that no other taxon falls within a similar size range in the fauna. Due to the state of breakage on the dp3 on OMNH 68766, OMNH 25505 gives important information on the morphology of the deciduous premolar. The specimen is similar to previously identified dp3s (Clemens, 1966; Cifelli et al., 2016), with an open trigonid, resulting from the paraconid anteriorly placed and nearly in line with the protoconid; the paraconid and metaconid significantly smaller than the protoconid (only about half the height), and a wider talonid than trigonid.

Upper molars for this taxon are known from isolated specimens, with only a single complete molar known (MNA V7556, Fig. 4.2D). As is typically the case for Late Cretaceous marsupialiforms, stylar shelf morphology appears to be of some importance for identifying tooth locus. Stylar cusps B, C, and D are variable in relative size among the recovered specimens. OMNH 69354 (Fig. 4.2A) is heavily worn, but cusp B is much smaller than cusps C and D. The relative sizes between C and D cannot be determined due to the advanced wear. The relative cusp sizes on MNA V7556 are difficult to ascertain due to wear, but, cusp B was probably larger than cusp C due to the greater amount of wear and larger base. The D region on MNA V7556 is multicuspate, with two distinct cusps, both of which are considerably smaller than the B and C cusps. The multicuspate D morphology is seen on an additional specimen, OMNH 24635, suggesting that this morphology may be due to tooth position, and not simply intraspecific variation. OMNH 69354 is most likely a first molar, because the stylar shelf labial to the paracone is narrow when compared with MNA V7556, the typical condition for metatherian first molars (Clemens, 1966). Accordingly, variation in stylar cusp size among referred upper molars is most likely due to tooth position, with cusp B increasing in size, and cusp D decreasing in size through the molar series. Following this trend, MNA V7556 is identified as a third molar. On all specimens preserving the B and C regions on the stylar shelf, an accessory cusp is present, positioned halfway between the B and C cusps. The accessory cusp is further labial than cusp C on all specimens.

The protocone is the tallest cusp and leans anteriorly, except on M1, where it is relatively symmetrical and untilted. The protocone is inflated and anteroposteriorly broad. The preprotocrista runs past the paracone and terminates on the parastyle. The postprotocrista does not extend past the base of the metacone. Conules are present, positioned closer to the paracone and metacone than to the protocone. Internal cristae are present for both the paraconule and metaconule, and run partway up the lingual face of the paracone and metacone, respectively. The paracone and metacone have heavy apical wear, with a greater amount of wear on the paracone, resulting in a height differential between these cusps on MNA V7556.

A single, fragmentary upper deciduous premolar, OMNH 23001 (unfigured), is tentatively referred to the species based on its appropriate size. The DP3 preserves the protocone, paracone, and parastyle. The specimen is typical of metatherian deciduous premolars (see Clemens, 1966; Cifelli et al., 2016) where the paracone is the largest cusp, the protocone is small and anteroposteriorly broad, and the anterior stylar shelf is highly reduced, lacking a stylocone.

Comments. — *Scalaria* is unquestionably an aquiladelphid, based upon numerous shared characters, such as the diverging paracone and metacone; rounded, inflated cusps; multiple or subdivided B cusps on the stylar shelf; reduced anterior width of the stylar shelf; and anteroposteriorly broad protocone and talonid. The most notable difference between *Aquiladelphis* and *Scalaria* is in the construction of the stylar cusps. Stylar cusp C in *Aquiladelphis* dominates the stylar shelf, with cusps B and D markedly smaller by comparison. An interesting observation on the morphology of the stylar cusps of both genera, however, is the remarkable variation in the relative sizes of the cusps. In both *Scalaria* and *Aquiladelphis*, the relative sizes of cusps B and D are variable between individual specimens (see Fox, 1971 and Davis et al., 2016 for differences in cusp B and D size in *Aquiladelphis incus*), but in *Aquiladelphis*, cusp C is consistently the largest cusp. With *Scalaria diversicuspis*, the difference in relative size of the stylar cusps may have some positional significance, but additional specimens will be required to clarify this variation. The presence of Meckel's groove suggests that Meckel's cartilage was present, linking the middle ear to the dentary, although whether the element was ossified or not remains to be seen.

Scalaria aquilana, gen. et sp. nov.

Fig. 4.3; Table 4.2

Etymology. — Aquila, from Latin meaning eagle, in reference to the close morphological similarity to the genus *Aquiladelphis*.

Holotype. — OMNH 29078, right M3.

Type Locality. — OMNH locality V60, Smoky Hollow Member of the Straight Cliffs Formation, Kane County, Utah, USA.

Distribution. — Middle Turonian Smoky Hollow Member of the Straight Cliffs Formation, Utah, and Moreno Hill Formation, New Mexico.

Referred material. — OMNH 29514, left M1; OMNH 29065, left m1?; MNA V6361, left mx, missing the entoconid and hypoconulid; OMNH 69363, right mx, missing the entoconid and hypoconulid; OMNH 29482, left mx, missing the majority of the talonid; OMNH 69365, left trigonid of mx; and OMNH 29497, left mx.

Tentatively-referred material.— MNA V7557, left DP3, missing the parastyle; and MNA V6362, left DP3.

Diagnosis. — The larger of the two species in the genus. Further differs from *Scalaria diversicuspis* in that the preparacrista does not connect to stylar cusp B, and the postmetacrista is reduced. Similar to *Aquiladelphis* with stylar cusp C as the largest stylar cusp.

Description. — Lower molars are known from mostly fragmentary isolated teeth and are similar to *Scalaria diversicuspis*, although larger (Table 4.2). The only complete lower molar, OMNH 29065 (Fig. 4.3C_1), has a talonid wider than the trigonid, with an anteroposteriorly long basin. OMNH 69363 and MNA V6361 preserve the trigonid and the labial half of the talonid, and both appear to have a talonid that was equal in width to the trigonid. The hypoconid and entoconid are subequal in height, and are both taller than the hypoconulid. The hypoconulid is closer to the entoconid than it is to the hypoconid, although not to the degree seen in alphadontids or even *Aquiladelphis*, and a postcingulid is present (Cifelli, 1990; Fox, 1971). The cristid obliqua attaches to the back of the trigonid wall labial to the protocristid notch. Apical wear is present on all three of the talonid cusps. Wear on the shearing crests is concentrated along the labial side of the basin, with the entocristid virtually unworn. The cusps are all rounded and inflated. The trigonid is similar to that seen on lower molars of *Scalaria diversicuspis*, with the protoconid as the tallest cusp, the paraconid leaning anteriorly, and the metaconid as the shortest cusp. The entoconid, metaconid, and paraconid are not in line, with the paraconid positioned slightly labial to the metaconid. Apical wear is present on all three trigonid cusps, with wear facets on the shearing crests larger on the protocristid than the paracristid. Faint carnassial notches are present on both the paracristid and protocristid.

Two upper molars are included in the species, including the holotype, OMNH 29078, a right M3 (Fig. 4.3B); and OMNH 29514, a left M1 (Fig. 4.3A). Upper molars are generally similar to *Scalaria diversicuspis*, although much larger. The protocone is the largest cusp, and is anteroposteriorly long, corresponding with a broad trigon basin. The deepest part of the basin is situated close to the paracone and metacone. The paracone and metacone diverge, leaning anteriorly and posteriorly, respectively. The centrocrista does not invade the stylar shelf, connecting the two cusps in a straight line. The paracone and metacone are subequal in height, although the paracone is slightly taller on OMNH 29514. All three main cusps are inflated, with rounded faces. Conules are present, and are situated closer to the paracone and metacone than to the protocone. Internal cristae are weakly developed, and attach to the separate bases of the paracone and metacone. The anterior protoconal cingulum may be present on OMNH 29078, although the anterior face of the protocone is broken. OMNH 29514 has no protoconal cingula. The postprotocrista is variable in its development. On the first molar, OMNH 29514, the postprotocrista appears to terminate at the base of the metacone (base of the tooth is broken), while on the M3, OMNH 29078, the crest extends past the metacone and terminates at the postmetacrista, although the crest is crenulated along its margin and thins at the metacone. The preprotocrista for both specimens terminates at the parastyle. On OMNH 29514, the stylar shelf is worn and some enamel is flaked off, but important morphological information remains clear. Stylar cusps B and C are the largest cusps, although it cannot be determined which one was larger. Cusp B is positioned directly labial to the paracone. The ectoflexus is shallow, and stylar cusp C is slightly posterior to it. Stylar cusp D is positioned directly posterior to cusp C, and is anteroposteriorly elongate. The postmetacrista is short and low, with no evidence for the presence of cusp E. The presence of a cuspule situated between cusps B and C cannot be determined due to enamel breakage. OMNH 29078 gives additional morphological data for the stylar shelf, as well as information on variation between tooth loci. The parastyle has a crenulated rim, with a distinct cusp positioned halfway between the paracone and stylar cusp B. A preparacrista is present between the paracone and stylar cusp B, but is not continuous. Cusp B is the tallest cusp on the stylar shelf, and is highly inflated. A deeper ectoflexus is present, when compared with OMNH 29514, with cusp C still positioned slightly posterior. Cusp C is also tall, and has a distinct crest connecting from the apex to the notch in the centrocrista. A small cuspule is present halfway between cusps B and C. In the D region, a complex of cusps are present, with a larger central cusp flanked by two small, accessory cusps. The central D cusp is rounded and shorter than both the B and C cusps. The posterior side of the central D cusp slopes posteriorly towards the roots, creating a smooth area bordered by the postmetacrista. A tiny E cusp is present, and is the smallest structure on the stylar shelf, situated at the end of the postmetacrista. The postmetacrista is very low and poorly developed, connecting with the postprotocrista labial to the base of the metacone before terminating on the stylar shelf.

Comments. — The stylar shelf in *Scalaria aquilana* is more cuspate than that seen in *Scalaria diversicuspis*, with a number of accessory cuspules positioned among the B, C, and D cusps. These accessory cuspules are mainly seen on OMNH 29078 and not OMNH 29514, but the stylar shelf on OMNH 29514 is damaged, so the exact morphology in that region of the tooth cannot be adequately determined. The amount of variation between the stylar shelf morphologies in OMNH 29514 and OMNH 29078 may also be explained by positional differences (OMNH 29514 is an M1, while OMNH 29078 is an M3), but additional specimens will be required to further investigate.

Aquiladelphis Fox, 1971

Type species. — *Aquiladelphis incus* Fox, 1971

Included species. — The type, *Aquiladelphis minor* Fox, 1971, *Aquiladelphis laurae* Eaton, 2006, and *Aquiladelphis analetris*, sp. nov.

Distribution. — Late Santonian Milk River Formation, Alberta, Canada, late Santonian Eagle Formation, Montana, USA, Campanian ?Wahweap Formation, Utah, USA, late Campanian Judith River Formation, Montana, USA, and late Campanian Kirtland Formation, New Mexico, USA.

Emended diagnosis. — Moderate to large-sized aquiladelphid. Differs from *Scalaria* with a smaller stylar cusp B, and with stylar cusp C as the largest cusp on the stylar shelf. Cusp D is variable in size relative to cusp B. Species tend to have more carnassial notches and sharper crests than *Scalaria* or *Dakotadens*.

Comments. — *Aquiladelphis laurae* is formally included in the genus *Aquiladelphis* based on a number of shared characteristics, such as a reduced stylar cusp B, stylar cusp

C the largest stylar cusp, and a greater anteroposterior development of the protocone and trigon basin. The protoconal region in *Aquiladelphis laurae* is particularly instructive for investigating wear stages due to the variability in amount of wear between structures. The wear surfaces are widest along the shearing crests, indicating that they are more heavily worn than the basin. This suggests that wear started along the crests before the trigon basin and the conules.

Aquiladelphis analetris sp. nov.

Fig. 4.4A–B; Table 4.3

Etymology.— An-, Greek for without, and aletris, Greek for grinding, in reference to the lighter-built protocone, the portion of the upper molar responsible for the grinding action in tribosphenic molars, in comparison to the type species, *Aquiladelphis incus*.

Holotype.— UCMP 131240, left Mx

Type Locality.— UCMP locality V82117, Judith River Formation.

Distribution.— Late Campanian Judith River Formation, Montana.

Included material.— UCMP 235745, left Mx, missing the paracone and anterior portion of the stylar shelf.

Diagnosis.— Similar in size to *Aquiladelphis incus*, but with smaller stylar cusps. Most similar to *Aquiladelphis laurae* but differs in the presence of both anterior and posterior protoconal cingula. Cusps are slightly less inflated and protocone is anteroposteriorly narrower than other members of the genus.

Description.— UCMP 131240 (Fig. 4.4A) has been previously described by Montellano (1986), and the only additional morphological information to note is that the centrocrista runs straight between the paracone and metacone apices. UCMP 235745 (Fig. 4.4B) is largely similar, and may even represent the same tooth locus, but gives important information on intraspecific variation. Both the anterior and posterior protoconal cingula on UCMP 235745 are much smaller, and the protocone is expanded posteriorly to a greater extent than in UCMP 131240. UCMP 235745 is also larger (Table 4.3), but still within the expected range for intraspecific variation. The last minor difference is in the construction of the stylar cusps in the metastylar region. On UCMP 131240, these two cusps are of nearly equal size and are equally spaced between the cusp posterior to the ectoflexus (most likely equivalent to stylar cusp C) and the termination of the postmetacrista, while on UCMP 235745, the anterior cusp is nearly half the size of the posterior cusp and is appressed against stylar cusp C. On both specimens, apical wear is not dramatic, with wear along the shearing crests dominating.

Comments.— *Aquiladelphis analetris* differs from *Aquiladelphis incus* and *Aquiladelphis minor* in having smaller stylar cusps, although an additional cusp between the B and C cusps is present. The protocone is transversely narrower than in the other species of *Aquiladelphis*. UCMP 131240 is slightly smaller than *Aquiladelphis incus* and UCMP 235745. *Aquiladelphis analetris* is most similar to *Aquiladelphis laurae*, in having reduced stylar cusps, two small cusps in the D position, and a greater posterior expansion of the protocone, compared with *Aquiladelphis incus* and *Aquiladelphis minor*. The anterior protoconal cingulum is present on both *Aquiladelphis* *laurae* and *Aquiladelphis analetris*, but *Aquiladelphis laurae* lacks a posterior protoconal cingulum. Within Aquiladelphidae, the presence of protoconal cingula appears to be related to body size, with larger taxa more likely to have cingula. *Aquiladelphis laurae* is intermediate in size, being smaller than *Aquiladelphis analetris* and *Aquiladelphis incus*, but larger than *Scalaria*, while also intermediate in its development of the protoconal cingula (well-developed protoconal cingula present in *Aquiladelphis incus* and *Aquiladelphis analetris*, while absent in *Scalaria*). The protoconal cingula may be important for enhancing the crushing function of the protocone, by giving additional surface area in which to break apart food resources between the upper and lower molars, as proposed for *Gypsonictops* by Crompton and Kielan-Jaworowska (1978). However, additional functions that have been proposed for cingula include protection of the gingiva from food particles or to reinforce the enamel from crack propagation (Allen et al., 2015). The presence of protoconal cingula could then suggest that perhaps larger taxa may have incorporated harder objects (such as seeds) into their diet than the smaller taxa. The addition of harder objects would necessitate protecting the gingiva and reinforcing the enamel from the increase forces on the teeth. The proposed crushing function in aquiladelphids is most likely different from the inferred durophagy crushing function for stagodontids, primarily based on the shape of the protocone. Stagodontid protocones are transversely wide and anteroposteriorly short, while aquiladelphids have anteroposteriorly long protocones. An expanded talonid region and protocone are often seen in mammals that specialize in frugivory, such as primates (White, 2009). At first glance, the wear patterns between *Aquiladelphis laurae* and *Aquiladelphis analetris* differ but this is probably due to the amount of wear on the specimens. All known molars of *Aquiladelphis laurae* show extreme wear, where just about every surface of the molars are worn. The two specimens of *Aquiladelphis analetris* have a moderate amount of wear, and may just represent an earlier stage of wear for this taxon.

Pediomyidae Marsh, 1889

Leptalestes sp. Davis, 2007

Fig. 4.4C; Table 4.3

Referred material. — OMNH 68752, left M2, missing the protocone.

Locality. — OMNH locality V1404, Smoky Hollow Member of the Straight Cliffs Formation, Utah.

Description. — The paracone is taller and narrower than the metacone, with small cuspules attached to the labial side of the cusp (Fig. 4.4C). The centrocrista is sharp and strongly V-shaped in the vertical plane. The metacone leans posteriorly and is connected to a tall, well-developed postmetacrista. The stylar shelf is reminiscent of Late Cretaceous pediomyids, with the complete reduction of the anterior stylar shelf and lack of a stylocone. A well-developed D cusp is present directly labial to the apex of the metacone. A small, subdivided C cusp is also present, with the anteriorly placed cuspule connected to a crest that attaches to the labial base of the paracone. The parastyle is slightly labial to a line through the apices of the paracone and metacone. The internal conular cristae attach at the bases of the paracone and metacone, but the relative size of the cristae cannot be determined. A remnant of the postprotocrista extends beyond the base of the metacone, terminating nearly at the posterolabial corner of the tooth (not visible in Fig. 4.4C).

Comments. — *Leptalestes* has been previously diagnosed as a small, primitive pediomyid, but OMNH 68752 is large, and within the size range of *Protolambda florencae* (Clemens, 1966: table 12). However, morphological evidence suggests OMNH 68752 is more similar to *Leptalestes* than *Protolambda*, as the parastyle is not lingually placed to the extent seen in *Protolambda* (the parastyle is in line with the apices of the paracone and metacone in *Protolambda*) and the paracone and metacone of OMNH 68752 are closer together when compared with specimens of *Protolambda florencae*, suggesting the cusps may be significantly connected at their base (difficult to ascertain with the missing protocone and trigon basin) (Davis, 2007). However, significant differences exist between *Leptalestes* and OMNH 68752, such as the presence of a subdivided C cusp and a well-developed D cusp on OMNH 68752. The presence and relative construction of these stylar cusps are interpreted here as the ancestral condition, as both of these cusps are well developed in *Pediomys elegans*.

Glasbiidae Clemens, 1966

Glasbius Clemens, 1966

Type species. — *Glasbius intricatus* Clemens, 1966.

Included species. — The type, *Glasbius twitchelli*, and *Glasbius piceanus* sp. nov.

Distribution. — Lancian NALMA: Lance Formation, Wyoming, USA; Hell Creek Formation, Montana, USA; and Frenchman Formation, Saskatchewan, Canada; and "Edmontonian" NALMA, Williams Fork Formation, Colorado, USA.

Emended diagnosis. — See Davis (2007), with variable presence of a basal labial cingulid.

Glasbius piceanus sp. nov.

Fig. 4.4D; Table 4.3

Etymology. — Named after the Piceance Basin, from where the specimens were found.

Holotype. — UCM 57354, right m3.

Type Locality. — UCM locality 86018, Williams Fork Formation, Rio Blanco County, Colorado.

Distribution. — "Edmontonian" NALMA Williams Fork Formation, Colorado.

Included material. — UCM 57350, right mx.

Diagnosis. — Differs from *Glasbius intricatus* and *Glasbius twitchelli* in much larger size, absence of a basal labial cingulid, and a taller protoconid than metaconid in m3.

Description. — Both specimens are large with highly inflated cusps. UCM 57350 is heavily worn, but otherwise nearly identical to the holotype, UCM 57354 (Fig. 4.4D). The trigonid and talonid are nearly equal in height, with the entoconid only slightly shorter than the metaconid. In lingual view, the metaconid is posteriorly expanded with the apex leaning posteriorly. The protoconid is the tallest cusp, with the paraconid shorter than the metaconid and entoconid. The paraconid is positioned slightly labial to the metaconid and is slightly appressed to that cusp. A carnassial notch is present in the paracristid, but the crest is not blade-like. A well-developed precingulid is present and wraps around to the labial side of the protoconid. The talonid is transversely broad and wider than the trigonid, with a correspondingly wide and shallow basin. The entoconid is wall-like, the tallest cusp on the talonid, and is twinned with the hypoconulid. The postcingulid is positioned as a straight crest running from the hypoconulid to the labial edge of the hypoconid. The cristid obliqua meets the posterior trigonid wall labial to the protocristid notch. A carnassial notch is present in the cristid obliqua and the entocristid at the junction between the talonid and the trigonid.

Comments. — When compared with *Glasbius intricatus*, UCM 57354 is determined to be an m3 due to the relative width of the trigonid/talonid and acutely angled trigonid. The Williams Fork specimens were originally referred to *Aquiladelphis*, but based on a number of differences, are no longer referable to the family Aquiladelphidae. These differences include greater degree of inflation in the cusps than in other lower molars referred to Aquiladelphidae, lesser trigonid/talonid height differential, and a labially placed paraconid. These differences in the lower molars are more reminiscent of the Lancian genus *Glasbius* than to *Aquiladelphis*, despite the similarity in size with *Aquiladelphis incus* (Diem, 1999). These genera were closely allied in the analysis by Davis (2007), suggesting the possibility that the Aquiladelphidae lineage may have given rise to *Glasbius* as this genus appears suddenly, and without clear morphological antecedents, during the Lancian. The recent analysis by Wilson et al. (2016) lends support to this relationship, with *Glasbius* and *Pediomys* recovered as sister taxa

(*Aquiladelphis* was not included). Members of Aquiladelphidae have a deeper record in the Late Cretaceous, and share similar morphological trends with *Glasbius* when compared with generalized Late Cretaceous marsupialiforms (i.e., *Alphadon*), such as an anteroposterior broadening of the trigon basin with a correspondingly long talonid, a taller protocone, and an inflation of the cusps (including the stylar cusps). Despite these trends, the only specific character that unites the Williams Fork specimens with Aquiladelphidae is large size. In contrast, morphological characters shared between the Lancian *Glasbius* and the Williams Fork specimens include a low trigonid/talonid height differential (with the metaconid and entoconid nearly equal in height), a tall, wall-like entoconid, taller metaconid than paraconid, and a posteriorly expanded metaconid. *Glasbius intricatus* and *Glasbius piceanus* have a very low talonid/trigonid height differential, with the entoconid being nearly equal in height with the metaconid. The lingual half of m3 and m4 of *Glasbius intricatus* is taller than the labial half (i.e. the metaconid is taller than the protoconid), unlike that seen in *Glasbius piceanus*. The paraconid is appressed to the metaconid on the m3 and m4 only, with a correspondingly more open trigonid for the anterior lower molars. On all molars (except the ultimate molar) the talonid is wider than the trigonid. A few points of difference between the Williams Fork *Glasbius* and the Lancian *Glasbius* include the much larger size of the Williams Fork specimens, taller protoconid than metaconid on an m3, and the lack of any labial cingulid. The precingulid on UCM 57354 ends at the labial margin of the protoconid but does not continue along the labial margin of the tooth.

Discussion

The presence of specimens definitively referable to Pediomyoidea from both Aquiladelphidae and Pediomyidae by the middle Turonian implies that the emergence of these two families occurred earlier in the Cretaceous than previously thought. Taxa from the Smoky Hollow fauna already show important advanced characteristics found in later members of the families, including the reduction of the anterior stylar shelf in *Leptalestes* sp. and the expanded protocone and stylar shelf cusps in *Scalaria*.

Earlier tribosphenidans of unknown affinities to Late Cretaceous groups include members of the Cenomanian genus *Dakotadens*, which has been difficult to assign to clade, owing to poor knowledge of transitional faunas between the Cenomanian and the better-known late Santonian–Campanian (Cifelli et al., 2016; Eaton, 1993). New evidence of definitive pediomyoids from the Turonian suggests that *Dakotadens* may be a basal pediomyoid, based upon the labial attachment of the cristid obliqua to the back of the trigonid wall, a broad talonid that is as wide or wider than the trigonid, and slight labial placement of the paraconid on lower molars. Morphology of the upper molars suggests further that *Dakotadens* may belong to Aquiladelphidae, based upon an anteroposteriorly long protoconal region, a shallow ectoflexus, and divergent paracone and metacone culminating in a wide, U-shaped, straight centrocrista in *Dakotadens morrowi* (Cifelli et al., 2016; Eaton, 1993). As for other therians of uncertain affinities, the relationships of early Cenomanian *Culicolestes kielanae* cannot be determined, due to the fragmentary nature of the specimens. Large marsupialiforms include stagodontids, pediomyids, and aquiladelphids, and *Culicolestes* can be excluded from all groups based upon the wide anterior stylar shelf (contrary to Pediomyidae) and the transversely narrow protocone (contrary to Aquiladelphidae and Stagodontidae). Looking further back into the Early Cretaceous, affinities for tribosphenidans become even murkier, exacerbated by the fragmentary nature of these taxa (Cifelli and Davis, 2015). There are a few taxa of interest to the origin of large-bodied Late Cretaceous groups (e.g. *Argaliatherium robustum* and *Carinalestes murensis*), but additional specimens will be required to elucidate the relationships of these early therians.

Aquiladelphid molars have a number of morphological features consistent with crushing specialization, such as the anteroposteriorly expanded talonid, transversely wide protocone, and inflated cusps (Davis, 2007; Fox, 1971). Crushing dentitions are typically seen in frugivorous and durophagous taxa, but the morphological traits in the basal members of Aquiladelphidae (*Scalaria* spp., and perhaps *Dakotadens* spp.) are more consistent with frugivorous taxa (*Aquiladelphis* has numerous adaptations for carnivory, including sharp crests and carnassial notches). Frugivorous taxa tend to have a transversely wide protocone nearly equal in size with the paracone and metacone, while also including the protoconal region with the addition of protoconal cingula or a developed hypocone, deeper trigon and talonid basins, and anteroposteriorly and transversely expanded lower molars (White, 2009). In highly specialized durophagous taxa, all cusps are reduced to low, rounded flat surfaces, leaving little room for the entrapment of food (e.g. *Enhydra lutris*), but in generalist durophagous taxa such as *Crocuta crocuta*, *Didelphodon vorax*, and *Fumodelphodon pulveris*, the crushing surfaces tend to retain aspects of the teeth to grasp and hold food items during mastication (i.e. carnassial notches). On upper molars, the paracone and metacone tend to be taller relative to the protocone, with a shallower trigon and talonid basin, when present.

Prior to the Late Cretaceous, tribosphenidans were mostly relegated to smaller body size and a presumed insectivorous diet, with a tendency toward increasing body size during the Late Cretaceous (Grossnickle and Polly, 2013; Grossnickle and Newham, 2016). This trend has been linked to the emergence of lineages known for large body size (i.e. Stagodontidae and Aquiladelphidae) (Grossnickle and Polly, 2013; Wilson et al., 2012). Large marsupialiforms (herein defined arbitrarily as upper molar AP length 3 mm or larger) from the Smoky Hollow fauna show that these clades emerged early in the Late Cretaceous and, surprisingly, that they were more diverse than in younger faunas. The Smoky Hollow assemblage includes two stagodontids, *Fumodelphodon pulveris* and *Hoodootherium praeceps*; two aquiladelphids, *Scalaria aquilana* and *Scalaria diversicuspis*; and a large pediomyid, *Leptalestes* sp., while typical Lancian marsupialiform faunas only have two stagodontids, *Didelphodon vorax* and *Didelphodon padanicus*; two large pediomyids, *Protolambda florencae* and *Protolambda hatcheri*; and one large alphadontid, *Turgidodon rhaister* (Clemens, 1966; Cohen, 2017; Lillegraven, 1969). Large marsupialiforms from the Smoky Hollow support the hypothesis that increasing body size through the Cretaceous is related to the emergence of Stagodontidae and Aquiladelphidae, and this increase is most likely a response to additional selective pressures, such as changes in diet (either increased carnivory or herbivory). Large marsupialiforms from the Smoky Hollow tend to be smaller than their counterparts from the Lancian faunas, with the exception of

Leptalestes sp., showing that there was progressive size increase through time in these clades.

The increase in body size and diversity of tribosphenidans through the Cretaceous has been linked to two potential factors: the extinction and subsequent replacement (whether via direct competition or passive replacement is unknown) of large, carnivorous mammalian taxa from archaic lineages (i.e. eutriconodonts) and the radiation of angiosperms during the medial Cretaceous, providing new, rich food resources (i.e. fruits, nectar, pollen, etc.) (Grossnickle and Polly, 2013). There is some evidence to suggest that these factors can at least partially explain why mammal body size and diversity increased through the Cretaceous, leading up to the adaptive radiation after the K-Pg extinction event (Wilson et al., 2012; Wilson, 2013). Stagodontids and cimolestids both achieved large body size by the end of the Cretaceous and have been linked to an increased carnivorous diet (Clemens, 1966; Cohen, 2017; Fox and Naylor, 2006; Fox, 2015; Wilson et al., 2016). With the decline of eutriconodonts during the Cenomanian, there is a subsequent emergence of large, carnivorous marsupialiforms by the middle Turonian: the first unequivocal stagodontids (Cifelli et al., 2016; Cohen, 2017). Pediomyoids have been shown to have an increased herbivorous diet, highlighting a possible response to the angiosperm radiation (Wilson, 2013). Pediomyoids may have first emerged during the Cenomanian, much earlier than previous evidence suggests, with the emergence of the putative pediomyoid, *Dakotadens*, and undoubtedly diversified by the middle Turonian, with morphological adaptations for increased herbivory, such as a transversely wide protocone, anteroposteriorly broad trigon and talonid basins, and an anteroposteriorly expanded lower molar. At larger body sizes, basal mammals must incorporate larger and more abundant food resources in order to correctly balance energy intake and output (Clauss et al., 2013). Terrestrial mammals subsisting on invertebrate prey only have a net energy gain at smaller body sizes; larger tribosphenidans such as aquiladelphids and stagodontids most likely relied on supplementing invertebrate prey with either vertebrate prey or highly nutritious plant parts (i.e., reproductive parts such as fruits and seeds) in order to survive (Clauss et al., 2013; Hiiemae, 2000). Within Aquiladelphidae, *Aquiladelphis* and *Scalaria* appear to have had different adaptations and strategies for supplementing their diets. *Aquiladelphis* teeth differ from those of *Scalaria* with sharper crests and carnassial notches, both features important for processing vertebrate tissue, yet *Aquiladelphis* still retains the anteroposteriorly wide protocone seen in *Scalaria*. *Scalaria* lacks the sharper crests and carnassial notches, instead relying on the crushing and grinding function associated with inflated cusps and anteroposteriorly expanded protocone (Hiiemae, 2000).

The first readily identifiable pediomyoids from the middle Turonian consist of two moderately well represented species of aquiladelphids and one pediomyid based on a single, incomplete molar. Aquiladelphidae was a moderately successful marsupialiform family that probably first emerged in the early Cenomanian with the genus *Dakotadens*, and survived until the Late Campanian with *Aquiladelphis analetris*. Aquiladelphidae apparently did not survive into the Maastrichtian. This family provides the first evidence for increased frugivory/granivory within Metatheria, shortly after the initial diversification of angiosperms during the end of the Early Cretaceous. The first record of Pediomyidae is pushed back to the middle Turonian; however, *Leptalestes* already possesses upper molar specializations (e.g., reduction of the mesial stylar shelf) that hamper identification of antecedents earlier in the Cretaceous. The Smoky Hollow fauna is surprisingly diverse with respect to large marsupialiforms, highlighting a probable reaction to multiple factors co-occurring during the early Late Cretaceous, with the decline and subsequent extinction of archaic lineages such as eutriconodonts, and the radiation and dominance of angiosperms.

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FIGURE 4.1. Lower dentition of *Scalaria diversicuspis* gen. et sp. nov. A, OMNH 68766, holotype, left dentary fragment with dp3–m2, in occlusal stereopair (A_1) and lingual (A_2) views. B, OMNH 25505, left dp3, in occlusal stereopair (B_1) and lingual (B_2) views. C, OMNH 69398, right p3, in occlusal stereopair (C_1) and lingual (C_2) views. D, MNA V6363, right m1, in occlusal stereopair (D_1) and lingual (D_2) views. E, OMNH 68778, right m2 or m3, in occlusal stereopair (E_1) and lingual (E_2) views.

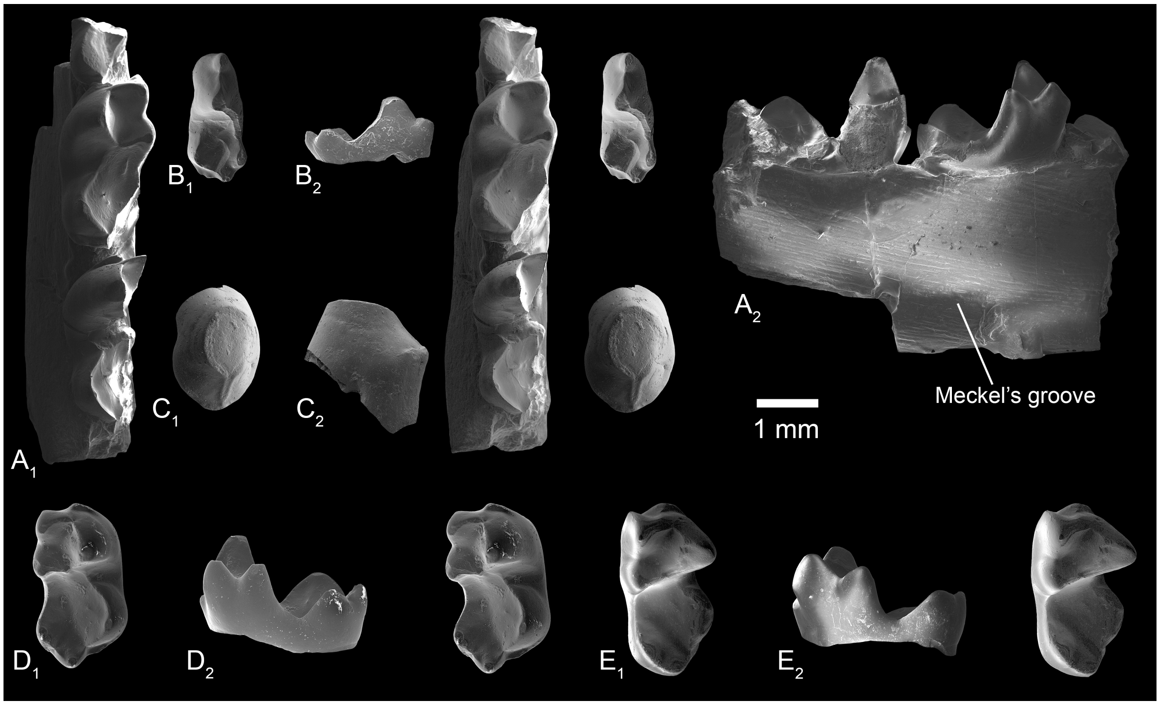

FIGURE 4.2. Upper dentition of *Scalaria diversicuspis* gen. et sp. nov. A, OMNH 69354, left M1?, in occlusal stereopair. B, OMNH 24635, right Mx, in occlusal stereopair. C, OMNH 69354, right M1?, in occlusal stereopair. D, MNA V7556, right M3, in occlusal stereopair.

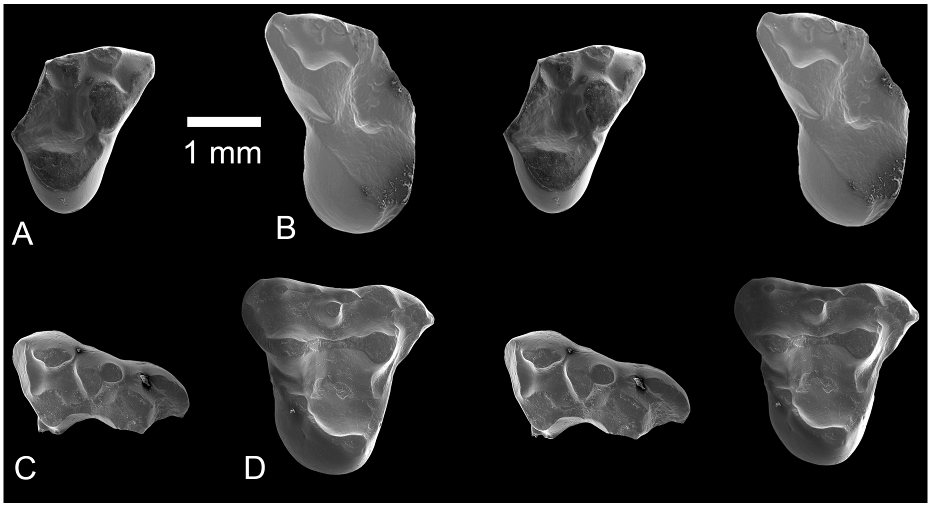

FIGURE 4.3. ***Scalaria aquilana* gen. et sp. nov. A, OMNH 29514, left M1, in occlusal stereopair. B, OMNH 29078, right M3, in occlusal stereopair. C, OMNH 29065, left mx, in occlusal stereopair (C_1) and lingual (C_2) views.**

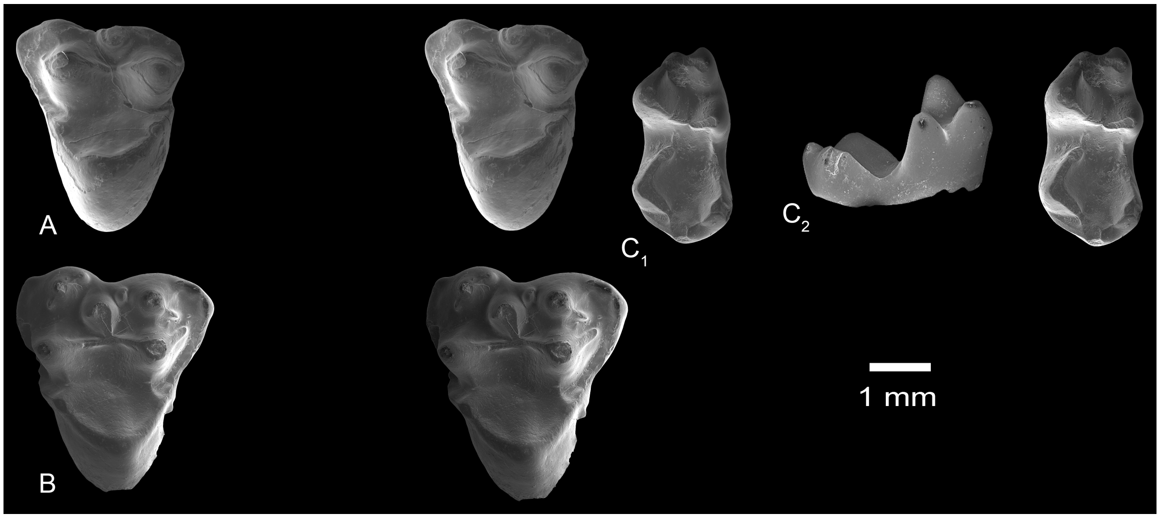

FIGURE 4.4. Pediomyoidea A–B *Aquiladelphis analetris* sp. nov. A, UCMP 131240, left Mx, in occlusal stereopair. B, UCMP 235745, left Mx, in occlusal stereopair. C, *Leptalestes* sp. OMNH 68752, left M2, in occlusal stereopair. D, *Glasbius piceanus* sp. nov., UCM 57354, right m3, in occlusal stereopair (D_1) and lingual (D_2) views.

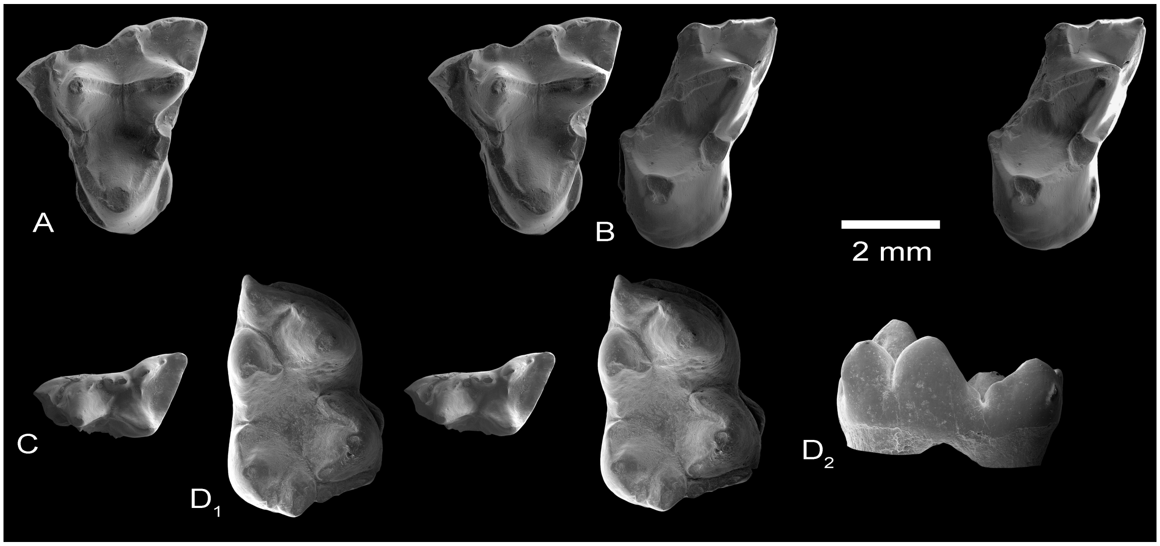

Table 4.1. Dental measurements (in mm) of *Scalaria diversicuspis* gen. et sp. nov. * denotes holotype. ANW = anterior width, POW = posterior width, AP = anteroposterior length.

Specimen	Tooth	ANW	POW	AP
OMNH 69398	p3			
OMNH 25505	dp3	0.94	1.16	2.56
OMNH 68766*	dp3	—	1.35	—
*	m1	1.91	1.79	3.06
*	m2	—	—	3.29
MNA V6363	m1	1.60	1.79	3.11
OMNH 68778	m2 or m3	1.80	1.74	3.29
OMNH 68767	mx	—	1.86	—
MNA V6945	M1?	—	2.70	—
OMNH 69354	M1?	—	—	3.14
MNA V7556	M3	2.96	3.12	3.16
OMNH 24635	Mx	—	3.31	—

Table 4.2. Dental measurements (in mm) of *Scalaria aquilana* gen. et sp. nov. * denotes holotype.

Specimen	Tooth	ANW	POW	AP
OMNH 29065	mx	1.95	2.02	3.68
OMNH 29482	mx	2.14	—	—
OMNH 29497	mx	1.93	1.99	3.61
MNA V6361	mx	2.19	—	—
OMNH 29514	M1	3.81	3.73	3.33
OMNH 29078*	M3	4.37	4.48	4.09

Table 4.3. Dental measurements (in mm) of *Aquiladelphis analetris* sp. nov., *Leptalestes* sp., and *Glasbius piceanus* sp. nov. * denotes holotype.

Specimen	Taxon	Tooth	ANW	POW	AP
UCMP 131240*	*Aquiladelphis analetris*	Mx	4.80	5.28	4.78
UCMP 235745	*Aquiladelphis analetris*	Mx	—	5.76	—
OMNH 68752	*Leptalestes* sp.	M2	—	—	3.66
UCM 57354*	*Glasbius piceanus*	m3	3.26	3.68	5.04
UCM 57350	*Glasbius piceanus*	mx	3.23	3.64	4.57

CHAPTER 5: A TRANSITIONAL MAMMALIAN FAUNA FROM THE LATE CRETACEOUS (TURONIAN) OF NORTH AMERICA

Abstract

The increasing knowledge of the mammalian faunas during the medial Cretaceous of North America has come about via a concerted collecting effort over the last few decades. The collecting effort has resulted in a large, well-preserved mammalian fauna from the Turonian-aged Smoky Hollow Member of the Straight Cliffs Formation. Previous studies from Turonian-aged rocks of North America have resulted in faunal elements more similar to Campanian–Maastrichtian-aged faunas, rather than the temporally closer Cenomanian faunas. Previous work has described the stagodontid and pediomyoid marsupialiforms and eutherians from the Smoky Hollow Member of the Straight Cliffs Formation. Herein I describe the alphadontid marsupialiforms, which constitute the most taxonomically diverse yet dentally conservative group of tribosphenidans from the Smoky Hollow Member. The alphadontids are generally small, and include one of the smallest Cretaceous tribosphenidans known to date; all were presumably insectivorous. Included taxa are: *Varalphadon* sp., *Eoalphadon lillegraveni*, *Eoalphadon clemensi*, *Kokopellia musicus* sp. nov., *Apidelphys minuscularia* gen. et sp. nov., and ?*Anchistodelphys delicatus*. Along with previously described elements of the Smoky Hollow mammalian fauna, a comparison to earlier and later faunas demonstrates that elements from both the Cenomanian and the Campanian–Maastrichtian are present during the Turonian of Utah. The unique faunal signature, including elements from both older and younger assemblages, is also characterized by

lowered diversity among archaic mammalian groups (i.e., symmetrodonts and triconodonts) concomitant with significant morphological and taxonomic diversification of Tribosphenida. In some cases, at least, newly-appearing tribosphenidans may have occupied niches like those postulated for predecessors among archaic clades (e.g., diminutive alphadontid marsupialiforms replacing symmetrodonts as small insectivores; stagodontid marsupialiforms replacing triconodontids as carnivores and/ or durophagous faunivores) via either direct competition or passive replacement.

Introduction

The record of mammals from the Late Cretaceous of North America has steadily increased in recent decades, most noticeably filling in gaps during the medial Cretaceous, from the Cenomanian to the Campanian (Cifelli et al., 2016; Cohen, 2017; Davis et al., 2016; Eaton, 2006a, 2006b, 2009, 2013). Yet many of these records are based on small sample sizes and notoriously incomplete fossils (often isolated teeth, sometimes broken), so that the systematics and paleobiology of these mammals remain poorly understood. The Late Cretaceous Turonian age (about 89–94 Ma ago) stands out as having one of the poorest records for mammals and other terrestrial vertebrates in North America, due to the global marine transgression at this time (Kirkland and Wolfe, 2001). Vertebrate-bearing terrestrial deposits from the Turonian of North America are rare, with the main source of information for vertebrate faunas coming from the Smoky Hollow Member of the Straight Cliffs Formation of southern Utah and the Moreno Hill Formation of western New Mexico. Nearly all vertebrate groups from these formations include the first appearance of taxa commonly associated with later Cretaceous (Campanian–Maastrichtian) assemblages (Cohen, 2017; Cohen et al., in review; Nydam, 2013; Sweeney et al., 2009; Wolfe and Kirkland, 1998). Given that the overwhelming majority of Turonian mammals and other microvertebrates from North America come from the Smoky Hollow Member of the Straight Cliffs Formation, this unit provides a critical and unique source of data in documenting the continent's changing ecosystem during the mid-Cretaceous transition (Cifelli, 1990a; Cifelli and Gordon, 1999; Cohen, 2017; Eaton, 1995; Nydam, 2013). Early Cretaceous and earliest Late Cretaceous therian mammal assemblages tend to be dominated by archaic lineages (i.e. symmetrodonts and triconodonts), with tribosphenidans rare and often regarded as basal, with uncertain affinities to later Cretaceous faunas (Cifelli, 1997, 2004; Cifelli and Davis, 2015; Cifelli et al., 2016). In contrast, the Smoky Hollow fauna exhibits elements of later Cretaceous mammalian faunas, such as definitive stagodontids, aquiladelphids, pediomyids, and eutherians (Cohen, 2017; Cohen and Cifelli, in prep; Cohen and Davis, in prep).

Materials and Methods

Most of the specimens included in this study resulted from a long-term collecting program (1983–present) led by Richard L Cifelli, first of the Museum of Northern Arizona, Flagstaff (1983–1986) and, later, the Sam Noble Oklahoma Museum of Natural History, Norman (1986–present) in the Cretaceous System of the Kaiparowits region, southern Utah. Additional specimens were collected under the auspices of parallel, collaborating efforts of Jeffrey G. Eaton (based sequentially at the University of Colorado, Boulder; the Museum of Northern Arizona, and Weber State University, Ogden, Utah). Ironically, until these collecting programs began in the early 1980s, the terrigenous Cretaceous of southern Utah was noteworthy for being virtually devoid of vertebrate fossils (e.g., Gregory and Moore, 1931; Peterson, 1969). Most of the outcrops (and hence fossil localities) are on Federal lands administered by the U.S. Department of the Interior, Bureau of Land Management (BLM); and the U.S. Department of Agriculture, Dixie National Forest. In 1996, most of the study area was designated part of the Grand-Staircase-Escalante Monument, which remains under BLM jurisdiction and is the largest national monument in the U.S. By law, access to vertebrate fossil sites on Federal lands is restricted; precise locality data are on file with the Utah State Office, BLM (440W 200S, No. 500, Salt Lake City, Utah 84101; https://www.blm.gov/office/utah-state-office).

Samples were collected following bulk screen washing techniques described by Cifelli et al. (1996). Standard measurements (following Lillegraven and McKenna, 1986) were collected using a Reflex Microscope (see MacLarnon, 1989, Consultantnet Ltd, 94 High Street, Linton, Cambridge, CB21 4JT, UK; http://www.reflexmeasurement.co.uk/). Scanning electron micrographs were taken using a Denton Vacuum Desk II sputter coater (Denton Vacuum LLC, 1259 North Church Street Building 3, Moorestown, New Jersey 08057, USA; https://www.dentonvacuum.com/) and a LEO 1450VP SEM (Carl Zeiss NTS LLC, One Corporation Way, Peabody, Massachusetts 01960, USA; http://www.microscopy.info/organization/Details/505).

Measurement abbreviations. — ANW, anterior width (trigonid width of lower molars); AP, anteroposterior length; POW, posterior width (talonid width of lower molars).

Institutional abbreviations. — MNA, Museum of Northern Arizona, Flagstaff, Arizona, USA; OMNH, Sam Noble Oklahoma Museum of Natural History, Norman, Oklahoma, USA.

Systematic Paleontology

Marsupialiformes Vullo et al., 2009

"Alphadontidae" Marshall et al., 1990

Included genera. — *Alphadon*, *Turgidodon*, *Protalphadon*, *Varalphadon*, *Eoalphadon*, *Albertatherium*, *Nortedelphys*, and *Aenigmadelphys*.

Comments. — The current status of the family "Alphadontidae" is relegated to a paraphyletic morphological grade (Kielan-Jaworowska et al., 2004) and is supported by phylogenetic anlayses by Johanson (1995) and Wilson et al. (2016). The "family" includes a number of genera from the Cenomanian to the Maastrichtian of North America. The genera all have generalized insectivorous molars, and share a number of morphological characters including the presence of stylar cusps A, B, and D, well developed conules, stylar cusp D separated by a well developed notch, and an uncompressed protocone (Eaton, 2009; Kielan-Jaworowska et al., 2004). Stylar cusp C is a variable character within "Alphadontidae" because of the relative size and variable presence within *Varalphadon* (variably present), *Eoalphadon* (present, but variable in relative size and position), *Aenigmadelphys* (absent), and *Protalphadon* (variably present) (Johanson, 1995; Kielan-Jaworowska et al., 2004; Eaton, 2009). The variability in both the relative size and presence of the stylar cusp C might be another symptom of the paraphyly of "Alphadontidae" since stylar cusp C has been shown to be independently acquired within the "alphadontids" and Pediomyoidea (Cohen, 2017; Rougier et al., 2015; Wilson et al., 2016).

Varalphadon Johanson, 1996

Varalphadon sp.

Fig. 5.1; Table 5.1

Included material. — OMNH 29073, left M1; OMNH 29076, left M1; OMNH 29082, right M1; OMNH 29074, right M1; OMNH 29513, left M1; OMNH 26112, left M1; MNA V7351, left M2; MNA V7338, right M1; MNA V7347, right M2; OMNH 68755, left M3?; OMNH 24633, right Mx; OMNH 26115, left Mx; OMNH 26108, left dp3; MNA V7336, right dp3; MNA V7342, left dp3; OMNH 69345, right m1; OMNH 29069, left m1; OMNH 29059, left m1; OMNH 29053, right m2; MNA V7334, left m2; MNA V7343, left m2; OMNH 29062, right m2; OMNH 29057, right m2; OMNH 29058, right m2; MNA V6949, left m2; OMNH 25494, left m2; OMNH 23101, right m3; OMNH 25493, left m3; OMNH 29071, right m3; OMNH 29072, left m3; OMNH 20380, right m3; OMNH 29498, left m4; OMNH 29070, left m4; OMNH 29067, eroded left m4; OMNH 68780, right m4; OMNH 29054, left m4; OMNH 26110, left mx missing lingual half of tooth; OMNH 29500, left mx missing protoconid, entoconid, and hypoconulid; OMNH 29060, eroded right mx; and OMNH 68774, right mx missing the protoconid.

Description. — Upper molars are generally small, with a relatively narrow protocone and moderately defined crests. The paracone and metacone are nearly identical in height, but the cusps diverge, with the paracone leaning slightly anteriorly and the metacone leaning slightly posterior (Fig. 5.1A). In labial view, the metacone is anteroposteriorly wider than the paracone. The lingual faces of the paracone and metacone are angular, resulting in a keeled appearance for the lingual edge of the paracone and metacone. The labial faces of the paracone and metacone are slightly inflated and rounded, rather than flat. The centrocrista runs straight between the paracone and metacone, and is not sharply defined, nor does it exhibit much wear on more worn specimens. The postmetacrista is tall and bears a vaguely cusp-like swelling on the anterior side and slightly closer to the metacone than to the metastylar angle of the tooth margin. Between this swelling and the metacone is a pronounced dip, or notch, in the postmetacrista. The stylar shelf does not have cusps in the C or E positions. Stylar cusp A is low. The B cusp is tall and conical, connected to the paracone with a preparacrista. In anterior view, the preparacrista is V-shaped, with stylar cusp B only about half as tall as the paracone. Stylar cusp D, the largest of the stylar cusps, is elongate and forms a wall-like margin that extends almost the length of the metastylar lobe, along the margin of the stylar shelf. Cusp D is subequal in height with stylar cusp B. The ectoflexus is shallow on M1 and deeper on M2, suggesting that is deepens through the series M1–3. The protocone is relatively narrow, but has well-developed para- and metaconules, closer to the protocone than to the paracone and metacone, respectively. The internal cristae are present, and extend to the base of their respective cusp. The postprotocrista ends at the base of the metacone, while the preprotocrista extends all the way to the parastyle. The protocone is tall and conical, resulting in a deep trigon basin. Differences between tooth loci are not apparent, with the only major differences in morphology being the depth of the ectoflexus and the length of the preparacrista (Fig. 5.1A, C).

The dp3 (not illustrated) is similar to other described Cretaceous marsupialiform deciduous premolars, with an open trigonid, resulting from an anteriorly placed paraconid, and a wide talonid. The protoconid dominates the trigonid and is curved. The metaconid and paraconid are subequal in height, with the paraconid leaning anteriorly, and the metaconid having a larger base. The talonid is well developed, with all three main cusps present. The hypoconid is the largest cusp, with the entoconid and hypoconulid closely approximated and twinned. A weak postcingulid is present, extending from the hypoconulid.

All molars in the lower molar series are known, and trends through the molar series are similar to other marsupialiforms. The talonid narrows and elongates relative to the trigonid through the molar series, with the first molar being the smallest of the four. The protoconid is the tallest cusp of the trigonid, with the paraconid the smallest. The paraconid leans anteriorly on the first molar, resulting in an open trigonid, although not to the same degree as seen in the dp3. Moving posteriorly through the molar series, the paraconid leans anteriorly to a lesser degree, until the third molar, where it is nearly parallel with the protoconid and metaconid, giving the trigonid a more compressed look when compared with the first and second molars. The paraconid also shifts lingually through the molar series, but is never completely in line with the metaconid and entoconid. The metaconid has an anteroposteriorly long base and is positioned slightly posterior to the protoconid on all four molars (e.g., Fig. 5.1D_2). The talonid is deeply basined and is bordered by strong crests. The entoconid is wall-like and is the tallest cusp on the talonid. The hypoconulid and entoconid are twinned with a strong postcingulid connected. The postcingulid wraps around to the lingual side of the tooth on at least the m2 and m3 loci (specimens attributed to m1 or m4 are not as well preserved and do not adequately preserve the morphology).

Comments. — *Varalphadon* sp. from the Smoky Hollow fauna appears to be morphologically intermediate between *Varalphadon wahweapensis* Cifelli 1990b from the Campanian and *Sinbadelphys schmidti* from the early Cenomanian, especially with regard to the construction of the D cusp. In *Varalphadon wahweapensis*, the D cusp is more conical when compared with *Varalphadon* sp., which is long and more wall-like. *Sinbadelphys*, however, has a poorly developed D cusp (if at all), with a long swelling on the stylar shelf in the D position.

Lower molars herein referred to *Varalphadon* sp. are remarkably similar to those of *Varalphadon wahweapensis*, differing only in the relative inflation of the cusps: those of *Varalphadon* sp. are slightly more inflated than specimens of *Varalphadon* *wahweapensis*. In both, posterior molars have the paraconid and metaconid more closely appressed than in anterior molars; the talonid basin is deep, with a tall, wall-like entoconid; and the postcingulid is strongly developed, extending to the lingual side of the tooth. Most of these characters are also shared with *Sinbadelphys schmidti*; in particular, the strong postcingulid extending to the lingual side of the tooth, the tall, wall-like entoconid, and the deep talonid basin. Differences between *Sinbadelphys schmidti* and *Varalphadon* sp. include greater cusp inflation in *Varalphadon* sp. and, provisionally, lesser approximation between the paraconid and metaconid in *Varalphadon* sp. (few lower molars, mostly incomplete, are known for *Sinbadelphys schmidti*).

Varalphadon sp. is the most abundant tribosphenidan from the Smoky Hollow Member of the Straight Cliffs Formation, but the majority of upper molars are referable to M1. There are at least three specimens included in the hypodigm that is from either the M2 or M3, shown by the increased depth of the ectoflexus. The abundance of specimens representing M1 is curious, especially in comparison to another well-sampled species, *Eoalphadon clemensi*, in which each locus is known by a similar number of referred specimens. The apparent overrepresentation of M1 referable to *Varalphadon* sp. might be due to misidentification of M2 as M1, which would occur in the event the two teeth were more similar (e.g., in depth of the ectoflexus) than is generally the case among alphadontids. Additional specimens are required to further investigate this possibility.

Eoalphadon Eaton, 2009

Eoalphadon lillegraveni Eaton, 1993

Fig. 5.2; Table 5.2

Referred material. — MNA V6124, left M3; OMNH 23114, left M4; OMNH 29064, right m3 missing the entoconid and hypoconulid; and OMNH 26107, left m4?.

Distribution. — Upper Cenomanian Naturita Formation, Utah; and middle Turonian Smoky Hollow Member of the Straight Cliffs Formation, Utah.

Description. — Upper molars are known from an M3 lacking the paracone (Fig. 5.2A) and a complete M4 (Fig. 5.2B). On the penultimate molar, the protoconal region is relatively wide, transversely, and the paraconule and metaconule are closer to the protocone than to either the paracone or metacone, respectively. The internal conular cristae are weakly developed, with the postparaconular crista slightly better developed than the premetaconular crista. The preprotocrista connects to the parastyle, terminating at stylar cusp A, and the postprotocrista runs nearly the entire length of the crown, terminating slightly lingual to the distobuccal corner of the metastyle. The metacone is conical, taller than the protocone, and has a separate, distinct base from the paracone. The bases between the paracone and metacone suggest that the two cusps were similar in size, with a straight centrocrista that did not invade the stylar shelf. The postmetacrista is weakly developed, to the point where it nearly disappears halfway between the metacone and the distobuccal corner of the metastyle. The distobuccal corner of the metastyle has a moderately developed stylar cusp E, separate from the postmetacrista and stylar cusp D. Stylar cusps C and D form a wall-like ridge along the buccal margin of the tooth, and the two cusps can be differentiated along the ridge by a faint notch at the posterior end of a deep ectoflexus. The stylocone is positioned buccal to where the paracone would be situated, and would have been connected by a low preparacrista. The preparacrista splits into two crests halfway between the paracone and stylocone, with the spur crest directed towards the parastyle and stylar cusp A, but does not connect with the stylar cusp. Stylar cusp A is positioned on the parastyle and is low.

The last upper molar is typical in its morphology for ultimate molars belonging to marsupialiforms, in having a reduced metacone and metastylar lobe, and an expanded parastylar lobe. The protocone is not as transversely wide as seen in the third molar, but has the paraconule closer to the protocone than it is to the paracone. A preprotocrista runs along the mesial edge of the tooth, and terminates at the anterobuccal corner of the parastyle. In terms of stylar cusps, a moderately sized stylar cusp is present between the paracone and metacone and three small cuspules are present at the anterobuccal corner of the parastyle. The paracone has a preparacrista running along the parastyle; this does not terminate at any cusp, but curves anteriorly, intersecting with the preprotocrista.

The lower molar morphology is known from two nearly complete specimens, OMNH 26107 (Fig. 5.2C) and 29064 (Fig. 5.2D). OMNH 29064 is missing the entoconid and hypoconulid, while 26107 is missing the protoconid, so nearly all of the morphology is known between these specimens. OMNH 26107 is most likely a last molar due to a posteriorly projecting hypoconulid and narrower talonid. The metaconid is slightly taller than the paraconid, although the difference in height on OMNH 29064 appears larger due to the preferential wear on the paracristid. Due to the higher degree of wear on the paracristid, it is uncertain how tall the protoconid would have been, but it would have likely been taller than the metaconid. For the talonid, the entoconid and hypoconulid are twinned, and both most likely were taller than the hypoconid, but this is uncertain due to the amount of wear on the talonid. The cristid obliqua meets the back of the trigonid wall directly below the protocristid notch.

Comments. — The Smoky Hollow specimens attributed to *Eoalphadon lillegraveni* are similar to the specimens from the Naturita Formation, but are slightly smaller (Table 5.2). Upper molars share a variety of characters, including having a straight centrocrista, weak internal cristae, a transversely wide protoconal region, and presence of stylar cusps B, C, D, and E. Lower molars share some similarities as well, with a subequal or slightly taller metaconid compared to the paraconid, but appear to differ in having a hypoconulid and entoconid taller than the hypoconid.

Eoalphadon clemensi Eaton, 1993

Fig. 5.3; Table 5.3

Referred material. — OMNH 65955, right M1, missing the metastylar region; OMNH 29520, left M1, missing the metacone and metastylar region; OMNH 29087, left M2; MNA V7558, left M2; OMNH 29085, right M2; OMNH 29080, right M2; OMNH 25507, right M2, missing the protocone; OMNH 29517, left M2, missing the protocone; MNA V6752, right M2, missing the protocone; MNA V7559, left M3; OMNH 69448, left M3; OMNH 20373, left M3, missing the protocone; OMNH 68759, right M3, missing the protocone; MNA V6895, left M4; MNA V6753, left M4; OMNH 69346, left Mx, preserving the paracone and anterior stylar shelf; MNA V6355, left Mx, missing the paracone and parastylar region; OMNH 29516, left Mx, missing the metacone and the metastylar region; OMNH 69344, right Mx, missing the parastylar region; MNA V7335, right Mx, missing the parastyle and labial edge of the stylar shelf; OMNH 26109, left dp3; OMNH 29052, left m1; MNA V6125, right m2; OMNH 29051, left m2; OMNH 69347, left m3; MNA V6115, right m3; OMNH 23108, right dentary fragment with m3; OMNH 29068, eroded left mx; OMNH 23102, right mx, missing the paraconid; MNA V6126, right mx, missing the paraconid, entoconid, and hypoconulid; OMNH 23106, right mx.

Distribution. — Upper Cenomanian Naturita Formation, Utah; and middle Turonian Smoky Hollow Member of the Straight Cliffs Formation, Utah.

Description. — Nearly the entire molar series is represented, both upper and lower. The first upper molar is incompletely known from the Smoky Hollow, with both specimens (OMNH 65955 and 29520) missing the metastylar region and metacone. OMNH 65955 (Fig. 5.3A) is the better-preserved specimen of the two, with almost no wear. The paracone and protocone are not inflated and have sharp shearing crests that are well developed. The protocone leans slightly anteriorly and has well-developed para- and metaconules. The paraconule is closer to the protocone than the metaconule, but both conules have well-developed internal cristae. The paracone is tall and straight, with a well-developed preparacrista. The preparacrista connects with the stylocone. The parastyle is tall, but shorter than the stylocone, with well-developed crests connecting to the stylocone and the protocone.

The succeeding molars are similar to the first molar, with sharp crests and uninflated cusps. The paracone and metacone are subequal in height, with a straight centrocrista connecting the cusps. The postmetacrista is well developed and longer on the third molars than on the second. The ectoflexus is deepest on the third molars. The parastylar region is expanded labially on third molars, compared to the second molars, while the metastylar region tends to be more extensive labially on the second molars. The stylocone is the largest of the stylar cusps, followed by stylar cusp D. Cusp C is variably placed within the ectoflexus notch, from anterior to the deepest part of the ectoflexus, to posterior to the deepest part of the ectoflexus. Cusp C is occasionally expressed as a poorly developed raised mound (Fig. 5.3B).

The single dp3 (not illustrated) attributed to *Eoalphadon clemensi* from the Smoky Hollow fauna is nearly complete, missing the metaconid and damaged enamel along the labial edge of the tooth. As is typical for deciduous lower premolars, the trigonid is open and narrower than the talonid, with the paraconid positioned anterior and between the protoconid and metaconid. The protoconid is the tallest cusp of the trigonid. The talonid is well developed, with the entoconid as the tallest cusp. The hypoconulid is closer to the entoconid, with a poorly developed postcingulid. Lower molars follow the general marsupialiform pattern, with the first molar being the smallest and a relative narrowing of the talonid through the molar series. The first molar is known from a single specimen, OMNH 29052 (Fig. 5.3D), missing only the tips of the metaconid and entoconid. The trigonid is relatively open, with the paraconid slightly anterior, when compared with the second and third molars. Judging from the size of their bases, the paraconid was smaller than the metaconid, with the protoconid dominating the trigonid. The protoconid leans posteriorly, with a well-developed, nearly blade-like preprotocristid. The talonid is wider than the trigonid, as is generally true of alphadontid first molars, with all three cusps present. The hypoconulid and entoconid are twinned, with a well-developed postcingulid originating from the apex of the hypoconulid and wrapping around to the labial margin of the hypoconid. The hypoconid was most likely the largest cusp on the talonid (the entoconid is broken, so this cannot be confirmed), and has a well-developed cristid obliqua, attaching to the trigonid wall below the protocristid notch. The talonid basin is deep and bowl-like. The second molar (Fig. 5.3F) is poorly preserved, but adds important information regarding molar proportions. The talonid is wider than the trigonid, but the trigonid is not open, as seen in the first molar. The paracristid is also more blade-like than in the first molar, with a carnassial notch present. The blade-like paracristid and carnassial notch are also observed on the third molars (Fig. 5.3G). The third molar is the best-represented locus of the lower dentition, with three specimens: OMNH 69347 (Fig. 5.3G), 23108, and MNA V 6115. These specimens complement each other on the molar morphology. OMNH 23108 (not illustrated) is the poorest preserved molar, but preserves a fragment of the dentary, where, notably, a faint Meckel's groove can be observed. The talonid and trigonid of m3 are subequal in width and have the greatest talonid/trigonid height differential. The paraconid is positioned closer to the metaconid, in comparison to the first and second molars. The metaconid is taller than the paraconid, but the entoconid and hypoconid are subequal in height.

Comments. — *Eoalphadon clemensi* from the Smoky Hollow fauna is virtually identical to specimens recovered from the Naturita Formation. *Eoalphadon clemensi* is the second-most abundant taxon of tribosphenic mammal from the Smoky Hollow fauna.

Incertae sedis

Kokopellia Cifelli, 1993

Type species. — *Kokopellia juddi* Cifelli, 1993

Distribution. — Cenomanian–Turonian, Cedar Mountain Formation; and Smoky Hollow Member of the Straight Cliffs Formation, Utah.

Diagnosis. — See Cifelli (1993).

Kokopellia musicus sp. nov.

Fig. 5.4; Table 5.4

Etymology. — Musicus from Latin meaning musician, after the depiction of the southwest Native American deity Kokopelli as a flute-player.

Holotype. — OMNH 24634, left M3.

Type locality. — OMNH locality V60, middle Turonian Smoky Hollow Member of the Straight Cliffs Formation, Garfield County, Utah.

Included material. — OMNH 69343, right M3 missing the parastylar lobe; OMNH 29083, right M4; OMNH 29046, right p3; OMNH 23107, right m3; OMNH 24628, left m3; MNA V6105, right m4; OMNH 68770, trigonid of left mx; OMNH 20017, trigonid of left mx; and OMNH 20128, left dp3.

Distribution. — Turonian, Smoky Hollow Member of the Straight Cliffs Formation, Utah.

Diagnosis. — Similar to *Kokopellia juddi*, but differs in: smaller size, metacone and paracone do not diverge, stylar cusp D is larger and better developed, precingulid shelf-like, and a lower trigonid/talonid height differential.

Description. — The paracone and metacone of upper molars are subequal in height, and are separated by a deep, narrow valley. The two cusps do not diverge. In occlusal view, the centrocrista does not run straight, but is slightly invasive toward the stylar shelf. The stylar shelf is buccolingually wide, and has a correspondingly long preparacrista and postmetacrista. The preparacrista is tall and connects with a well-developed stylocone. The parastyle is well developed, with a crest connecting between the stylocone and stylar cusp A. The preprotocrista runs along the entire anterior face of the molar, connecting between the protocone and stylar cusp A. The ectoflexus is deep on the presumed M3. On the holotype, a slightly raised cuspule is present, anterior to the deepest part of the ectoflexus, and on OMNH 69343, a small cusp is present at the deepest part of the ectoflexus, but no definitive C cusp is present. Stylar cusp D is well developed, but smaller than the stylocone; no cusp E is present. The postmetacrista is well developed and is oriented nearly straight buccolingually on the M3 (Fig. 5.4A). The protoconal region is narrow, but encompasses a well-developed, deep basin. The protocone is tall, although not as tall as the paracone and metacone. The lingualmost extent of the protocone is compressed, giving the lingual margin a keeled appearance. The paraconule and metaconule are best preserved on OMNH 69343 (Fig. 5.4B), and are located closer to the protocone than to either the paracone or metacone, respectively. Internal conular cristae are well developed and sharp, and extend part of the way up the lingual face of the paracone and metacone.

The last upper molar is broadly similar to the M3s, with a narrow protocone, internal conular crista well developed and running partially up the lingual face of the paracone, and a preprotocrista running the entire length of the anterior face of the tooth, from the protocone to the parastylar region (Fig. 5.4C). The preprotocrista is well developed and long. Typical reductions for the last upper molar are observed, with a much larger paracone than metacone, reduction in the metastylar region of the stylar shelf, and reduction of the metaconule. The stylar shelf has poorly developed stylar cusps that are manifested as slightly raised bumps along the buccal margin of the tooth.

The single p3 is two-rooted, and the paraconid is slightly recurved (Fig. 5.4D). The paraconid dominates the tooth, with a slightly developed anterior keel. A posterior keel is better developed than the anterior, and ends at a basined heel. The basined heel is formed from a single posterior cusp and crests defining the lingual and buccal edges of the basin, with the buccal crest continuous with the posterior keel of the paraconid. Short pre- and postcingulids are present, originating from the anterior keel and posterior cusp of the basined heel, respectively.

The lower deciduous premolar (not illustrated) is nearly complete, with a damaged talonid missing the hypoconid and entoconid. The tooth is overall similar to other described deciduous premolars, with a wider talonid than trigonid, a wide-open trigonid, and an anteriorly placed and low paraconid. The protoconid is the tallest cusp, with the apex recurved. Sharp crests descend on either side of the protoconid, connecting with the paraconid and metaconid, with slight wear observed on the metacristid. Due to the damage on the talonid, relative cusp heights cannot be determined.

The lower molar series is represented by two m3s, a single m4, and two trigonid fragments. Overall, lower molars are characterized as having the trigonid dominated by a tall protoconid, with the paraconid and metaconid subequal in height. The cusps are tall, slender, and mostly conical. The paracristid is well developed, with a faint carnassial notch present on most specimens. On the anterior face of the trigonid, the precingulid is shelf-like, with variable development of cusps e and f. Cusp e, when present, connects with a preparacristid, descending down from the apex of the paracone (OMNH 24628 and MNA V6105). The paraconid is positioned slightly buccal, in comparison with the metaconid, and is not in line with the metaconid and entoconid. On the m3s, the talonid and trigonid are subequal in width, while on the last molar; the talonid is narrower than the trigonid, with the hypoconulid pointing straight back. The hypoconulid and entoconid are taller than the hypoconid, with the entoconid slightly taller than the hypoconulid. The hypoconulid is slightly closer to the entoconid than the hypoconid, but is not twinned. A buccal postcingulid is present and variably connects to the hypoconulid. On MNA V6105 (Fig. 5.4G), the buccal postcingulid does not connect with the hypoconulid, while on OMNH 24628 (Fig. 5.4E), the buccal postcingulid does connect, while OMNH 23107 (Fig. 5.4F) preserves a morphology in between the two extremes. On the last molar, the cristid obliqua is continuous with a distal metacristid, with both creating a well-developed crest bordering the anterobuccal portion of the deep talonid basin. Additional variation between the penultimate and ultimate lower molars includes the presence of an entocristid on OMNH 23107 and 24628. The cristid obliqua meets the back of the trigonid wall below the protocristid notch. The trigonid-talonid height differential is overall not large by comparison to outgroup taxa such as *Pappotherium*.

Comments. — *Kokopellia musicus* is remarkably similar to *Kokopellia juddi* from the Lower Cenomanian Mussentuchit Local Fauna, but differs in a number of important features. *Kokopellia musicus* is slightly smaller (Table 5.4), the paracone and metacone do not diverge, has a better-developed D cusp on the stylar shelf (no specific cusp is present in *Kokopellia juddi*), a shelf-like precingulid, and a lesser trigonid-talonid height differential. While the amount of intraspecific variation in each species is unknown, these features can unequivocally separate the early Cenomanian and middle Turonian species. The presence of a D cusp in *Kokopellia musicus* is of interest, as Cifelli and de Muizon (1997) hypothesized the absence of cusp D as primitive for marsupialforms. The presence of a D cusp in the later-occurring species *Kokopellia musicus* supports this hypothesis and suggests that the D cusp independently evolved multiple times within Cretaceous marsupialiforms (Clemens and Lillegraven, 1986; Cifelli and de Muizon, 1997). Further evidence for the independent evolution of the D cusp can be seen in the published phylogeny of Wilson et al. (2016) and Cohen (2017).

Apidelphys, gen. nov.

Etymology. — Api- after the western honey bee, *Apis mellifera*, in allusion to Utah, whose motto is "The Beehive State," and -delphys, Greek for womb, a common suffix for opossums or opossum-like marsupialiforms.

Type species. — *Apidelphys minuscularia*, gen. et. sp. nov.

Distribution. — As for the type and only species.

Diagnosis. — As for the type and only species.

Apidelphys minuscularia, gen. et sp. nov.

Fig. 5.5; Table 5.5

Etymology. — Minuscule, for the tiny size of the teeth.

Holotype. — OMNH 29090, eroded left M3.

Type locality. — OMNH locality V60, middle Turonian Smoky Hollow Member of the Straight Cliffs Formation, Garfield County, Utah.

Included material. — OMNH 29504, left M1 missing the protocone; MNA V6480, left M1 missing the protocone; OMNH 29515, left M2 missing the protocone; OMNH 29521, right M3 missing metastylar region and metacone; OMNH 24625, right m1? missing the paraconid; and MNA V7332, left mx, missing the protoconid.

Distribution. — Middle Turonian Smoky Hollow Member of the Straight Cliffs Formation, Utah.

Diagnosis. — One of the smallest tribosphenidans from the Cretaceous of North America. Most similar to the early Cenomanian *Adelodelphys muizoni*, with a buccally directed postmetacrista, a very deep ectoflexus, and a buccally projecting parastylar process on the penultimate upper molar. Differs from *Adelodelphys muizoni* in the presence of stylar cusp D and an anteroposteriorly shorter protocone. Anteroposteriorly short protocone is similar to *Aenigmadelphys archeri*, but differs in having a buccal orientation of the postmetacrista on M3, a buccally projecting parastylar lobe, and a deeper ectoflexus.

Description. — Upper molars are mostly fragmentary, with only the holotype, OMNH 29090, complete (Fig. 5.5D). The paracone and metacone are subequal in height and connected to each other at their base. The cusps are tall, slender, with the apex curved buccally, and in occlusal view, circular. The size and development of the preparacrista increases throughout the molar series, starting out small and weakly developed in M1 to salient and strongly developed in M3. The postmetacrista, on the other hand, is well developed throughout the molar series, only the direction changing from more posterobuccally oriented in M1 (Fig. 5.5A), to nearly directly buccal in M3. The anterior stylar shelf increases in buccal width posteriorly through the molar series, to the point where the parastylar lobe is positioned further buccal than the metastylar lobe in M3. The largest stylar cusp is the stylocone. Stylar cusp A and D are the only other stylar cusps present. Cusp D is wall-like, and oriented posterobuccally. The protoconal region is only preserved in the M3s, and best seen on OMNH 29521 (Fig. 5.5C). The protocone is transversely wide, but anteroposteriorly short, with sharp, gracile crests, resulting in a transversely broad trigon basin, bordered by tall, thin walls. The apex of the protocone curves buccally. The paraconule and metaconule are both present and well developed. The metaconule is positioned closer to the protocone than the paraconule, giving the protoconal region a staggered appearance. The paraconule is larger than the metaconule, and both the paraconule and metaconule protrude beyond the anterior and posterior face of the protocone, respectively. This protrusion gives the protoconal region a lobed appearance. Internal conular crests are present, but weakly developed.

Two incomplete lower molars are known, but the preserved morphology in each specimen is complementary. The talonid is narrower than the trigonid, which is consistent with the narrow protocone on the upper molars. The cusps are generally tall and sharp, with a large height differential between the trigonid and talonid. The relative heights of the paraconid and metaconid cannot be determined, as neither specimen has both cusps preserved together. The metaconid, however, is buccolingually compressed and has an anteroposteriorly longer base, while the paraconid is much narrower with a nearly cylindrical base. The difference in base size suggests that the metaconid may have been taller than the paraconid. On OMNH 24625 (Fig. 5.5E_1), a wear facet is situated along the protocristid. The cristid obliqua meets the back of the trigonid wall below the protocristid notch. The hypoconulid and entoconid are strongly twinned and tall, with the lingual wall of the talonid nearly vertical. Wear striations are present in the vertical direction along the wall-like hypoconulid-entoconid complex, indicating that the structure was most likely used as a vertical shear surface. The hypoconid is low, with the talonid basin low angled and continuous with the lingual face of the hypoconid. A postcingulid is present, but poorly developed.

Comments. — *Apidelphys minuscularia* is similar to *Adelodelphys muizoni* from the Cedar Mountain Formation, but differs in the presence of stylar cusp D (absent in *Adelodelphys*) and the proportions of the protocone. The protoconal region of *Apidelphys* is shorter anteroposteriorly, compared to *Adelodelphys*. *Apidelphys* is also much smaller (see Table 5.5). Similarities to *Adelodelphys* include in M3, postmetacrista directed buccally, very deep ectoflexus, and a buccally projecting parastylar process. *Apidelphys* is also similar to *Aenigmadelphys* in its anteroposteriorly short protoconal region. Differences between *Aenigmadelphys* and *Apidelphys* include the lingual placement of the paraconule and metaconule in *Aenigmadelphys* and greater size of the conules in *Apidelphys*, as well as the stylar shelf anatomy. The stylar shelf for *Apidelphys* is more similar to *Adelodelphys* than it is to *Aenigmadelphys*. In the M3 of *Aenigmadelphys*, the postmetacrista is oriented distobuccally, the parastylar lobe does not project buccally to the same extent as it does in *Apidelphys* and *Adelodelphys*, and the ectoflexus is shallow.

Anchistodelphys Cifelli, 1990b

Type species. — *Anchistodelphys archibaldi* Cifelli, 1990b.

Distribution. — Turonian–Campanian, Smoky Hollow Member and John Henry Member of the Straight Cliffs Formation, Utah; Wahweap Formation, Utah.

Emended diagnosis. — Following Cifelli (1990b), upper molars with a anteroposteriorly narrower protocone than *Eoalphadon*, but wider than seen in

Varalphadon. Differs from "alphadontids" in slight development or absence of cusps C and D.

Comments. — Some confusion in the literature persists on the validity of *Anchistodelphys* as a genus, mainly due to the transferral of a specimen (OMNH 20968, Cifelli 1990b: fig. 4B) previously described as *Anchistodelphys archibaldi* to *Varalphadon wahweapensis* by Johanson (1996) during the erection of the genus *Varalphadon* (Eaton, 2006b; Eaton and Cifelli, 2013). Johanson (1996) transferred OMNH 20968 to *Varalphadon wahweapensis* due to the presence of stylar cusps C and D (variably present within *Anchistodelphys*), an anteroposteriorly compressed protocone, reduced width of the anterior stylar shelf, and a well developed posterior stylar shelf. Johanson (1996) noted that stylar cusps C and D are smaller than those typically seen within *Varalphadon wahweapensis*, but attributed it to intraspecific variation. *Anchistodelphys* is considered here a valid genus that can be differentiated from *Varalphadon* using the emended diagnosis above.

?*Anchistodelphys delicatus* Cifelli, 1990a

Fig. 5.6; Table 5.6

Type specimen. — OMNH 20374, left M2 or 3, lacking the protocone and anterior corner of the stylar shelf.

Type locality. — OMNH locality V4, middle Turonian Smoky Hollow Member of the Straight Cliffs Formation, Garfield County, Utah.

Included specimens. — OMNH 20375, left M4, missing the protocone; OMNH 20034, right M4, missing the protocone; OMNH 25502, right M1, missing the metacone and metastylar region; OMNH 22996, right m2, missing the entoconid and hypoconulid; OMNH 20384, left m1; MNA V5786, left m1; MNA V5788, eroded left m1; OMNH 26104, right m2; OMNH 68768, left m2; OMNH 20377, left m3, missing the paraconid; OMNH 23105, right m3; OMNH 68765, left m3, missing the apices of the protoconid, paraconid, and metaconid; OMNH 29055, left m3; OMNH 68769, left m3, missing the apex of the paraconid and protoconid; OMNH 29496, left m4; and OMNH 69348, right m4; MNA V5688, left eroded m4.

Description. — The only new information available for the upper dentition is from a single specimen, OMNH 25502 (Fig. 5.6A), a first molar missing the metacone and metastylar region. The overlapping morphology with the holotype, OMNH 20374, agrees with the referral of OMNH 25502 to the same species, with a straight centrocrista, a slightly convex labial face of the paracone, and the presence of a stylar cusp C. OMNH 25502 adds important morphological information regarding the construction of the protocone and parastylar region. The protocone is tall and sharp, with the apex leaning slightly labially. Both paraconule and metaconule are present, with the paraconule closer to the protocone. The paraconule has a sharp internal crista, but the metaconule is damaged, so the construction of the internal cristae cannot be ascertained on this specimen. The trigon basin is deep and is confined mesially by a wall-like postparaconular crista. The preparacrista terminates at the labial margin of the paracone, and does not connect directly with the parastyle. Stylar cusp B is present, well developed, and connected to the paracone by the preparacrista. A small cuspule is present posterior to stylar cusp B and anterior to the ectoflexus.

Newly-discovered lower molars support allocation of the seven specimens tentatively referred to this species by Cifelli (1990a) possible. Lower molars can be attributed to ?*Anchistodelphys delicatus* based on size and the *Alphadon*-like construction of the lower molars. As is typical for marsupialiforms, the first molars are noticeably smaller than m2–4 (Table 5.6), have an open trigonid, and a wider talonid than trigonid (Fig. 5.6B_1). For all the lower molars, the protoconid dominates the trigonid and is the tallest cusp. The metaconid is larger and taller than the paraconid, which is low and positioned anterior to the protoconid (Fig. 5.6D_2). A carnassial notch is present in the paracristid, but not the protocristid. The talonid is well developed, with the hypoconulid and entoconid "twinned." The entoconid is the tallest cusp. The hypoconid is taller than the hypoconulid, and the cristid obliqua attaches to the trigonid wall below the protocristid notch. Going through the molar series, typical marsupialiform characters can be used to differentiate molar loci, such as relative talonid/trigonid width, openness of the trigonid, and anteroposterior length of the talonid.

Comments. — ?*Anchistodelphys delicatus* is one of the smallest mammals in the fauna, larger only than *Apidelphys minuscularia*. With the larger sample size now available, the issue with the original assignment of the lower molars to the upper molars can now be resolved. No other marsupialiform is within the same size range, making it plausible (along with the available morphological evidence) that all molars described in Cifelli

(1990a) can be assigned to the uppers, along with a number of additional specimens. The additional specimens also help to elucidate the variation in the lower molars discussed by Cifelli (1990a) in the original description based upon tooth loci, with the exception of MNA V5787 and OMNH 20302. These two specimens that were tentatively referred to the species cannot be confirmed as belonging to the same taxon. For the upper molars, only one specimen can be added to the hypodigm, an incomplete first molar. Without further evidence from the upper molars, ?*Anchistodephys delicatus* cannot be confirmed as belonging to the genus.

Discussion

The marsupialiforms treated herein conclude description of the mammalian fauna from the Turonian-aged Smoky Hollow Member of the Straight Cliffs Formation. The Turonian is a time interval for which terrestrial fossil-bearing horizons are rare globally. The Smoky Hollow Member of the Straight Cliffs Formation has yielded the most diverse array of terrestrial microvertebrates hailing from the Turonian. Within North America, the Smoky Hollow fauna is especially important owing to the scarcity of terrestrial microvertebrates from the succeeding Coniacian–Santonian interval: hence, the Turonian is the only well-represented interval between the Cenomanian and terminal Santonian. Of the 2977 specimens catalogued in the OMNH collections, 1335 are mammals. The virtues of such large samples are fairly obvious: they increase likelihood of recovering rare taxa, providing a more complete understanding of a given fauna; and they increase sampling for individual taxa, providing some basis for understanding variation and increasing morphological representation (through recovery of informative individual specimens and more complete representation of an entire dentition). In the case of the Smoky Hollow Member, sampling of rare taxa has permitted recognition of the appearance and earliest radiations of stagodontid and pediomyoid marsupialiforms, as well as the first North American appearance of dentally advanced eutherians (Cohen, 2017; Cohen and Cifelli, in prep; Cohen and Davis, in prep). To date, the mammalian fauna of the Smoky Hollow Member includes at least 23 distinct taxa (Table 5.7), rivaling the well-sampled earliest Cenomanian Mussentuchit Local Fauna and latest Cretaceous NALMAs (Cifelli et al., 2004, 2016; Kielan-Jaworowska et al., 2004).

While the Smoky Hollow fauna is similar in size to the earliest Cenomanian Mussentuchit Local Fauna, the taxonomic makeup of the faunas differ (Table 5.7; Cifelli et al., 2016: table 2). Prior to the Turonian, Cretaceous tribosphenidan faunas are characterized by low taxonomic diversity and abundance (Cifelli and Davis, 2015; Cifelli et al., 2016). Excluding multituberculates (most Early Cretaceous, North American taxa remain unpublished), archaic groups, including the triconodontids and spalacotheriids, are important or dominant elements in Albian–early Cenomanian faunas (Cifelli et al., 2016). Composition changed dramatically by the Turonian, where tribosphenidans are more taxonomically and morphologically diverse, and comprise more than half of total species diversity (Table 5.7). The Turonian marks the first appearance of taxonomic groups more typical of later Late Cretaceous faunas, including dentally advanced eutherians, stagodontids, aquiladelphids, and pediomyids. Of particular interest from the Smoky Hollow fauna include the presence of eutherians and a deltatheroidan (Cohen and Cifelli, in prep; Cifelli, 1990a). Both of these groups are known from both earlier and later faunas, but appear to have undergone a local extinction in North America during the Cenomanian (deltatheroidans are rare elements from the Late Cretaceous of North America, so a collection bias cannot be ruled out) (Cifelli et al., 2016; Fox, 1974; Fox et al., 2007; Wilson and Riedel, 2010). The reappearance of these taxa suggests that an immigration event may have taken place between Asia and North America by at least the middle Turonian, as both groups have strong affinities with Asian taxa (Cohen and Cifelli, in prep; but see Wilson and Riedel, 2010 for an argument against a second immigration event for deltatheroidans).

Tribosphenidans from the late Early and early Late Cretaceous of North America tend to be basal and unspecialized in terms of tooth morphology, with some notable exceptions, such as *Argaliatherium robustum*, *Culicolestes kielanae*, *Pariadens*, and *Dakotadens* spp. All of these taxa depart from the typical insectivorous tribosphenic tooth type, with more robust cusps and larger size (Cifelli and Davis, 2015; Cifelli et al., 2016). This departure is further developed during the Turonian, with the appearance of increasingly specialized lineages, including the pediomyoids and stagodontids (Cohen, 2017; Cohen and Davis, in prep). However, the Turonian also exhibits a diversification of more typical insectivorous tribosphenidans, including the "alphadontids", *Kokopellia,* ?*Anchistodelphys*, and *Apidelphys*. The diversification of these generalized, insectivorous taxa highlights the change within the mammalian fauna from the Cenomanian to the Turonian, with the reduction in diversity and abundance of spalacotheriid symmetrodonts (Cifelli et al., 2016). Spalacotheriids are generally small, and hypothesized to have been strictly insectivorous (Cifelli and Gordon, 1999; Cifelli and Madsen, 1999). It is unknown whether insectivorous tribosphenidans directly outcompeted spalacotheriids or whether it was a passive replacement, with insectivorous tribosphenidans radiating into the empty niches left behind by spalacotheriids. Either way, the increase in insectivorous tribosphenidans, including one of the smallest tribosphenidans from the Cretaceous of North America (*Apidelphys minuscularia*) is most related to the reduction in diversity and abundance of spalacotheriids from southern Utah.

In addition to including elements from later Cretaceous faunas, two genera from the Cenomanian of North America are present in the Smoky Hollow fauna: *Kokopellia* and *Eoalphadon*. The presence of these taxa serves to connect the typical early Late Cretaceous fauna with later Cretaceous faunas, highlighting a faunal turnover from basal, insectivorous tribosphenidans to more dentally advanced tribosphenidans, such as: aquiladelphids, pediomyids, stagodontids, and eutherians (Fig. 5.7). Interestingly, Cifelli and Gordon (1999), Eaton (1995), and Nydam (2013) found within the Smoky Hollow fauna a similar pattern for spalacotheriids, multituberculates, and squamates, where elements from both older and younger faunas are present together. Squamates appear to parallel mammals in the Smoky Hollow fauna with characteristics from both the Cenomanian and the Campanian–Maastrichtian, and high taxonomic diversity (Nydam, 2013). Overall, mammals from the Smoky Hollow fauna exhibits transitional elements between the earliest Late Cretaceous and later Cretaceous faunas from North America, comprising the transition from archaic lineage-dominated to tribosphenidan-dominated, and the transition from solely basal tribosphenidans to including dentally-advanced tribosphenidans. The presence of elements from later Cretaceous faunas indicates that, at least in part, the taxonomic framework of the Campanian–Maastrichtian mammalian faunas had been established.

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FIGURE 5.1. ***Varalphadon*** **sp. A, OMNH 29088, right M1 in, occlusal stereopair. B, OMNH 69345, right m1, in occlusal stereopair (B_1) and lingual (B_2) views. C, OMNH 68755, left M3?, in occlusal stereopair. D, MNA 7334, left m2, in occlusal stereopair (D_1) and lingual (D_2) views. E, OMNH 25493, left m3, in occlusal stereopair (E_1) and lingual (E_2) views. F, OMNH 29498, left m4, in occlusal stereopair (F_1) and lingual (F_2) views.**

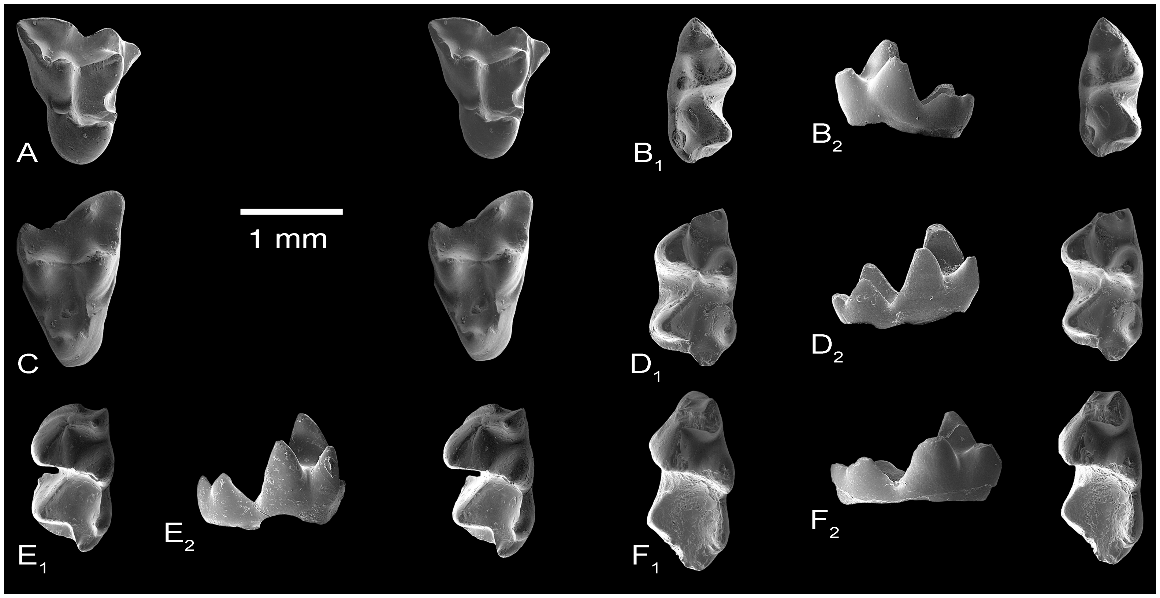

FIGURE 5.2. ***Eoalphadon lillegraveni*. A, MNA V6124, left M3, in occlusal stereopair. B, OMNH 29084, right M4, in occlusal stereopair. C, OMNH 26107, left m4?, in occlusal stereopair (C_1) and lingual (C_2) views. D, OMNH 29064, right mx, in occlusal stereopair (D_1) and lingual (D_2) views.**

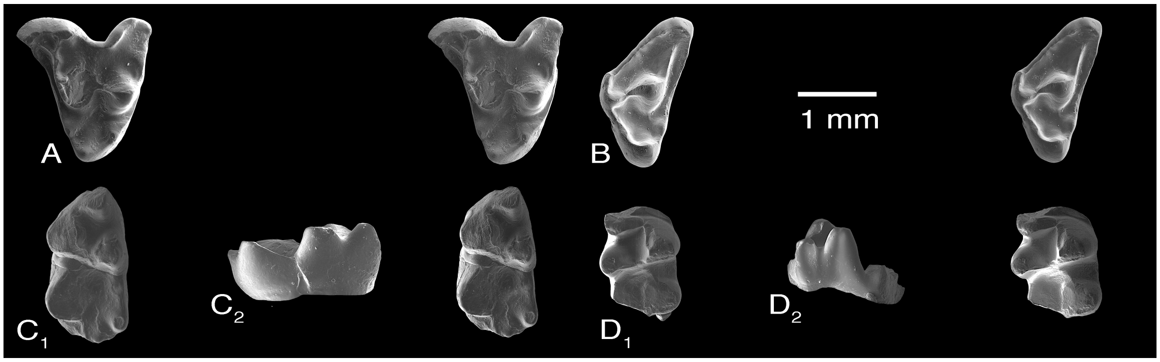

FIGURE 5.3. ***Eoalphadon clemensi*****. A, OMNH 65955, right M1, in occlusal stereopair. B, MNA V7559, left M2, in occlusal stereopair. C, OMNH 29080, left M2, in occlusal stereopair. D, OMNH 29052, left m1, in occlusal stereopair (D_1) and lingual (D_2) views. E, MNA V6753, left M4, in occlusal stereopair. F, OMNH 29051, left m2, in occlusal stereopair (F_1) and lingual (F_2) views. G, OMNH 69347, left m3, in occlusal stereopair (G_1) and lingual (G_2) views.**

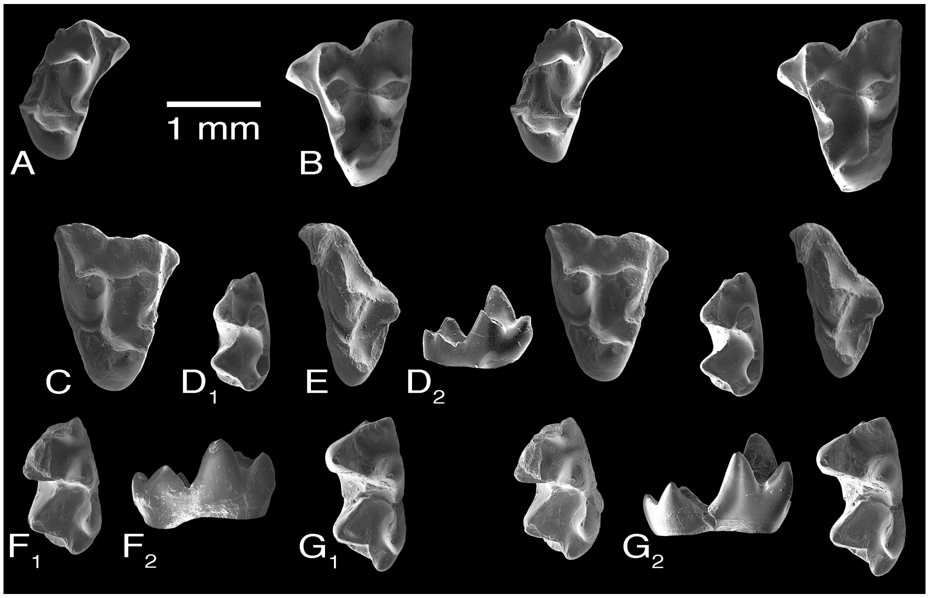

FIGURE 5.4. ***Kokopellia musicus*** **sp. nov. A, OMNH 24634, the holotype, left M3, in occlusal stereopair. B, OMNH 69343, right M3, in occlusal stereopair. C, OMNH 29083, right M4, in occlusal stereopair. D, OMNH 29046, right p3, in occlusal stereopair (D_1) and lingual (D_2) views. E, OMNH 24628, left m3, in occlusal stereopair (E_1) and lingual (E_2) views. F, OMNH 23107, right m3, in occlusal stereopair (F_1) and lingual (F_2) views. G, MNA V6105, right m4, in occlusal stereopair (G_1) and lingual (G_2) views.**

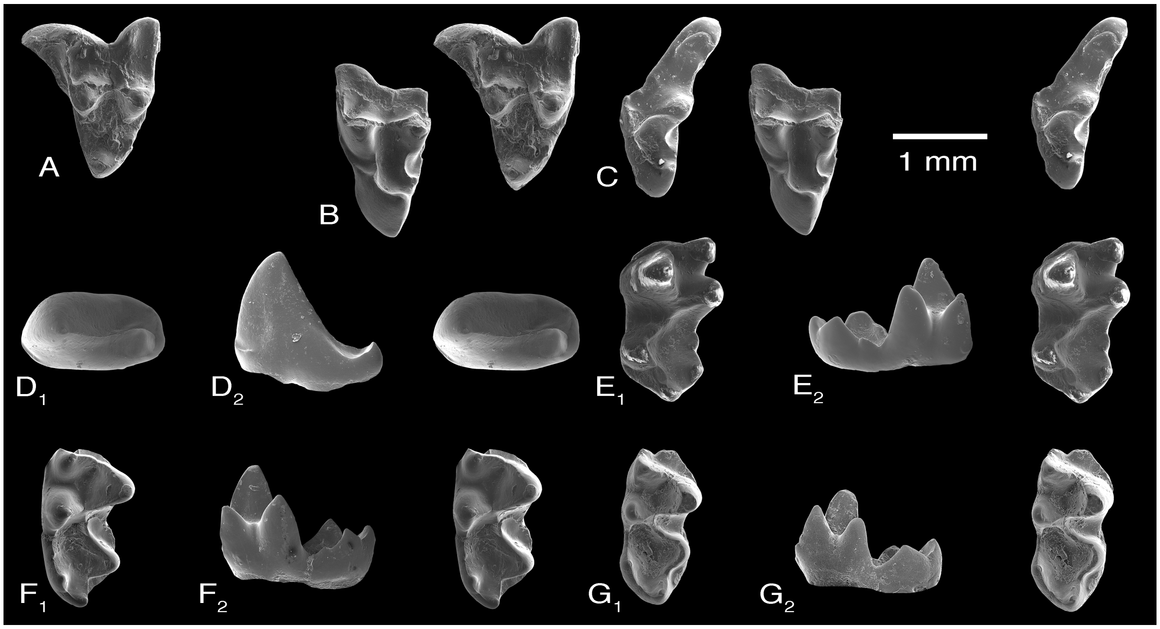

FIGURE 5.5. ***Apidelphys minuscularia*** **gen. et sp. nov. A, OMNH 29504, left M1, in occlusal stereopair. B, OMNH 29515, left M2, in occlusal stereopair. C, OMNH 29521, right M3, in occlusal stereopair. D, OMNH 29090, the holotype, left M3, in occlusal stereopair. E, OMNH 24625, right mx, in occlusal stereopair (E_1) and lingual (E_2) views. F, MNA V7332, right mx, in occlusal stereopair (F_1) and lingual (F_2) views.**

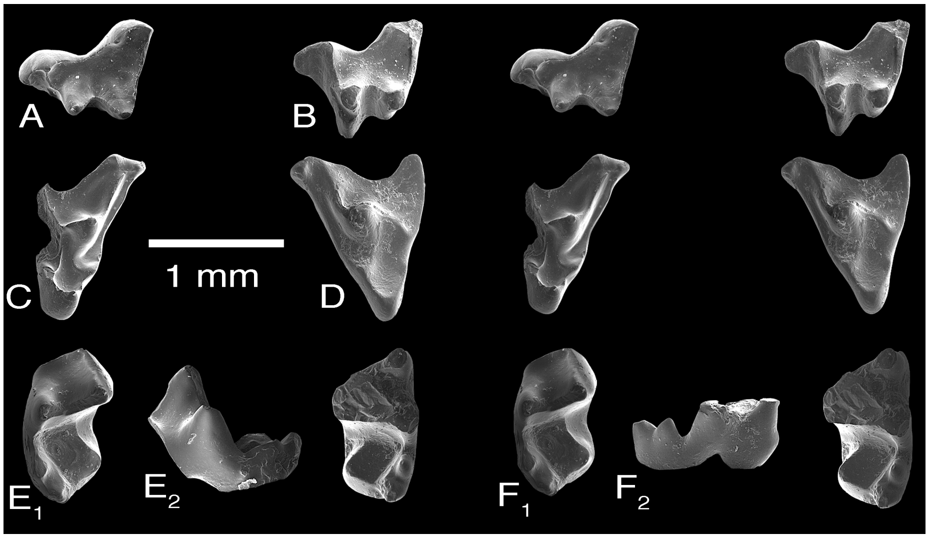

FIGURE 5.6. ?*Anchistodelphys delicatus*. A, OMNH 25502, right m1, in occlusal stereopair. B, OMNH 20384, left m1, in occlusal stereopair (B_1) and lingual (B_2) views. C, OMNH 22996, right m2, in occlusal stereopair (C_1) and lingual (C_2) views. D, OMNH 23105, right m3, in occlusal stereopair (D_1) and lingual (D_2) views. E, OMNH 69348, right m4, in occlusal stereopair (E_1) and lingual (E_2) views.

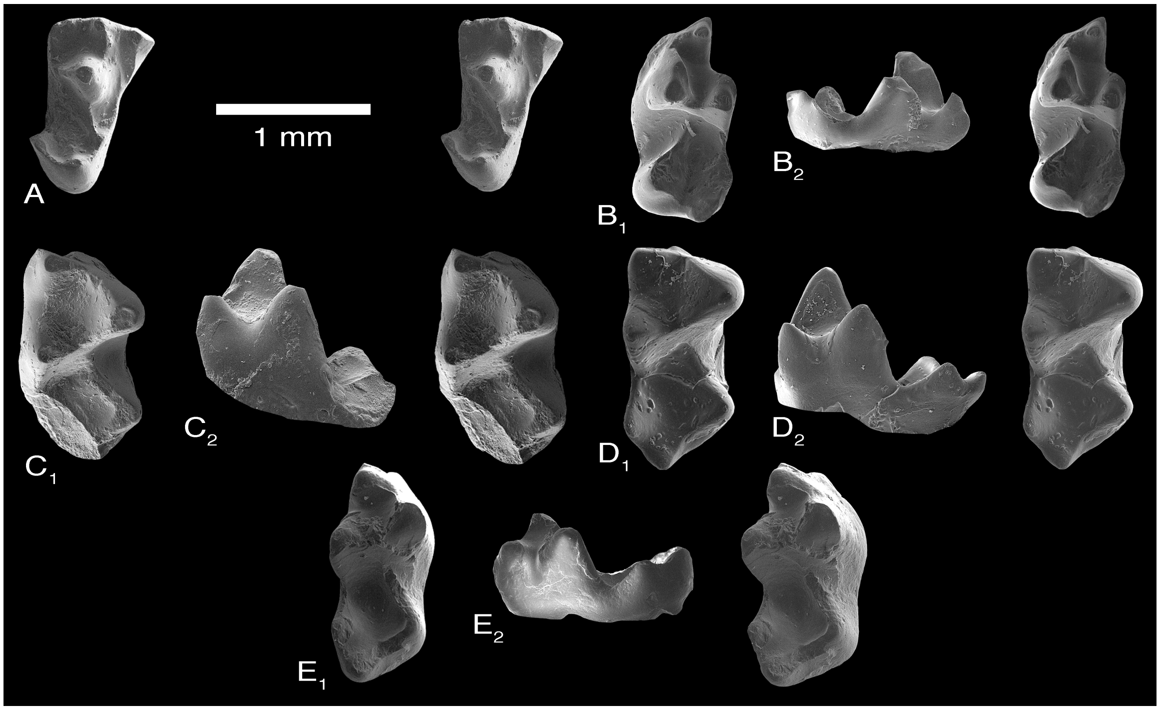

FIGURE 5.7. Tribosphenidan mammals from the Smoky Hollow fauna and affinities with older and younger faunas of North America. Mammal faunas in bold indicate NALMAs. Dark bars represent definitive occurrences, and dashed lines represent inferred occurrences.

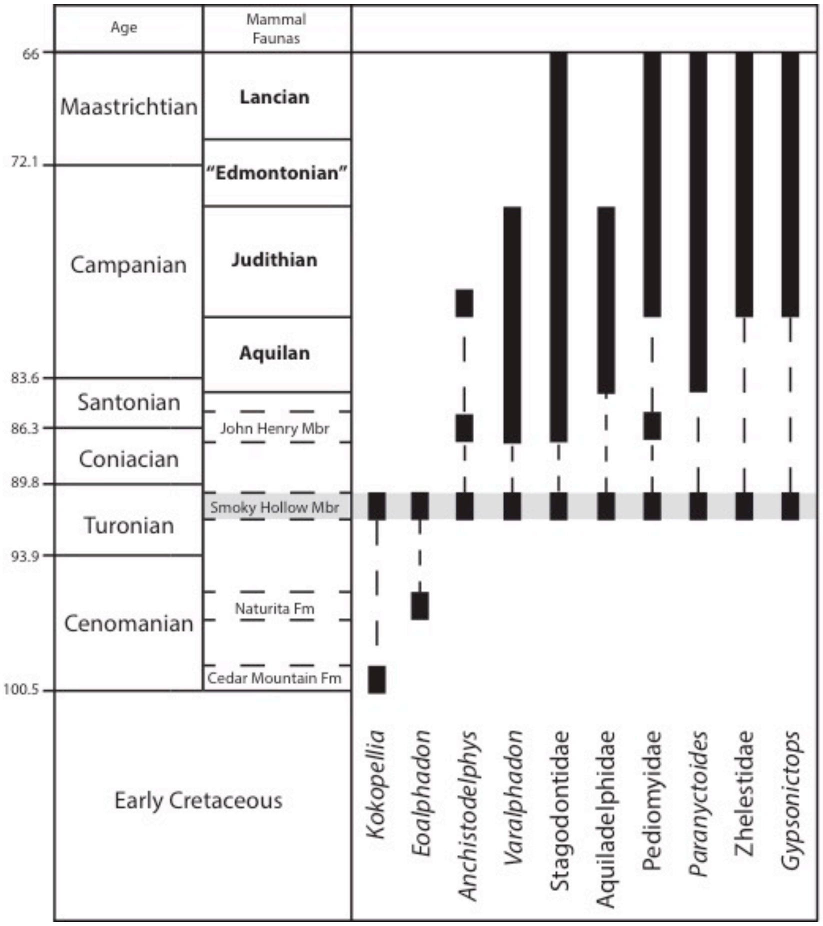

Table 5.1. Dental measurements (in mm) of *Varalphadon* sp. ANW = anterior width, POW = posterior width, AP = anteroposterior length.

Specimen	Tooth	ANW	POW	AP
OMNH 29088	M1	1.48	1.61	1.47
OMNH 29073	M1	1.41	1.54	1.59
OMNH 29076	M1	1.73	1.80	1.53
OMNH 29082	M1	1.45	1.63	1.59
OMNH 29074	M1	1.63	—	—
OMNH 29513	M1	—	—	1.58
OMNH 26112	M1	1.40	1.58	1.43
MNA V7351	M2	1.58	1.74	1.63
MNA V7338	M1	1.57	1.83	1.59
MNA V7347	M2	1.64	1.81	—
OMNH 68755	M3?	1.71	1.90	—
OMNH 26115	Mx	—	1.63	—
OMNH 26108	dp3	0.59	0.56	1.22
MNA V7336	dp3	0.48	0.43	1.16
MNA V7342	dp3	0.50	0.60	1.25
OMNH 69345	m1	0.76	0.75	1.51
OMNH 29059	m1	0.72	0.72	1.50
OMNH 29069	m1	0.77	0.77	1.50
OMNH 29053	m2	0.97	0.99	1.75

Table 5.1. (Continued)

Specimen	Tooth	ANW	POW	AP
MNA V7334	m2	0.94	1.01	1.63
MNA V7343	m2	1.02	0.97	1.65
OMNH 29062	m2	1.04	1.04	1.82
OMNH 29057	m2	1.23	1.13	1.71
OMNH 29058	m2	0.87	0.88	1.57
MNA V6949	m2	0.96	0.94	1.72
OMNH 25494	m2	1.12	—	—
OMNH 23101	m3	1.08	1.06	1.75
OMNH 25493	m3	1.01	1.01	1.70
OMNH 29071	m3	0.97	1.01	1.65
OMNH 29072	m3	1.09	1.01	1.71
OMNH 20380	m3	1.07	1.07	—
OMNH 29498	m4	0.98	0.92	1.88
OMNH 29070	m4	0.92	0.81	1.67
OMNH 29067	m4	1.17	0.85	1.78
OMNH 68780	m4	0.96	0.82	1.68
OMNH 29054	m4	1.01	0.91	1.81
OMNH 29500	mx	1.01	—	—
OMNH 29060	mx	1.03	1.10	1.64
OMNH 68774	mx	1.05	1.01	1.63

Table 5.2. Dental measurements (in mm) of *Eoalphadon lillegraveni*.

Specimen	Tooth	ANW	POW	AP
MNA V6124	M3	2.28	2.39	2.13
OMNH 23114	M4	2.19	1.72	1.69
OMNH 29064	m3	1.26	—	—
OMNH 26107	m4?	1.07	0.95	1.83

Table 5.3. Dental measurements (in mm) of *Eoalphadon clemensi*.

Specimen	Tooth	ANW	POW	AP
OMNH 65955	M1	1.72	—	—
OMNH 29087	M2	1.86	1.97	1.87
MNA V7558	M2	1.94	2.17	1.86
OMNH 29085	M2	1.85	1.92	1.79
OMNH 29080	M2	1.88	2.00	1.71
MNA V7559	M2	1.95	2.22	1.88
OMNH 25507	M2	—	—	1.81
OMNH 29517	M2	—	—	1.76
OMNH 20373	M3	—	—	1.63
OMNH 68759	M3	—	—	1.90
MNA V6895	M4	1.95	1.19	1.23
MNA V6753	M4	1.96	1.28	1.32
MNA V6355	Mx	—	2.03	—
OMNH 29516	Mx	1.87	—	—
OMNH 69344	Mx	—	2.12	—
OMNH 26109	dp3	0.64	0.67	1.44
OMNH 29052	m1	0.85	0.85	1.55
MNA V6125	m2	1.11	1.12	1.83
OMNH 29051	m2	1.09	1.07	1.77

Table 5.3. (Continued)

Specimen	Tooth	ANW	POW	AP
OMNH 69347	m3	1.07	1.03	1.90
MNA V6115	m3	1.12	1.03	1.92
OMNH 23108	m3	0.92	0.89	1.67
OMNH 29068	mx	1.13	1.11	1.88
OMNH 23102	mx	1.09	1.08	1.69
MNA V6126	mx	1.03	1.03	1.82
OMNH 23106	mx	0.98	1.02	1.73

Table 5.4. Dental measurements (in mm) of *Kokopellia musicus* sp. nov. * denotes holotype.

Specimen	Tooth	ANW	POW	AP
OMNH 24634*	M3	2.18	2.23	1.98
OMNH 69343	M3	1.88	2.12	—
OMNH 29083	M4	1.97	1.21	1.21
OMNH 29046	p3	0.97	—	1.65
OMNH 23107	m3	1.06	0.94	1.81
OMNH 24628	m3	1.10	0.96	1.94
MNA V6105	m4	1.06	0.94	1.87
OMNH 68770	mx	1.14	—	—
OMNH 20128	dp3	0.75	0.74	1.74

Table 5.5. Dental measurements (in mm) of *Apidelphys minuscularia* gen. et sp. nov. * denotes holotype.

Specimen	Tooth	ANW	POW	AP
OMNH 29504	M1	—	—	1.12
MNA V6480	M1	—	—	1.11
OMNH 29515	M2	—	—	1.14
OMNH 29521	M3	1.43	—	—
OMNH 29090*	M3	1.43	1.35	1.19
OMNH 24625	m1?	0.73	0.73	—
MNA V7332	mx	0.75	0.63	1.19

Table 5.6. Dental measurements (in mm) of ?*Anchistodelphys delicatus*. **indicates measurements taken from Cifelli, 1990a.

Specimen	Tooth	ANW	POW	AP
OMNH 25502	M1	1.20	—	—
OMNH 20384**	m1	0.76	0.71	1.35
MNA V5788**	m1	0.67	0.70	1.30
OMNH 26104	m2	0.98	0.96	1.65
OMNH 22996	m2	0.85	—	—
OMNH 68768	m2	0.87	0.80	1.54
OMNH 20377**	m3	0.90	0.94	—
OMNH 23105	m3	0.84	0.78	1.51
OMNH 68765	m3	0.97	0.84	1.60
OMNH 29055	m3	0.87	0.79	1.51
OMNH 68769	m3	0.85	0.83	1.68
OMNH 29496	m4	0.90	0.73	1.55
OMNH 69348	m4	0.72	0.65	1.46
MNA V5688**	m4	0.75	0.86	1.72

Table 5.7. Mammals of the Smoky Hollow Fauna.

- Multituberculata Cope, 1884
  - Cimolodontidae indet.
  - ?Taeniolabididae indet.
  - Family incertae sedis
    - cf. *Paracimexomys* sp., cf. *P. robinsoni* Eaton and Nelson 1991
    - *Bryceomys fumosus* Eaton, 1995
    - *Bryceomys hadrosus* Eaton, 1995
- Trechnotheria McKenna, 1975
  - Family, gen., et sp. indet.
  - Spalacotheriidae Marsh, 1887
    - *Spalacotheridium mckennai* Cifelli, 1990a
    - *Symmetrodontoides oligodontos* Cifello, 1990a
- Deltatheroida Kielan-Jaworowska, 1982
  - Deltatheridiidae Gregory and Simpson, 1926
- Marsupialiformes Vullo et al., 2009
  - "Alphadontidae" Marshall et al., 1990
    - *Varalphadon* sp.
    - *Eoalphadon clemensi* Eaton, 1993
    - *Eoalphadon lillegraveni* Eaton, 1993
  - Stagodontidae Marsh, 1889
    - *Fumodelphodon pulveris* Cohen, 2017
    - *Hoodootherium praeceps* Cohen, 2017

Table 5.7. (Continued)

Incertae sedis

?*Anchistodelphys delicatus* Cifelli, 1990a

Apidelphys minuscularia gen. et sp. nov.

Kokopellia musicus sp. nov.

Pediomyoidea Simpson, 1927

Aquiladelphidae Davis, 2007

Scalaria diversicuspis Cohen and Davis, in prep

Scalaria aquilana Cohen and Davis, in prep

Pediomyidae Simpson, 1927

Leptalestes sp.

Eutheria Gill, 1872

Gypsonictopidae Van Valen, 1967

Gypsonictops lewisi Sahni, 1972

?Zhelestidae Nessov, 1985

Incertae sedis

Paranyctoides sp