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PIPESTONEOMYIDAE, A NEW FAMILY OF FOSSIL RODENTS (MAMMALIA) FROM THE DUCHESNEAN (LATE MIDDLE EOCENE, BARTONIAN) TO ORELLAN (EARLY OLIGOCENE, PRIABONIAN) OF NORTH AMERICA

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ABSTRACT—Additional specimens of the problematical rodent *Pipestoneomys* Donahoe, 1956, have allowed for recognition of a new family, Pipestoneomyidae. A new genus and species of pipestoneomyid is recognized from the late middle Eocene (Duchesnean North American Land Mammal Age; Bartonian), *Argorheomys septendrionalis*, which is morphologically more primitive than *Pipestoneomys* and demonstrates that this new family has been distinct since the Duchesnean. The Pipestoneomyidae share a number of derived characters with the Geomorpha, especially the two-part inner layer of incisor enamel of the Eoymidae. The Pipestoneomyidae differ from the Eomyidae in lacking the basic "omega" pattern of the cheek teeth of the former, so are in the Eomyoidea as a distinct family.

INTRODUCTION

DONAHOE (1956) NAMED a new genus and species of rodent from the Chadronian (late Eocene, Priabonian) of Montana, *Pipestoneomys bisulcatus*, and referred it to the family Aplodontidae. Alf (1962) named a second species, *P. pattersoni*, from the Chadronian of Nebraska and suggested that the genus was more likely a beaver (Family Castoridae). Some later authors have followed the Alf (1962) referral to the Castoroidea, but with question (Black 1965; Flynn and Jacobs, 2008). However, Wood (1980) included the genus in "cf. Aplodontidae" and synonymized the two named species under *P. bisulcatus*. McKenna and Bell (1997) included *Pipestoneomys* in a primitive suborder of rodents, the Sciruavida, but did not include it in any recognized family. All of these allocations were based on a limited knowledge of *Pipestoneomys*. Both named species being represented only by several isolated teeth and a few maxillary fragments from Montana and Nebraska. Additional and more complete specimens from the type locality of *P. bisulcatus*, as well as other localities in Montana, consist of complete mandibles with lower incisors and more complete maxillae that have allowed for a better understanding of the genus.

Dental terminology is modified from that of Wood and Wilson (1936; Fig. 1). Capital letters indicate upper teeth; lowercase letters indicate lower teeth (e.g., M1 or m1). Abbreviations for institutions: CM, Carnegie Museum of Natural History; FMNH, Field Museum of Natural History; MCZ, Museum of Comparative Zoology, Harvard; RSM, Royal Saskatchewan Museum; USNM, National Museum of Natural History, Smithsonian.

SYSTEMATIC PALEONTOLOGY

Order RODENTIA Bowdich, 1821
Infraorder GEOMORPHA Thaler, 1966
Superfamily EOMYOIDEA Winge, 1887
Family PIPESTONEOMYIDAE new family

Included genera.—*Pipestoneomys* Donahoe, 1956, and *Agrorheomys* n. gen.

Diagnosis.—Rodents with sciuromorphous skull and sciurognathous mandible; anterior end of masseteric fossa expanded laterally on mandible; ascending ramus widely separated from tooth row; plane of angular process inclined medioventrally making medial surface of mandible strongly concave, tooth row not vertically aligned with lower incisor; cheek teeth brachydont to mesodont and lophate; dental formula 1/1–0/0–1/1–3/3; P4–p4 progressively larger relative to M1/m1; distinct anteroconid on p4; uniserial microstructure of incisor enamel with two-part *portio interna* but lacking a longitudinal ridge along the anterolateral edge (typical of eomyids); molars decrease in size from M1/m1 to M3/m3; ectoloph complete on upper cheek teeth; endolophid complete on lower cheek teeth; hypoflexus continuous to anterobuccal corner of tooth on uppers, hypoflexid continuous to posterolingual corner of tooth on lowers; metalophulid I forms anterior cingulid on lower molars; mesoconid on lower cheek teeth enlarged and positioned at center of talonid basin.

Occurrence.—Duchesnean (late middle Eocene, Bartonian) of Saskatchewan, Chadronian (late Eocene, Priabonian) of Montana, North Dakota, Nebraska, and Orellan (early Oligocene, early Rupelian) of Nebraska.

Remarks.—Although the zygomassteric structure of the skull (sciuromorphy; small, unmodified infraorbital foramen; long infraorbitral canal; sciurognathous mandible), dental formula (P4/p4 always present), and uniserial microstructure of the incisor enamel with two-part *portio interna* of the Pipestoneomyidae are shared by the Eomyidae (Wahlert and Koenigswald, 1985; Flynn, 2008), the former is maintained as a distinct family because of the drastically different morphology of the cheek teeth (see Conclusions).

GENUS PIPESTONEOMYS DONAHOE, 1956

Type species.—*Pipestoneomys bisulcatus* Donahoe, 1956.
Other species.—*P. pattersoni* Alf, 1962.

Diagnosis.—Pipestoneomyid with mesodont cheek teeth; P3 lacking on all species; P4 larger than M1; anteriorly expanded anterocone on P4; hypoflexus (-id) continuous on molars until late stages of wear.

Occurrence.—Chadronian (late Eocene, Bartonian) of Montana, Nebraska, North Dakota, Saskatchewan, and Orellan (earliest Oligocene, early Rupelian) of Nebraska.

PIPESTONEOMYS BISULCATUS DONAHOE, 1956
Figures 2–5

2011 *Pipestoneomys* sp. Kihm, p. 86, figs. 4H, 4I.

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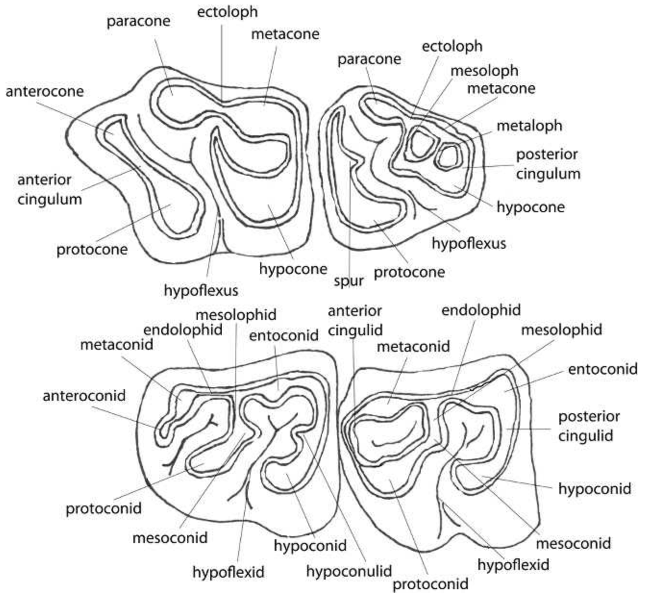

FIGURE *1*—Nomenclature used for cheek teeth of *Pipestoneomys*. Left P4-M1 (above) and left p4-m1 (below). Anterior to left.

Diagnosis.—Largest species of the genus; p4 larger than m1; M2/m2 larger relative to M1/m1 than in *P. pattersoni*; p4 wider relative to length than that of *P. pattersoni*; M1 wider than long.

Description.—The only evidence of the skull of *Pipestoneomys* is a portion of the maxilla preserved on two specimens, CM 18814 and CM 18815, both consisting of a P4 and the base of the zygomatic arch (Fig. 2). The zygomatic plate is tilted nearly vertically in a sciuromorphous condition. The ventral border of the infraorbital foramen is preserved; it is small and apparently oval. Although not complete, the infraorbital canal on CM 18815 measures 2 mm in length, similar to that of other Geomorpha that are characterized by long infraorbital canals (Wahlert, 1978, 1985).

All cheek teeth are mesodont in crown height. They are widest at the base and taper towards the occlusal surface. As noted by Alf (1962) for *Pipestoneomys pattersoni*, there is no evidence of an alveolus on any of the maxillary fragments for a P3. P4 is the largest of the upper cheek teeth. It is widest at the paracone and tapers posteriorly from that point. The anterocone is as large as the paracone or protocone and is in the anterobuccal corner of the tooth. It is directly attached to the protocone via the anterior cingulum. On the least worn specimen, CM 18814, there is a minute re-entrant valley on the lingual side of the anterocone, a small pit on the buccal side of the protocone, and the posterior wall of the anterior cingulum is irregular. After slightly more wear, these two small re-entrants are worn into minute, circular enamel lakes. After only moderate wear, any vestige of these valleys or lakes is eliminated and both the protocone and anterocone have large circular wear facets, and the posterior margin of the anterior cingulum is a smooth loph. The loph connecting the anterocone and protocone is separated from the remainder of the tooth by a deep valley that extends obliquely (anterobuccal to posterolingual) across the entire tooth (=hypoflexus). The paracone is circular in occlusal outline. The metacone is compressed into a slightly oblique loph at the posterobuccal corner of the tooth that connects to the center of the paracone anteriorly. The hypocone is crescentic in shape. Anteriorly, a short loph extends buccally from the hypocone. In some specimens, it fuses with the union of the paracone and metacone, whereas in others is ends just before meeting it. The

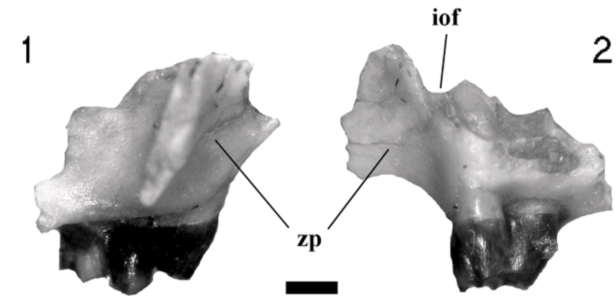

FIGURE *2*—*1, 2*, right maxillary fragment of *Pipestoneomys bisulcatus* with P4, CM 18815: *1*, lateral view; *2*, anterior view. Abbreviations: iof=infraorbital foramen; zp=zygomatic plate. Scale=1 mm.

posterior cingulum is continuous from the posterior side of the metacone to the posterior side of the hypocone, isolating a small crescentic enamel lake between the metacone and hypocone.

M1 is slightly wider than long, its greatest width being at the anterior margin of the tooth, and tapering posteirorly. In general appearance, M1 is similar to P4 but lacks the enlarged anterocone. The anterior cingulum is attached directly to a crescentic protocone and bounded posteriorly by a continuous but narrow hypoflexus. In worn specimens, the paracone unites buccally with the buccal end of the anterior cingulum. There is a distinct posteriorly directed spur that originates at the center of the anterior cingulum that divides the hypoflexus into two smaller lakes. The buccal cusps are oval in occlusal outline being slightly transversely compressed; the metacone more than the paracone. The hypocone is crescentic and connected anteriorly to the lingual side of the paracone by an oblique loph. At the center of this loph is a mesocone that corresponds with the spur from the anterior cingulum. However, even on the most worn specimens, the mesocone and spur do not fuse, leaving the hypoflexus continuous to the anterobuccal corner of the tooth where it is either open or closed by the connection of the paracone and anterior cingulum. The hypocone connects to the metacone via two lophs, a short metaloph that runs from the anterobuccal margin of the hypocone to the posterobuccal corner of the metacone, and via the posterior cingulum that wraps around the posterior edge of the tooth. These connections produce two minute enamel lakes between the metacone and hypocone. In the holotype, FMNH 409, the anterior connection is lacking (Donahoe, 1956, fig. 1A; Alf, 1962, fig. 2). There is a small but distinct metastyle at the posterobuccal corner of the tooth that is connected to a low ridge that runs dorsally to the base of the crown.

The only reported M2 is that of the holotype, FMNH 409, best figured by Alf (1962, fig. 2). It is nearly identical to M1 in morphology but is slightly smaller. M3 is markedly smaller than the anterior molars and is nearly circular in occlusal outline. As with M2, the only known M3 of the species is in the holotype. The occlusal surface consists of a number of isolated enamel lakes, roughly corresponding to those of M1 and M2. The only distinguishable cusps are the paracone and protocone (Alf, 1962, fig. 2).

The mandible (Fig. 4) is relatively shallow but robust (transversely thick). The condyles and angle of the mandible are not preserved in any of the available specimens. The body of the mandible is concave medially. The ascending ramus is angled away from the alveolar margin leaving a wide furrow between the medial wall of the ascending ramus and the tooth row. The rotation of the horizontal ramus of the mandible has moved the tooth row out of alignment with the line of the incisor, similar to

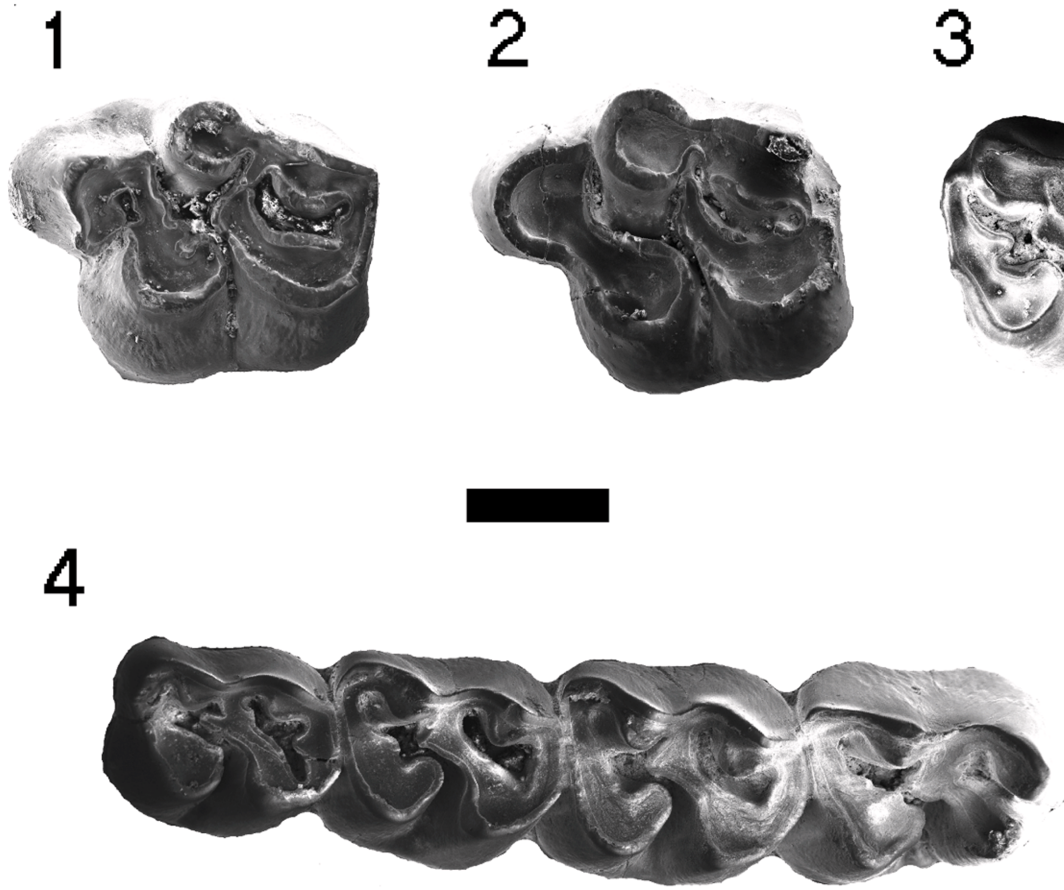

FIGURE 3—*1–4*, dentition of *Pipestoneomys bisulcatus*: *1*, CM 18814, left P4; *2*, CM 16911, left P4; *3*, CM 86164, left M1; *4*, CM 86166, right p4–m3. Anterior to left on *1–3*, anterior to right on *4*. Scale=1 mm.

the condition in hystricognathous rodents (see Korth, 1994, fig. 2.6). The masseteric scar extends anteriorly in a V-shape to a point below the front half of p4. The diastema is shallow and its length is approximately 75% the length of the tooth row. The mental foramen is single, small, and situated just posterior to the center of the diastema at approximately one-third the depth of the mandible. Ventrally, there is a small digastric process at the posterior end of the mandibular symphysis.

The lower incisor is slightly longer than wide in cross-section. The anterior enamel surface is smooth, gently convex with no ornamentation, and the anterolateral corner of the surface is rounded. Enamel extends only about one third the height of the tooth on the lateral side. The micorstructure of the enamel is uniserial (Fig. 5). Typically, the *portio externa* is oriented radially. Two layers of the *portio interna* can be distinguished. In the transverse section of the lower incisor (Fig. 5.2) the inner layer can be distinguished by the steeper angle of the Hunter-Schreger bands (HSB) that are crossed by interprismatic crystals. In the outer layer, the HSB are at a lesser angle and the interprismatic crystals appear parallel to the HSB. In longitudinal section (Fig. 5.4) the HSB appear nearly parallel to the long axis of the incisor.

As with the upper dentition, p4 is the largest of the lower cheek teeth and narrower anteriorly than posteriorly. The anterior part of the occlusal surface is dominated by the protoconid and metaconid. Both are obliquely compressed ovals that do not meet anteriorly, but define a deep trigonid basin. The metaconid is always slightly more anterior than the protoconid. There is a distinct anteroconid on the anterior slope of the metaconid on all specimens but is variable in size. On some specimens it is a large cusp that blocks the trigonid basin anteriorly, whereas in others it is a minute cuspule and the trigonid basin remains open anteriorly. There is a distinct mesoconid in the center of the tooth that is connected buccally to the posterior edge of the protoconid. Lingually a short loph (mesolophid) extends from the mesoconid to the lingual edge of the tooth, fusing with the posterior side of the metaconid, enclosing the trigonid basin posteriorly. An anteroposteriorly oriented loph (=endolophid) runs along the lingual side of the tooth from the posterior end of the metaconid and connects to the posterolingual corner of the tooth and includes the entoconid. The hypoconid is crescentic and continuous with the posterior cingulid that joins the lingual loph of the tooth at the posterolingual corner. The anterior arm of the hypoconid extends into the center of the tooth. On little worn specimens it ends short of the mesoconid and the hypoflexid is continuous from the buccal margin of the tooth to the posterolingual corner. In later stages of wear it is continuous with the mesoconid, forming a deep enamel lake for the talonid basin. A hypoconulid is present in the form of a short spur extending into the talonid basin from the center of the posterior cingulid.

The m1 is slightly smaller than p4 and rectangular in occlusal outline, slightly longer than wide. The buccal cusps (protoconid, hypoconid) are crescentic in shape and the lingual cusps are oval. The protoconid and metaconid are united anteriorly by the anterior cingulid (=metalophulid I) along the anterior edge of the tooth. The posterior arm of the protoconid is similar to that of p4, united with a central mesoconid that is connected to the endolophid via a short mesolophid. This pattern of lophs isolates

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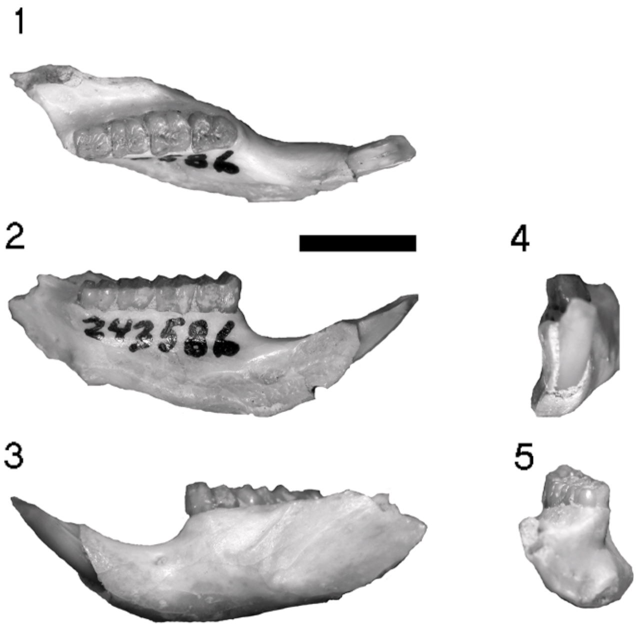

FIGURE 4—*1–5*, mandible of *Pipestoneomys bisulcatus*, USNM 243586: *1*, dorsal (occlusal) view; *2*, medial view; *3*, lateral view; *4*, anterior view; *5*, posterior view. Scale=5 mm.

a deep, crescentic trigonid basin between the protoconid and metaconid. The posterior half of the tooth is similar to that of p4 with the hypoconid and entoconid united posteriorly by the posterior cingulid. The hypoflexus is deep in unworn specimens, extending posterolingually from the center of the buccal margin of the tooth and ending posterolingually around the entoconid, forming a Y-shaped valley. In later stages of wear, as in p4, the anterior arm of the hypoconid can fuse with the mesoconid isolating a talonid basin. However, in some specimens the hypoflexid remains continuous even in late stages of wear. The hypoconulid is also variable in size but generally smaller than in p4, not being recognizable on heavily worn specimens.

The m2 is very similar to m1 in occlusal morphology and is only slightly smaller in size than m1. It is nearly equal in length and width. The greatest difference from m1 is the size of the hypoconulid. On some specimens it is as in m1, whereas in others it is a short loph that is directed anteriorly splitting the talonid basin into two.

The m3 is the smallest of the lower cheek teeth and significantly longer than wide. It is slightly narrower posteriorly than anteriorly. The occlusal morphology is nearly identical to that of m2.

Holotype.—FMNH UM409, right maxilla with M1–3.

Referred specimens.—FMNH UM408 fragmentary mandible with right p4 (partial)-m1; CM 10047, partial mandible with left p4-m1; CM 16910, partial mandible with right m1-m3; CM 29115right p4; CM 56986, fragmentary mandible with right p4-m2; CM 76909, mandible with left p4-m2; CM 78272, mandible with left p4-m3; CM 86165, mandible with right p4-m3; CM 86166, mandible with right p4-m3; USNM 243586, mandible with left i1 and p4-m3; USNM 243587 partial mandible with i1 and p4-m2; CM 16911, left P4; CM 18814, maxillary fragment with P4; CM 18815, partial maxilla with right P4; CM 21399, right M1; CM 21400, left M1; CM 27575, right M1; CM 86164, fragmentary maxilla with P4 (partial)-M1; PTRM 10974, right P4; PTRM 6167, left M1 or M2.

Occurrence.—Middle to late Chadronian (late Eocene, Priabonian). Holotype and CM 10047, 16910, 16911, 18814, 18815, 21399, 21400, 29115, 56986, 60691, 86164, 86165, from Pipestone Springs, Climbing Arrow Member, Renova Formation, Jefferson County, Montana. There are several fossil localities included in the general term "Pipestone Springs" and in the initial description of this species, Donahoe (1956) did not designate the specific locality. All of the specimens in the CM collections are from the locality known as "Little Pipestone Creek", which is slightly higher stratigraphically than the main pocket at Pipestone Springs (Kuenzi and Fields, 1971). USNM specimens are from Dry Hollow, Dunbar Creek Formation, Broadwater County, Montana. Previous specimens from this area indicate an Orellan age (early Oligocene; Korth, 1992, 2007). However, the University of Montana has reported Chadronian collections from this same area including specimens of the otherwise Chadronian eomyid *Aulolithomys bounites* (see Korth, 1992). It is evident that the rocks along Dry Hollow include exposures both of Chadronian and Orellan age. CM 28697 is from Pilgrim Creek fauna, Montana (Sutton and Black, 1975). CM 86166 is from of the Dunbar Creek Formation, Canyon Ferry area, (locality 24C16 of White, 1954, p. 396), Lewis and Clark County, Montana. CM 78272 is from a small exposure along US Highway 10 N in Broadwater County, Montana (Tabrum et al., 2001).

Remarks.—The additional and more complete specimens of *Pipestoneomys bisulcatus* from the type area, as well as other Chadronian localities, has allowed for the description of the zygomasseteric structure, mandible, incisor microstructure, and range of variation in the morphology of the cheek teeth that was not possible previously. This, in turn, has allowed for the allocation of the genus to a new family the Pipestoneomyidae.

Kihm (2011) identified two isolated cheek teeth (P4 and M1) from the Chadronian of North Dakota as *Pipestoneomys* sp. He could not assign the specimens to either of the described species of the genus because they had morphologies of both species that had been used originally to differentiate them. There were also a few characters that were not present in either of the named species. As Kihm (2011) suggested, it appears that the differences he noted between the North Dakota sample and *P. bisulcatus* are variations present in the larger sample of the latter, and the greater degree of wear on the North Dakota specimen of P4.

West and Korth (1994) documented the occurrence of *Pipestoneomys* from the Orellan of Nebraska based on a single isolated p4. The size and morphology of this tooth is well within the range of *P. bisulcatus*. However, because the Orellan record is only a single tooth, this specimen was referred to *Pipestoneomys* sp. rather than any of the two recognized species.

PIPESTONEOMYS PATTERSONI Alf, 1962
Figure 6.1–6.4

Diagnosis.—Emended, smallest species of the genus; p4 and m1 subequal in size; M2/m2 more reduced in size relative to M1/m1 than in *P. bisulcatus*; p4 narrower relative to length than in *P. bisulcatus*.

Holotype.—MCZ 7113 maxillary fragment with left M1-M2.

Referred specimens.—MCZ 7110, 7106, 7108, P4; MCZ 7102, M1; MCZ 7111, M2; MCZ 7104, 7107, p4; MCZ 7103, 7109, 7112, 7101; m1. (Also see Alf, 1962, p. 172.)

Occurrence.—Chadronian (late Eocene, Priabonian). Lower part of the Chadron Formation (below "lower purple-white layer" of Schultz and Stout, 1955), sec. 26, T33N, R53W, Sioux County, Nebraska.

Remarks.—Alf (1962) described the morphology of the cheek teeth of *Pipestoneomys pattersoni* in detail; no additional specimens of the species have been reported since that time. In the original description of the species, Alf (1962) cited three features of M1 that separated *Pipestoneomys pattersoni* from *P. bisulcatus*: 1) buccal cusps transversely compressed in *P. pattersoni*, rounded in *P. bisulcatus*; 2) anterior cingulum

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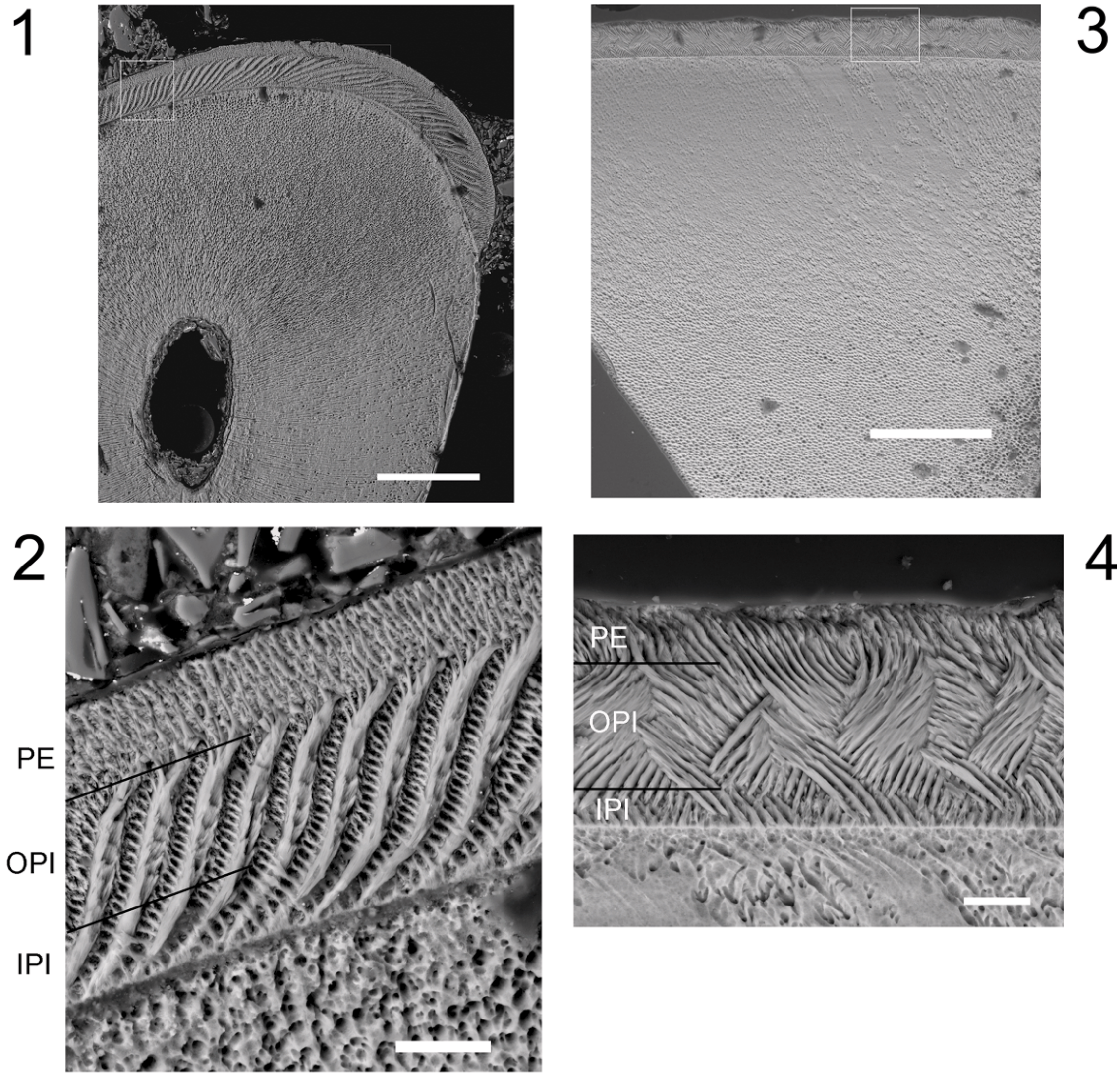

FIGURE 5—*1–4*, scanning electron micrograph of incisor enamel (lower left) of *Pipestoneomys bisulcatus*, USNM 243587: *1, 2*, transverse section; *3, 4*, saggital section. Scale=200 microns for *1,3*; scale=20 microns for *2*, *4*. Anterior enamel surface toward top of the figure. Abbreviations: PE=*portio externa*; IPI=inner layer of *portio interna*; OPI=outer layer of *portio interna*.

(=anteroloph) more widely separated from the paracone in *P. bisulcatus* than in *P. pattersoni*; and 3) enamel lakes posterior to the anterior cingulum (=anteroloph) smaller and not connected to one another in *P. pattersoni* (deeper and connected in *P. bisulcatus*). None of these features appear to separate these two species. With the additional specimens recognized of *P. bisulcatus*, these are all variable characters within the sample of the latter. The compression of the buccal cusps is identical in both species and the separation of the buccal end of the anterior cingulm from the paracone varies from wide and deep to actually fusing with the paracone. In the sample of *P. bisulcatus*, the enamel lakes posterior to the anterior cingulum are variable in size and appear to communicate with each other in all specimens of *P. pattersoni* as well as *P. bisulcatus*.

In an unpublished master's thesis, Ostrander (1980) identified over 100 isolated teeth of *Pipestoneomys bisulcatus* from the Chadronian Raben Ranch fauna of Sioux County, Nebraska (the same area and horizon as the type material of *P. pattersoni*). In this same fauna Ostrander (1980) also identified 28 isolated teeth of *P. pattersoni*. He used the differences cited by Alf (1962) to separate the two species. However, in the published faunal list of the Raben Ranch fauna (Ostrander, 1985, appendix II), only one species, *P. bisulcatus*, was identified. The tables of measurements given by Ostrander (1980, tables 51, 52) for these samples are difficult to use for comparison because he did not separate the first from the second molars; including them together in his tables. It is possible that Ostrander (1980) referred the smaller specimens of *Pipestoneomys* to *P. pattersoni*, and the larger in *P. bisulcatus*. (The specimens from this fauna were not available for this study.) The variable nature of the morphologic characters used by Alf (1962) to separate the two species led some authors to suggest that *P. bisulcatus* and *P. pattersoni* were possibly synonyms (Wood, 1980; Kihm, 2011).

The greatest observed difference between *Pipestoneomys pattersoni* and *P. bisulcatus* is in size and the relative proportions of the cheek teeth (Tables 1, 2). *P. pattersoni* is only slightly smaller in overall dental dimensions than *P. bisulcatus*. In *P. bisulcatus*, however, p4 is approximately 10% larger in both length and width dimensions compared to m1, whereas in *P. pattersoni*, p4 and m1 are nearly identical in dimensions. The size of M2/m2 relative to M1/m1 also differs between the species of *Pipestoneomys*. For *P. bisulcatus*, the second molar has dimensions over 90% that of the first molar but in *P. pattersoni*

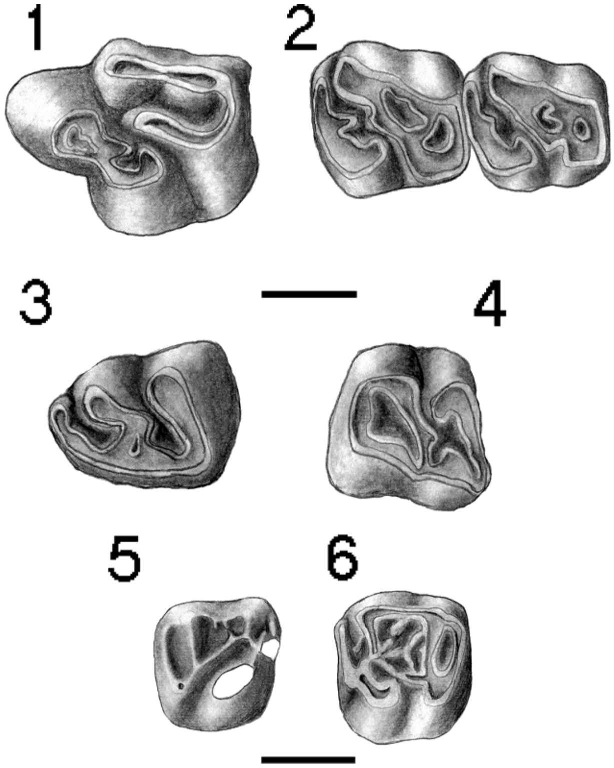

FIGURE 6—*1–4*, dentition of *Pipestoneomys pattersoni*: *1*, right P4 (reversed), MCZ 7110; *2*, left M1–M2, MCZ 7113, holotype; *3*, left p4, MCZ 7107; *4*, left m1, MCZ 7109, anterior to the left; *5*, *6*, dentition of *Argorheomys septentrionalis*: *5*, right P4, RSM P1899.568; *6*, left M1 or M2, RSM P1899.569, type. Scale=1 mm.

the second molar is approximately 80% the length and width of the first molar (more pronounced in the uppers). This means that the second molars in *P. patersoni* are relatively smaller compared to M1/m1 than in *P. bisulcatus*. Of these features, Alf (1962) only mentioned the relatively smaller p4 of *P. pattersoni* in his original diagnosis.

GENUS ARGORHEOMYS new genus

Type species.—*Argorheomys septentrionalis* n. sp. by monotypy.

Diagnosis.—As for species.

Etymology.—Greek, *argos*, swift, *rheos*, current, and *mys*, mouse; in reference to Swift Current, Saskatchewan, a town near the type locality of the type species.

Occurrence.—Duchesnean (late middle Eocene, Bartonian) of Saskatchewan.

ARGORHEOMYS SEPTENTRIONALIS new species
Figure 6.4, 6.5

1987 ?*Yoderimys* sp. Storer, p. 113, figs. 3A, 3B.

Diagnosis.—Pipestoneomyid with brachydont cheek teeth; anterocone on P4 small (not enlarged as in *Pipestoneomys*); upper molars larger than P4; hypoflexus on upper cheek teeth interrupted by loph from lingual end of paracone (=?protoloph); upper molars wider relative to length than in *Pipestoneomys*; trigonid basin on p4 closed anteriorly.

Description.—P4 is approximately square in outline. There is a small chip of enamel missing along the anterior border on the buccal half of the tooth, and the top of the protocone has been broken away, but the base remains. There is a minute parastyle or anterocone at the anterobuccal corner of the tooth. The protocone appears to be continuous with the anterocone, but is interrupted by the missing chip of enamel. Both of the lingual cusps, protocone and hypocone, are of similar size and are obliquely compressed (anterobuccal-posterolingual). The buccal cusps, paracone and metacone, are anteroposteriorly compressed. The paracone connects lingually with a loph that runs diagonally across the tooth to the hypocone, leaving a deep valley separating the protocone and anterior cingulum, thus defining a hypoflexus. On the lingual side of the paracone is a very short loph (?=protoloph) that blocks the hypoflexus from being completely continuous to the anterobuccal corner of the tooth. Between the buccal cusps is an ectoloph that isolates a small valley on its lingual side. There is also a small shelf formed on the buccal side of the ectoloph between the buccal cusps. Within the small valley are two short lophules that connect with the ectoloph, but end inside the valley, before uniting with any other loph or cusp. A metaloph extends lingually and slightly anteriorly from the metacone, uniting with the anterior arm of the hypocone. The posterior cingulum extends from along the entire width of the tooth on the posterior border, ending at the hypocone lingually and the metacone buccally, and isolating a large valley.

The upper molar, RSM P1899.569, is larger than the P4, wider than long and is moderately worn. The anterior cingulum arises from the crescentic protocone and extends the entire width of the tooth along the anterior border, ending at the anterobuccal corner of the tooth. There is a slight bend in the anterior cingulum at the buccal end of the protocone. There is a valley that runs obliquely across the tooth posterior to the anterior cingulum (=hypoflexus) as in P4, but it is interrupted in two places; near the lingual end where the posterior arm of the protocone crosses it, and near the center where a spur from the center of the anterior cingulum crosses it. In both cases, the union with the oblique loph is very thin (weak), suggesting that in early stages of wear, the hypoflexus may have been continuous. The buccal cusps, hypocone, posterior cingulum and ectoloph of the molar are similar to that of P4. The central basin of the tooth, bounded by the ectoloph, metaloph and oblique loph is filled with several irregular lophules.

The referred p4, RSM P1899.570, is heavily worn and broken along the lingual and posterior edges of the tooth, so little of the occlusal morphology is distinguishable. The tooth is wider posteriorly than anteriorly. There is a minute depression along the anterior margin of the tooth indicating the presence of a small trigonid basin, but no cusps are recognizable. Posteriorly, the hypoconid and entoconid are identifiable. Along the buccal side of the tooth is a low loph that runs obliquely from the center of the buccal margin to the lingual side of the hypoconid. No other morphologies can be discerned.

Measurements include: RSM P1899.568, P4, length=1.35 mm, width=1.33 mm; RSM P1899.569, M1 or M2, length=1.35 mm, width=1.60 mm; P1899.570, p4, length=1.43 mm, width=1.49 mm (measurements of this specimen represent minimums because the tooth is not complete).

Etymology.—Latin, *septentrionalis*, northern.

Holotype.—RSM P1899.569, left M1 or M2.

Referred specimens.—RSM P1899.568, right P4 and RSM P1899.570, right p4.

Occurrence.—Duchesnean (late middle Eocene, Bartonian). Lac Pelletier locality (RSM locality 72J04-0006), Cypress Hills Formation, Saskatchewan (see Storer, 1987, p. 112).

Remarks.—Storer (1987) referred four isolated teeth from the Duchesnean of Saskatchewan to the eomyid ?*Yoderimys*, an upper and lower premolar and an upper and lower molar. He also noted that this occurrence predated the previously earliest record of *Yoderimys* (Chadronian). Korth (1994) suggested that these specimens more closely resembled *Pipestoneomys* without discussion. Although Storer (1987) originally referred the

TABLE 1—Dental measurements of upper cheek teeth of *Pipestoneomys*. Abbreviations: N=number of specimens; M=mean; OR=observed range; SD=standard deviation; CV=coefficient of variation; L=anteroposterior length; W=transverse width. All measurements in mm.

	P4L	P4W	M1L	M1W	M2L	M2W	M3L	M3W
P. bisulcatus								
N	4	5	5	5	1	1	1	1
M	2.50	1.97	1.68	1.76	1.55	1.81	0.91	1.27
OR	2.17–2.71	1.89–2.08	1.64–1.78	1.67–1.95				
SD	0.23	0.08	0.06	0.11				
CV	9.34	4.14	3.50	6.18				
P. pattersoni								
N	2	3	2	2	2	2		
M	2.58	1.98	1.72	1.69	1.38	1.43		
OR	2.53–2.62	1.87–2.05	1.65–1.78	1.53–1.84	1.37–1.49	1.37–1.49		

specimens allocated here to *Argorheomys* to ?*Yoderimys*, the three of them are similar to *Pipestoneomys* and differ from yoderimyines in the following features of P4: 1) nearly complete hypoflexus; 2) paracone directly connected to hypocone via oblique loph across center of tooth; 3) endoloph incomplete; and 4) small, irregular lophules between buccal cusps, no mesoloph. Similarly, the upper molar of *Argorheomys* is similar to that of *Pipestoneomys* and differs from the least derived yoderimyine, *Litoyoderimys*, in the following features: 1) complete ectoloph (developed independently in *Yoderimys*); 2) protocone crescentic rather than obliquely compressed; 3) paracone directly connected to hypocone via oblique loph; 4) hypoflexus present (but interrupted); 5) protoloph connecting paracone to protocone lacking; 6) posterior "spur" at center of anterior cingulum; and 7) irregular lophules in place of mesoloph.

Argorheomys differs from *Pipestoneomys* in the following features: 1) brachydonty rather than mesodonty; 2) P4 smaller than M1; 3) upper molars wider relative to length (subequal in length and width in *Pipestoneomys*); 4) hypoflexus interrupted at the base of the paracone (continuous to anterobuccal corner of tooth in *Pipestoneomys*); and 5) anterocone on P4 small (enlarged in *Pipestoneomys*). In all of these features, *Argorheomys* is more primitive than *Pipestoneomys*.

The lower molar and referred to ?*Yoderimys* by Storer (1987) (RSM P1899.571) is that of a cylindrodontid, and is not referable to *Argorheomys*. It is most likely referable to *Pseudocylindrodon lateriviae*, a species that is present in the Lac Pelletier fauna (Storer, 1988).

CONCLUSIONS

Previously, the reference of *Pipestoneomys* to any known family of rodents has been difficult because of the unique occlusal morphology of the cheek teeth, and poor fossil record (almost entirely isolated teeth). Thus, in the past, no allocation to any family has been done with certainty. The mesodonty and the presence of hypoflexi (=ids) on the cheek teeth of *Pipestoneomys* led some authors to include it within the Castoridae (Alf, 1962; Black, 1965) or Eutypomyidae (Castoroidea; Flynn and Jacobs, 2008). However, it is clear from more complete material that it is identifiable as belonging to a distinct family of rodents. The sciuromorphous zygomatic structure, dental formula, microstructure of the incisor enamel, and long infraorbital canal of *Pipestoneomys*, is the same condition in all other Geomorpha (=Eomyoidea and Geomyoidea; Wahlert, 1978, table 2). Within the Geomorpha, *Pipestoneomys* is more like the Eomyoidea because of the lophodont dentition that is not bilophate as in all geomyoids. However, the occlusal pattern of the cheek teeth of pipestoneomyids is vastly different from the "omega" pattern of eomyids (Stehlin and Schaub, 1951) and eomyids never attain the degree of crown-height of the cheek teeth of *Pipestoneomys*. The morphology of the mandible of *Pipestoneomys* (concave medial surface, widely separated ascending ramus) is similar to the condition in derived yoderimyine eomyids. However, this appears to be independently developed within *Pipestoneomys* and the Yoderiminae because of the lack of its development in earlier species of the latter (Emry and Korth, 1993).

The most compelling character is the microstructure of the incisor enamel of *Pipestoneomys*. It has the unique two-part *portio interna* that is diagnostic of the eomyidae and the HSB of the *portio interna* are oriented nearly parallel to the long axis of the incisor, both diagnostic features of the Eomyidae (Wahlert, 1978; Wahlert and Koenigswald, 1985). However, the incisor lacks the distinct longitudinal ridge on the enamel surface of most eomyids (this ridge is also lacking on the incisors of *Yoderimys* [Emry and Korth, 1993]). It is difficult to include *Pipestoneomys* in the Eomyidae because of the markedly distinct morphology of the cheek teeth. Even in *Argorheomys*, the most primitive genus of pipestoneomyids, there is no indication of the characteristic "omega" occlusal pattern on the cheek teeth that is diagnostic of the Eomyidae. Because of this difference in cheek tooth morphology, and the fact that the pipestoneomyids can be traced back into the Duchesnean as a distinct clade, the Pipestoneomyidae is recognized as a distinct family, but included in the Superfamily Eomyoidea due to the shared characters of the skull, dental formula and incisor microstructure.

TABLE 2—Dental measurements of lower cheek teeth of *Pipestoneomys*. Abbreviations as in Table 1. Measurements in mm.

	p4L	p4W	m1L	m1W	m2L	m2W	m3L	m3W	p4-m3
P. bisulcatus									
N	9	9	10	10	8	8	3	3	3
M	1.89	1.68	1.71	1.59	1.59	1.45	1.49	1.23	6.83
OR	1.78–2.03	1.51–1.79	1.59–1.83	1.47–1.69	1.50–1.68	1.34–1.55	1.46–1.53	1.19–1.27	6.62–7.13
SD	0.10	0.09	0.08	0.07	0.05	0.07	0.04	0.04	0.27
CV	5.15	5.64	4.46	4.33	3.37	4.70	2.55	3.28	3.88
P. pattersoni									
N	2	2	2	2	1	1			
M	1.89	1.45	1.64	1.55	1.42	1.27			
OR	1.85–1.92	1.39–1.50	1.64–1.64	1.53–1.56					

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