Two new pocket mice (Mammalia, Rodentia, Heteromyidae) from the Miocene of Nebraska and New Mexico and the early evolution of the subfamily Perognathinae

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ABSTRACT
Two new genera and species of heteromyid rodents are described: *Eochaetodipus asulcatus* n. gen., n. sp. from the late Arikareean (earliest Miocene) of Nebraska and *Mioperognathus willardi* n. gen., n. sp. from the Barstovian (middle Miocene) of New Mexico. *Eochaetodipus asulcatus* n. gen., n. sp. is based on a nearly complete skull with associated mandibles and some postcranial material. This specimen is the earliest recognized member of the subfamily Perognathinae based on shared cranial and skeletal features with extant perognathines (mastoid inflation; reduction of incisive foramina; separation of the buccinator and masticatory foramina; more gracile skeleton). *Eochaetodipus* n. gen. is viewed as more primitive than other perognathines because it lacks a number of derived features of the latter. The cranium of *Mioperognathus* n. gen. was previously described as "*Perognathus minutus*". It differs from that of *Eochaetodipus* in a number of features that are considered derived for perognathines (loss of the accessory foramen ovale; greater inflation of the bulla and mastoid; reduction of the squamosal dorsal to the external acoustic meatus to a thin bar; presence of an unossifed area on the orbital wall; grooved upper incisors), but is distinct from extant perognathines in several characters interpreted as primitive (presence of temporal foramen; less inflated bulla; longer temporalis scar). A phylogenetic analysis shows that the perognathine clade arose from a mioheteromyine-like ancestor separate from the Heteromyinae.

KEY WORDS
Mammalia,
Rodentia,
Heteromyidae,
Perognathinae,
cranial foramina,
Barstovian,
Arikareean,
Miocene
new genera,
new species.

RÉSUMÉ

Deux nouvelles souris à poches (Mammalia, Rodentia, Heteromyidae) du Nebraska et du Nouveau-Mexique du Miocène et évolution primitive de la sous-famille Perognathinae.

Deux nouveaux genres et espèces de rongeurs Heteromyidae sont décrits : *Eochaetodipus asulcatus* n. gen., n. sp. de l'ancien Arikarain (lointain Miocène) du Nebraska et *Mioperognathus willardi* n. gen., n. sp. du Barstovian (du milieu du Miocène) du Nouveau-Mexique. *Eochaetodipus asulcatus* n. gen., n. sp. est basé sur un crâne presque complet avec les mâchoires associées et de la matière postcrânienne. Ce spécimen est le plus ancien membre reconnu de la sous-famille Perognathinae d'après les caractéristiques du crâne et du squelette qu'il partage avec les perognathines actuels (inflation mastoïde ; réduction des incisives foraminées ; séparation du buccinateur et des masticatrices foraminés ; squelette plus gracile). *Eochaetodipus* n. gen. est considéré comme plus primitif que d'autres perognathines parce qu'il lui manque un certain nombre de caractéristiques dérivées de ce dernier. Le crâne du *Mioperognathus* n. gen. fut préalablement décrit comme « *Perognathus minutus* ». Il diffère de celui d'*Eochaetodipus* n. gen. par certains traits qui sont considérés dérivés pour les perognathines (perte du foramen ovale accessoire ; plus grande inflation de la bulle et du mastoïde ; réduction du squamosal à une fine barre ; présence d'une région non ossifiée du mur orbital ; incisives supérieures cannelées), mais est différent des perognathines actuels par plusieurs caractéristiques interprétées comme primitives (présence de foramen temporaire ; bulle moins enflée ; cicatrice temporale plus longue). Il est considéré que le groupe perognathine est issu d'un ancêtre semblable aux Mioheteromynae, distinct des Heteromyinae.

MOTS CLÉS
Mammalia,
Rodentia,
Heteromyidae,
Perognathinae,
trous crâniens,
Barstovian,
Arikareean,
Miocène,
genres nouveaux,
espèces nouvelles.

INTRODUCTION

The systematics of the Heteromyidae have been in flux since Wood (1935) proposed the first detailed classification of the family, which included all known extant and fossil taxa. The extant genera are easily divided into three subfamilies, each of which contains two recognized genera: Heteromyinae Gray, 1868 (*Liomys* Merriam, 1902, *Heteromys* Desmarest, 1817); Perognathinae Coues, 1875 (*Perognathus* Wied-Neuwied, 1839, *Chaetodipus* Merriam, 1889); and Dipodomyinae Gervais, 1853 (*Dipodomys* Gray, 1841, *Microdipodops* Merriam, 1891; Wilson & Reeder 1993). These subfamilies are easily distinguishable based on drastically different morphologies of the skull, dentition and postcranial skeleton (Hafner & Hafner 1983; Williams *et al.* 1993).

Since the majority of the Tertiary fossil record of heteromyids is limited to teeth and jaws, all of the criteria for separating the extant taxa into subfamilies could not be used; only dental characters were used to put the fossil taxa into the subfamilies of the extant heteromyids. Wood (1935) primarily used the morphology of the premolars to assign the fossil taxa to subfamilies. This has been the standard for classification of the fossil heteromyids since that time (see Korth 1997: table 1, for list all of the previously published classifications of heteromyids that included Tertiary taxa). Some other subfamilies have been named that only included fossil heteromyids. In each case, it was because more complete cranial material was available. Wood (1936) named the Florentiamyinae as a subfamily of heteromyids, but it was later recognized as a distinct family of geomyoids (Wahlert 1983). Wahlert (1991) named the subfamily Harrymyinae for the nominal genus based on cranial as well as dental features, again due to the recovery of a nearly complete skull. Korth (1997) named a new subfamily, Mioheteromyinae, which included the majority of the fossil genera that previously had been included in different subfamilies by different authors. The diagnosis of the Mioheteromyinae included a number of cranial features based on newly described cranial material. It is apparent that the diversity among heteromyids is better reflected in the features of the skull and postcranial skeleton than it is in the dentition alone.

A newly discovered specimen of a heteromyid from the late Arikareean of Nebraska includes a nearly complete skull and jaws, and some associated postcranial bones. This specimen and a previously described nearly complete skull (referred to *Perognathus minutus* by Korth 1998) are compared to Recent heteromyids. Because of the completeness of these fossil specimens, it is possible to better reconstruct the phylogeny of the heteromyids, and better define the characters of the subfamilies of the Heteromyidae as they apply to fossil taxa.

Abbreviations

- AMNH Department of Mammals, American Museum of Natural History, New York;
- CM Section of Mammals, Carnegie Museum of Natural History, Pittsburgh;
- FAM Frick Collection, American Museum of Natural History, New York;
- UNSM University of Nebraska State Museum, Lincoln (Nebraska).

METHODS AND MATERIALS

Terminology

Dental terminology for heteromyids follows Korth (1997: fig. 1), and terminology for cranial foramina follows that of Wahlert (1974, 1985). Upper teeth are designated by capital letters, lower teeth by lower case letters.

Specimens examined

It was necessary to compare of the fossil specimens with Recent species of heteromyids for several reasons. First, the morphologies that define the different subfamilies of the Heteromyidae are based on those of the extant genera. Second, it was also necessary to determine whether the morphologies of the fossil species were distinct or part of a range of variation within a living species. Finally, because the fossil record is so incomplete, the diagnostic morphologies of each of the genera and families could only be determined by direct comparison with more complete material.

Fossil specimens. — *Eochaetodipus asulatus* n. gen., n. sp.: UNSM 130000, skull with associated mandibles and several postcranial bones from late Arikareean (earliest Miocene) UNSM locality Sh-112, Antelope Creek Formation, Sheridan County, Nebraska.

Mioperognathus willardi n. gen., n. sp.: FAM 129674, nearly complete cranium with incisors and right M1 (partial)-M3 from late Barstovian (middle Miocene) Lower Pojoaque Bluffs, Pojoaque Member, Tesuque Formation, New Mexico.

Extant specimens. — *Liomys pictus* (Thomas, 1893): AMNH 190257, 190263, 190265-190267, 190269, 190276.

Liomys irroratus (Gray, 1868): AMNH 172451, 172454, 172456, 172458.

Liomys salvini (Thomas, 1893): AMNH 126313-126319, 126321, 126323, 126324.

Heteromys anomalis (Thompson, 1815): AMNH 69679-69686, 69688, 69689.

Heteromys desnarestianus Gray, 1868: AMNH 79239, 79241, 74542, 79244, 79246, 79248.

Heteromys australis Thomas, 1901: AMNH 64678, 64680, 64681, 64689, 64690, 64696, 64863, 64866.

Chaetodipus hispidus Baird, 1858: CM 75174, 93588, 89207, 89208, 48912

Chaetodipus californicus Merriam, 1889: CM 71380, 71390, 71385.

Chaetodipus baileyi Merriam, 1894: CM 7517, 108271, 108272, 46366, 46367.

Perognathus fasciatus Wied-Neuwied, 1839: CM 46417-46419, 21187, 21189.

Perognathus amplus Osgood, 1900: CM 91004-91008.

Perognathus parvus (Peale, 1848): CM 65351-65353, 65365, 65366.

SYSTEMATIC PALEONTOLOGY

Order RODENTIA Bowdich, 1821
Family Heteromyidae Gray, 1868

Subfamily Perognathinae Coues, 1875

Included genera. — *Perognathus* Wied-Neuwied, 1839; *Chaetodipus* Merriam, 1889; *Oregonomys* Martin, 1984; *Eochaetodipus* n. gen., and *Mioperognathus* n. gen.

TABLE 1. — Cranial measurements (in mm) of the holotype of *Eochaetodipus asulcatus* n. sp. (UNSM 13000) and *Mioperognathus willardi* n. sp. (FAM 129674). *, actual length slightly greater, anterior end of nasals missing).

	UNSM 13000	FAM 129674
Total length	30.2*	26.05
Maximum rostral width	7.6	4.64
Maximum rostral depth	9.3	6.27
Length upper diastema	7.19	6.83
Minimum width, postorbital constriction	5.9	5.15
Greateast width of skull (parietals)	13.6	11.67
Posterior width	12.2	10.39
Depth of skull at M2	10.2	7.55
P4-M3 (alveolar)	5.0	3.51

Genus *Eochaeotodipus* n. gen.

TYPE SPECIES. — *Eochaetodipus asulcatus* n. sp.

RANGE. — Late Arikareean of Nebraska (earliest Miocene).

DIAGNOSIS. — Primitive heteromyid features: premolars (upper and lower) simple, four-cusped, with very weak development of lophodonty; cheek teeth brachydont; upper incisor asulcate; rostral perforation anterior to infraorbital foramen. Primitive characters shared with mioheteromyines not present in heteromyines, perognathines and dipodomyines: no bony flange dorsal to orbit; large temporal foramen on skull; accessory foramen ovale retained (enclosed posterior border); premaxillary-maxillary suture crosses midline of palate anterior to the posterior margin of the incisive foramina. Derived characters shared with heteromyines, perognathines, and dipodomyines, not present in mioheteromyines: length of incisive foramina less than 15% total length of the upper diastema; interparietal bone oval (transversely elongated); parapterygoid fossae shallower than in extant perognathines, but deeper than in mioheteromyines; limb bones thinner and skull less robust. Derived features shared with perognathines and dipodomyines: rudimentary inflation of the bulla and mastoid; masticatory and buccinator foramina separate on alisphenoid. Apomorphic features: posterior palatine foramina multiple.

ETYMOLOGY. — Greek, *eos*, dawn and *Chaetodipus*, extant genus of perognathine.

COMPARISONS

Eochaetodipus n. gen. is clearly referable to the Heteromyidae because of its generally small skull and skeleton and the presence of a rostral perforation anterior to the infraorbital foramen (diagnostic for heteromyids). It is separable from geomyids, entoptychines, and floreniamyids by thinner more delicate bones of the skull. It also lacks the cranial specializations of these groups (see Wahlert 1983, 1985; Wahlert & Sousa 1988). Florentiamyids also lack the lingual stylar cusps on the upper molars present on *Eochaetodipus* n. gen., and have teeth that are generally more robust.

Eochaetodipus n. gen. differs from the contemporaneous geomyoid *Tenudomys* Rensberger, 1973, again, in having a more gracile skull that is not as deep. The foramina of the medial orbital wall of *Tenudomys* are positioned more posteriorly than in *Eochaetodipus* n. gen. (Korth 1993) and the cheek teeth of the former are generally more hypsodont and lophate (Rensberger 1973; Korth 1993). The upper molars of *Eochaetodipus* n. gen. differ from those of *Tenudomys* by having non-continuous lingual cingula. In *Tenudomys*, the central transverse valley of the upper molars is blocked lingually by the lingual cingulum, whereas in *Eochaetodipus* n. gen. the transverse valley is continuous and two distinct cusps are present along the cingulum (protostyle and hypostyle).

Eochaetodipus n. gen. differs from the late Arikareean or early Hemingfordian *Trogomys* Reeder, 1960 from southern California by its larger size, slightly lower crowned and less lophate cheek teeth, and morphology of the lower premolar. In *Trogomys*, the cusps of the metalophid of p4 are joined anteriorly by a loph connecting their apices, giving the loph an anteriorly curved shape. In *Eochaetodipus* n. gen., the metaconid cusps are not joined by a loph and will probably not fuse until a much later stage of wear when the bases of the cusps fuse. *Trogomys* also has a distinct supraorbital flange (Reeder 1960) as in extant perognathines that is lacking in *Eochaetodipus* n. gen.

Eochaetodipus n. gen. differs from harrymyines in lacking the specialized occlusal pattern of the cheek teeth of the latter (V-shaped hypolophid that unites with the metalophid via anterior ridge on lower cheek teeth) and the nature of the inflation of the auditory bullae (Wahlert 1991).

TABLE 2. — Dental measurements (in mm) of the holotype of *Eochaetodipus asulcatus* n. sp. (UNSM 130000). Abbreviations: **a-p**, antero-posterior length; **tr**, maximum transverse width. Upper teeth are designated by capital letters, lower teeth by lower case letters.

P4		M1		M2		M3		I1		P4-M3	
a-p	tr	a-p	tr	a-p	tr	a-p	tr	a-p	tr		
1.51	1.81	1.33	1.74	1.22	1.68	1.00	1.37	1.65	0.91	5.00	(left)
–	–	1.27	1.77	1.11	1.61	0.98	1.24	1.62	0.90		(right)
p4		**m1**		**m2**		**m3**		**i1**		**p4-m3**	
a-p	tr	a-p	tr	a-p	tr	a-p	tr	a-p	tr		
1.23	1.20	1.31	–	1.18	2.04	1.04	1.32	–	–	4.84	(left)
1.27	1.20	1.28	1.42	1.19	1.58	1.11	1.34	1.68	0.70	4.76	(right)

Among the other subfamilies of heteromyids (Mioheteromyinae Korth, 1997, Perognathinae, Heteromyinae, Dipodomyinae), *Eochaetodipus* n. gen. has a mosaic of derived and primitive morphologies. The skull of *Eochaetodipus* n. gen. shares the following primitive features of the skull with mioheteromyines: 1) presence of a large temporal foramen; 2) position of the maxillary-premaxillary suture relative to the incisive foramina (crosses foramina anterior to posterior margin); 3) presence of an accessory foramen ovale on the alisphenoid that is enclosed posteriorly; 4) lack of a bony flange dorsal to the orbits; and 5) morphology of the temporalis scar on the skull (extends posteriorly to occipital).

The derived characters of *Eochaetodipus* n. gen. that are shared with heteromyines, perognathines and dipodomyines include shorter incisive foramina (less than 15% the length of the diastema), deeper parapterygoid fossa (not as deep as in extant heteromyids, but deeper than in mioheteromyines); and more gracile limb bones. *Eochaetodipus* n. gen. also shares some derived characters of the skull with perognathines (inflation of bulla and mastoid). The arrangement of the foramina on the lateral alisphenoid in *Eochaetodipus* n. gen. is unique among heteromyids. In *Eochaetodipus* n. gen. the accessory foramen ovale is large, and completely surrounded by bone, and the buccinator and masticatory foramina are separate from one another. This condition is known only elsewhere within the geomyoids in the entoptychines, a group clearly not closely allied with *Eochaetodipus* n. gen.

Eochaetodipus asulcatus n. sp.
(Figs 1-3; Tables 1; 2)

HOLOTYPE AND ONLY SPECIMEN. — UNSM 130000, skull with associated mandibles and several postcranial bones.

HORIZON AND LOCALITY. — UNSM locality Sh-112, Antelope Creek Formation, Sheridan County, Nebraska.

AGE. — Late Arikareean (earliest Miocene).

DIAGNOSIS. — Only species of the genus.

ETYMOLOGY. — Latin, *a-* prefix meaning without; and *sulcatus*, furrow; in reference to the ungrooved upper incisor of this species.

DESCRIPTION

The skull is nearly complete, lacking only the zygomatic arches and the anterior end of the rostrum (Fig. 1). Some damage has removed most of the bone from the orbital wall. The skull is similar in overall proportions and size to the extant perognathine species *Chaetodipus hispidus* Baird, 1858, but lacks the degree of inflation of the mastoids present in the latter. In dorsal view, the snout broadens anteriorly rather than tapering as in *Chaetodipus* Merriam, 1889. This may be affected by the breakage and dorsoventral crushing of the anterior part of the rostrum. The nasal bones end posteriorly anterior to the anterior margin of the orbits. The premaxillaries extend slightly farther posteriorly, level with the anterior margin of the orbits. There is no flange on the frontals dorsal to the orbits, which is a characteristic of extant heteromyids (Wahlert 1985). The crest formed by the temporalis is similar to that of

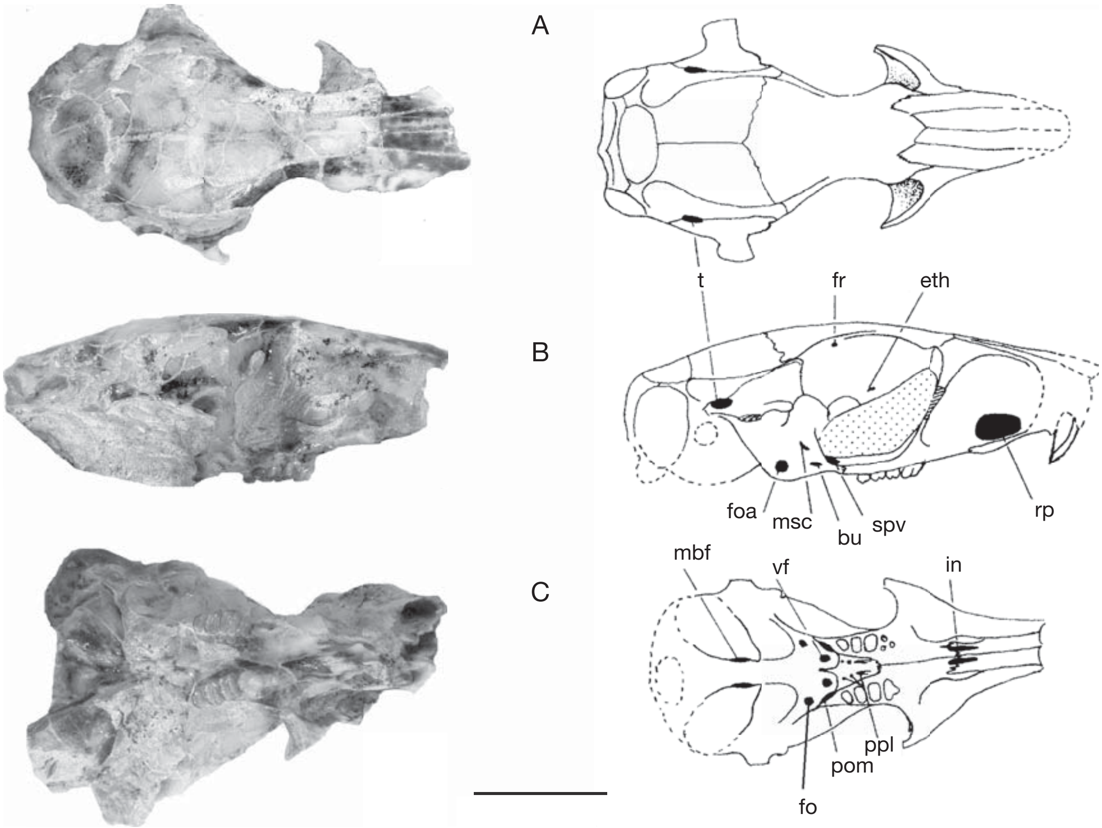

Fig. 1. — Photographs (left) and line diagrams (right) of the skull of *Eochaetodipus asulcatus* n. sp. based on the holotype UNSM 130000: **A**, dorsal view; **B**, lateral view (zygomatic arch removed); **C**, ventral view. Dashed lines indicate outlines of broken or covered areas; patterned area indicates missing bones. Abbreviations: **bu**, buccinator foramen; **eth**, ethmoid foramen; **fo**, foramen ovale; **foa**, accessory foramen ovale; **fr**, nutritive foramen in frontal; **in**, incisive foramen; **mbf**, fissure medial to bulla; **msc**, masticatory foramen; **spv**, sphenofrontal vacuity; **pom**, posterior maxillary foramen; **ppl**, posterior palatine foramen; **t**, temporal foramen; **rp**, rostral perforation (including infraorbital foramen); **vf**, venous foramen. Scale bar: 1 cm.

extant *Heteromys* Desmarest, 1817 (Wahlert 1985: fig. 2), mioheteromyines (Korth 1997: fig. 8), and *Harrymys* Munthe, 1988, originating above the orbits and extending posterodorsally to the nuchal crest (Wahlert 1991: fig. 1). The two ridges marking the attachment of the temporalis do not meet, and are separated by the width of the interparietal (6.35 mm). The interparietal is oval in shape and wider than the postorbital constriction, a condition in extant *Chaetodipus* and other heteromyids, that differs from extant *Perognathus* Wied-Neuwied, 1839 and dipodomyines where the interparietal is greatly reduced in size to accommodate bullar inflation. A large temporal foramen (0.75 mm in diameter) is present along the squamosal-temporal suture, level with the base of the zygomatic root. The mastoids are slightly swollen, not as much as in extant perognathines, but are inflated enough to project posteriorly, producing low, broad ridges along the lateral sides of the occiput. Although there is breakage on the mastoids, matrix has filled the broken areas, and it is not possible to determine if there is any cancellous bone present as in extant perognathines.

Damage to the rostrum has obliterated the pattern of the premaxillary-maxillary suture on the lateral sides. Along the ventral margin of the rostrum, the premaxillary-maxillary suture appears anterior to the rostral perforation and extends posteriorly along the ventral boundary of the infraorbital foramen before crossing the palatal surface. The infraorbital foramen is large with an associated rostral perforation (typical of heteromyids) that is situated low on the rostrum, near the ventral border. A small swelling of bone is ventral to the infraorbital foramen. As stated above, little of the morphology of the orbital wall is preserved, but there are three recognizable foramina preserved on the right side of the skull. A small, crescentic ethmoid foramen is present dorsal to M2, just above the center of the orbital wall. A small frontal foramen is also present along the dorsal border of the orbit, well posterior to the tooth row. The opening for the sphenopalatine vacuity is just dorsal to the tooth row and just posterior to M3. Although there is damage to the orbital wall, the contact between the orbitosphenoid and frontal is present on one side of the skull. In species of perognathines and dipodomyines there is an unossified area (Wahlert 1985; Korth 1998). This unossified area is clearly not present on UNSM 130000. The alisphenoid extends dorsally only as high as the glenoid fossa. There is no distinct muscle attachment on the dorsal alisphenoid as in geomyids, but ventral to the anterior margin of the zygomatic root on the squamosal is a bony knob. This knob of bone is slightly enlarged by distortion of the skull, but is similar to a recurved ridge present in perognathines along the anterior margin of the glenoid fossa. On the posterolateral portion of the alisphenoid are three foramina. The accessory foramen ovale is the largest (0.5 mm), most ventral, and most posterior. It is circular in shape. The other two foramina are the masticatory and buccinator. The masticatory foramen is dorsal and slightly posterior to the buccinator. It is crescentic in shape and opens anterodorsally. The buccinator is a small, nearly horizontal slit, just posterior to the tooth row.

The incisive foramen is small and tear-drop shaped. Its length (1.0 mm) is approximately 14% that of the total length of the upper diastema, well within the range of extant heteromyids (Wahlert 1985). The premaxillary-maxillary suture crosses the midline of the palate just anterior to the posterior end of the incisive foramen as in *Harrymys* and mioheteromyines (Korth 1997). The palatal surface is smooth and slightly concave ventrally with no grooves or ridges. The maxillary-palatine suture extends anteriorly on the palate to the level of the posterior margin of P4. There are three pairs of posterior palatine foramina medial to the molars. The posterior maxillary foramen is an elongated oval along the maxillary-palatine suture posteromedial to M3. The parapterygoid fossa is shallower than in *Chaetodipus* but deeper than in mioheteromyines with a large opening for the sphenofrontal canal in the center of the anterior margin of the fossa. Posterior and slightly lateral is the foramen ovale, along the posterolateral margin of the fossa.

None of the auditory bullae is fully preserved, but an anteroventral portion is preserved on both

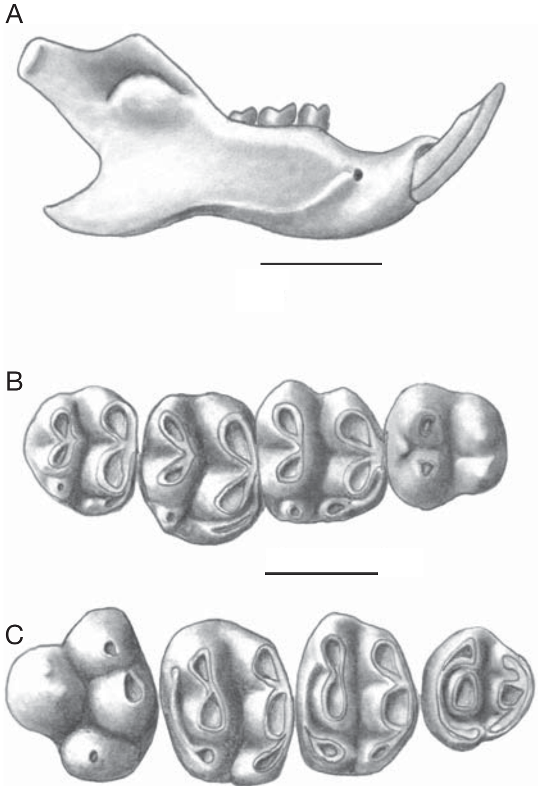

Fig. 2. — Mandible and cheek teeth of *Eochaetodipus asulcatus* n. sp. (UNSM 130000): **A**, lateral view of mandible; **B**, right p4-m3 (anterior to right); **C**, left P4-M3 (anterior to left). Scale bars: A, 5 mm; B, C, 1 mm.

sides. Where exposed, the bullar wall is a single lamina of bone. The bullae are slightly inflated and end anteroventrally in a point (directed anteromedially), but do not reach the center-line of the skull. There is a small, slit-like opening along the medial border of the bulla that appears to be the same as that identified by Wahlert (1985: fig. 2) as the "fissure medial to bulla" in extant *Heteromys*. No other foramina are recognizable in the basicranial area due to breakage.

No cranial foramina are recognizable on the back of the skull except the foramen magnum, again due to breakage. The nuchal crest is very low (not extending dorsal to the parietal bones) and has a small V at its center at the highest point on the skull. A low, rounded ridge runs ventrally from the apex of the occipital toward the foramen magnum. Laterally, the two ridges formed by the inflated mastoids are approximately as distinct as the central ridge of the occipital.

The mandible is slender, typical for heteromyids (depth below m1 = 4.1 mm and 4.0 mm: Fig. 2C). The diastema is nearly as long as the tooth row (4.1 mm) and shallow. The mental foramen is just above mid-depth of the mandible and just behind the center of the diastema. The masseteric fossa is shallow with only a ventral ridge. The ventral ridge runs anteriorly from the angle along the ventral border of the mandible, then angles anterodorsally from a point below p4 and ends at the posteroventral border of the mental foramen.

The ascending ramus originates lateral to m2 and blocks m3 from lateral view. The angle of the mandible has a sharp point posteriorly, similar to *Chaetodipus*, but does not flare laterally as in the former, it is in the same plane as the condyle. Anterior to the condyle is a rounded swelling for the base of the incisor. The coronoid process is not preserved on either of the mandibles, but the base of the process is recognizable, and very small, suggesting a minute process. There is no indication as to whether it was laterally deflected.

The upper incisors are separated from the skull, but both are present. In cross-section, they are longer (anteroposteriorly) than wide with a gently convex (nearly flat) anterior enamel surface that extends about one-fourth the height of the tooth on the lateral side.

The cheek teeth are brachydont as in species of perognathines. P4 is only preserved on the left side. It has a simple geomyoid pattern of four cusps (Fig. 2A). The protocone is the only cusp on the protoloph and is round in occlusal outline. There is a minute swelling on the buccal slope of the protocone (?paracone). The protocone is isolated, not connected to any of the cusps of the metaloph. The three cusps of the metaloph (hypostyle, hypocone, and metacone) are separated from one another by narrow valleys. The valley separating the hypocone and metacone is shallower, suggesting that the two cusps will fuse after moderate wear. The cusps of the metaloph form a curved loph that is concave anteriorly in occlusal outline.

M1 and M2 are nearly identical, M2 being slightly shorter (anteroposteriorly). These molars are the typical six-cusped, bilophate molars of heteromyids. The central cusps (protocone, hypocone) are the largest and the lingual styles (protostyle, hypostyle) are the smallest cusps. There is a narrow valley separating the styles, and a deeper valley that continues buccally, separating the rest of the protoloph and metaloph cusps. The anterior cingulum on M1 and M2 originates at the protostyle and runs buccally, anterior to the protocone, ending at the anterolingual corner of the paracone. The valley between the anterior cingulum and protoloph is narrow (narrower on M2) and will probably fuse with the protoloph after moderate wear.

M3 is the smallest molar and oval in occlusal outline. The protoloph is the same as in the anterior molars with three recognizable cusps. However, the posterior half of the tooth is reduced. There is no hypostyle present. A lingual cingulum runs posteriorly from the protostyle, then fuses with the hypocone posteriorly. There is no valley along the lingual border of the tooth as in the anterior molars. The metacone is reduced to a minute swelling at the buccal end of the metaloph.

The proportions of the lower incisor are similar to those of the upper incisor, but the anterior enamel surface is more strongly convex with no indication of flattening. The lower premolar is simple. It consists of four rounded, subequal cusps, with no indication of the development of lophodonty. The cusps of the metalophid (metaconid, protostylid)

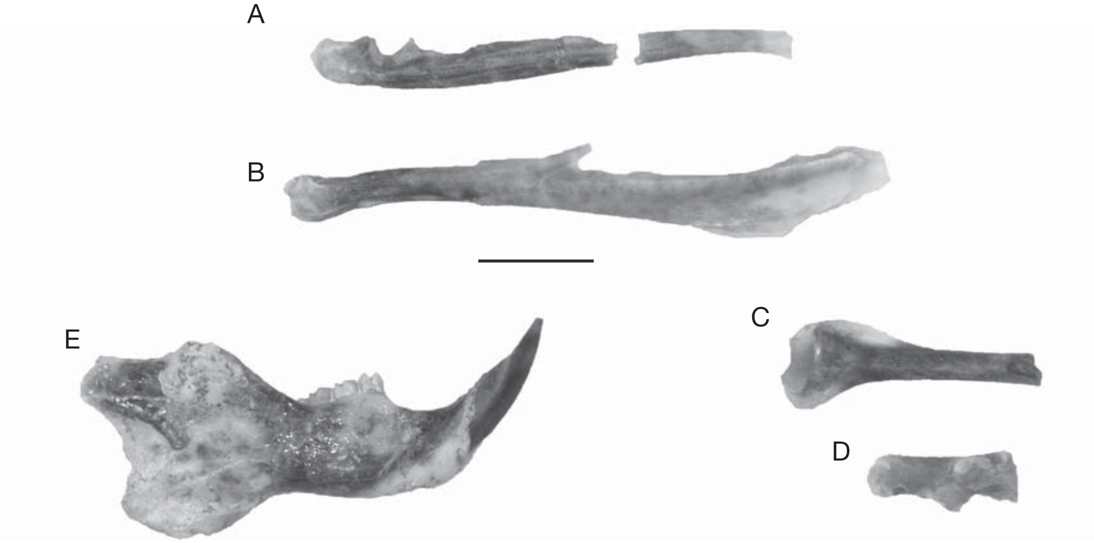

FIG. 3. — Postcranial elements and mandible of *Eochaetodipus asulcatus* n. sp. (UNSM 130000): **A**, ulna (distal end missing); **B**, tibiofibula (proximal end and fibula broken); **C**, humerus (proximal end missing); **D**, calcanium; **E**, lateral view of right mandible. Scale bar: 5 mm.

are closer together than the cusps of the hypolophid (hypoconid, entoconid). This makes the tooth narrower anteriorly than posteriorly (Fig. 2B). There is no indication that the anterior and posterior pairs of cusps will unite at the center of the tooth as in *Perognathus* and *Chaetodipus*. Instead, it appears that each of the cusps of the metalophid will unite with the hypolophid independently. The only other cuspule present on p4 is a minute hypoconulid between the hypolophid cusps along the posterior border of the tooth.

The first and second lower molars, as with their upper counterparts, are bilophate and six-cusped. The buccal stylids (protostylid, hypostylid) are the smallest cusps; the remainder are subequal in size. A deep valley runs transversely across the occlusal surface of the teeth separating the metalophid and hypolophid cusps. The only cingulum present is one that originates buccally at the anterior margin of the protostylid and wraps around the anterobuccal corner of the tooth, ending at the center of the anterior margin of the tooth. Both the metaconid and protoconid extend small arms to unite anteriorly with the cingulum. The arm is directed anterolingually from the protoconid and anterobuccally from the metaconid. The cusps of the hypolophid join by fusing at their anterior margins.

The last lower molar is smaller than the anterior molars, but with basically the same occlusal pattern. The hypolophid is slightly reduced by the reduction in the hypostylid and entoconid (similar to M3).

Among the postcranial fragments associated with UNSM 130000 are: humerus lacking proximal end; two tibia-fibulas lacking both ends; two calcanea (one broken); several vertebral fragments and phalanges (Fig. 3). Comparison of these bones with those of an equivalent-sized specimen of *Chaetodipus hispidus* shows very little difference in size and proportions. Korth (1997) stated that the limb bones of mioheteromyines were slightly more robust than those of extant heteromyids, but the bones associated with UNSM 130000 are equally proportioned with those of *Chaetodipus*.

DISCUSSION

Eochaetodipus n. gen. has several primitive characters that are shared with the mioheteromyines and extant heteromyines. The general shape of the mandible of *Eochaetodipus* n. gen. is similar to that of mioheteromyines and heteromyines with a deep emargination between the angle and the condyle, but the angle is not strongly deflected laterally as in perognathines and dipodomyines. On the cranium, the muscle scar for the temporalis in *Eochaetodipus* n. gen. extends the full length of the parietals as in mioheteromyines and extant heteromyines. In perognathines and dipodomyines, this scar is greatly shortened posteriorly, mainly due to the inflation of the bullae. The bulla in perognathines and dipodomyines is greatly inflated. The primitive condition in extant heteromyines and mioheteromyines, is a small bulla with little or no inflation. The bulla and mastoid in *Eochaetodipus* n. gen. is intermediate. It is only slightly enlarged and shows the beginnings of the inflation of the mastoid present in perognathines.

Eochaetodipus n. gen. has some derived features that appear to ally it with the perognathines and dipodomyines, but not the heteromyines. The primitive condition in geomyoids is that the buccinator and masticatory foramina are fused; this is the case in heteromyines and mioheteromyines (Korth 1997: fig. 11). In perognathines and dipodomyines, the two foramina are separated. The latter condition is present in *Eochaetodipus* n. gen. However, the primitive condition of the accessory foramen ovale is a large, round foramen on the posteroventral corner of the alisphenoid (Korth 1997). In the derived condition, the accessory foramen ovale is lost completely (perognathines and dipodomyines), or at least the posterior border is lost (heteromyines). The condition in mioheteromyines and harrymyines is a complete accessory foramen ovale and fused buccinator and masticatory foramina, believed to be the primitive condition for heteromyids. In *Eochaetodipus* n. gen., the entire accessory foramen ovale is retained as in mioheteromyines and harrymyines (primitive) but the buccinator and masticatory foramina are no longer fused similar to the perognathines and dipodomyines (derived). The condition in *Eochaetodipus* n. gen. appears to be transitional between the mioheteromyine condition and that of perognathines and dipodomyines but not with heteromyines.

Korth (1997) noted that the postcranial bones of mioheteromyines were more robust than those of extant heteromyids. The postcranial bones of *Eochaetodipus* n. gen. are more gracile than those of mioheteromyines and similar to those of extant perognathines and heteromyines.

The cheek teeth of *Eochaetodipus* n. gen. are brachydont and have a primitive heteromyid occlusal morphology. This bars *Eochaetodipus* n. gen. from inclusion in the Dipodomyinae, which are distinguished by much higher crowned cheek teeth (at least mesodont).

Wood (1935) separated fossil species into the Heteromyinae and Perognathinae, based on the union of the lophs of p4. In fossil perognathines, the union was central and in heteromyines, the union was either buccal or lingual of the center of the tooth, leaving a central basin. However, this distinction appears to break down in the more primitive species. In early heteromyids like *Proheteromys* and *Mookomys* Wood 1931, the cheek teeth are fairly low-crowned and the cusps of the metalophid of p4 do not form a distinct loph, but rather are isolated and circular in occlusal outline. The union of either of these metalophid cusps to the hypolophid is usually at the greatest anteroposterior diameter of the cusp (even with the center), so the ultimate union with the hypolophid is never central, but neither is it distinctly buccally or lingually placed to form a central basin. This suggests that the central union of the lophs in the premolar of extant perognathines is a derived condition, but so is the development of a central basin due to the buccal and lingual fusion of the lophs of the premolars in extant heteromyines. The premolars of *Eochaetodipus* n. gen. are brachydont and the cusps are simple and rounded, as would be expected in the primitive condition for heteromyids. The fusion of the lophs of the lower premolar lacks the derived condition of either the perognathines or heteromyines. Similarly, the lower premolars of several of the genera included in the Mioheteromyinae are not necessarily derived in the direction of extant heteromyines, but reflect their primitive nature (see Korth 1997 for figures).

It has also been the practice of authors to include fossil taxa with low-crowned cheek teeth in the Perognathinae because that is the condition in extant *Perognathus* and *Chaetodipus*. However, it is just as likely that these fossil taxa are simply earlier, primitive members of other subfamilies that have not yet modified their dentition towards hypsodonty. It is easy to exclude fossil species from the Perognathinae by the presence of mesodont or hypsodont cheek teeth, but inclusion for the primitive morphology (brachydonty) is not justified.

It appears that *Eochaetodipus* n. gen. represents a primitive perognathine based on skeletal and dental features, differing only from extant genera of the subfamily by the retention of several primitive heteromyid characters.

Three Tertiary species previously referred to *Perognathus* may be referable to *Eochaetodipus* n. gen.: *Perognathus trojectioansrum* Korth, 1979 from the late Barstovian of Nebraska, *P. ancenensis* Sutton & Korth, 1995 from the early Barstovian of Montana, and specimens referred to *P. minutus,* James, 1963 from the Barstovian of southern California (Lindsay 1972). There are several features that these species share with *Eochaetodipus* n. gen. that are distinct from all other Tertiary and Recent species of *Perognathus* (including Recent *Chaetodipus*).

The first morphology is the occlusal pattern of p4. On the holotype of *P. minutus*, UCMP 54575 from the Clarendonian (James 1963: fig. 45), the anterior cusps (metaconid and protostylid) unite posteriorly and form a short loph that runs posteriorly and joins the center of the hypolophid. This loph is not present on the stratigraphically lower referred specimens of *P. minutus* from the Barstovian of California (Lindsay 1972: fig. 22i). It is also lacking on the referred specimens of *P. trojectioansrum* (Korth 1979: fig. 3B) and *P. ancenensis* (Sutton & Korth 1995: fig. 9C, D) which is the same morphology of the p4 of *E. asulcatus* n. sp. (Fig. 2B). This character does not appear to be variable. All Recent specimens of *Chaetodipus* and *Perognathus* examined have this feature. In all other described Tertiary species of *Perognathus*, the loph connecting the anterior cusps of p4 to the hypolophid is present. It appears likely that the specimens identified by Lindsay (1972) as *P. minutus* are referable to a different species based on this character.

Another feature that unites these species to *Eochaetodipus* n. gen. is the morphology of the anterior cingulum of M2. On all other figured Tertiary species of *Perognathus*, the anterior cingulum is either absent or reduced to a minute cusp between the paracone and protocone along the anterior margin of the tooth (Sutton & Korth 1995). In the holotype of *Eochaetodipus asulcatus* n. sp., the anterior cingulum of M2 is nearly as complete as in M1, running nearly the entire width of the tooth anteriorly, joining the protostyle lingually. The only other species noted with this morphology was the specimens referred to "*P. minutus*" from the Barstow Formation (Lindsay 1972: fig. 22c) and *P. ancenensis* from Montana (Sutton & Korth 1995: fig. 9A, B). This feature was used to diagnose the latter species. Unfortunately, M2 is unknown for *P. trojectioansrum* (Korth, 1979).

The final distinctive feature of these species is the masseteric scar on the mandible. In all heteromyids, the anterior extent of the masseteric scar is a small shelf on the lateral side of the mandible that extends anterior to p4. In all Tertiary and Recent specimens of *Perognathus* and *Chaetodipus*, the anterior end of this shelf is dorsal to the mental foramen and extends anteriorly to at least the anterior margin of the foramen. On the mandible of *E. asulcatus* n. sp. this scar ends posterior to the mental foramen. This same condition is true for *P. trojectioansrum* (Korth 1979: fig. 3C). The mandible of *P. ancenensis* and the referred Barstovian specimens of "*P. minutus*" from Barstow are not known.

The similarities of these three species ("*P.*" *ancenensis*, "*P.*" *trojectioansrum*, and "*P. minutus*") to *E. asulcatus* n. sp. suggest that they may be referable to *Eochaetodipus* n. gen. However, all of these shared features appear to be primitive, so their presence in these species may exclude them from *Perognathus* or *Chaetodipus*, but it does not automatically include them in *Eochaetodipus* n. gen. Since all the characters are not known for all of the species, it is impossible to include them in *Eochaetodipus* n. gen. at this time.

Genus *Mioperognathus* n. gen.

Type species. — *Mioperognathus willardi* n. sp.

Range. — Middle Barstovian (middle Miocene) of New Mexico.

Diagnosis. — Derived perognathine features shared with *Perognathus* and *Chaetodipus*: mastoid and auditory bulla inflated; upper incisor grooved; accessory foramen ovale absent; unossified area present on medial orbital wall; premaxillary-maxillary suture crosses palate at posterior end of incisive foramina; buccinator and masticatory foramina separate; optic foramen greater than 1 mm in diameter. Primitive perognathine features: cheek teeth brachydont and bilophate; stapedial foramen present in bulla. Retained primitive heteromyid features lost in *Perognathus* and *Chaetodipus*: length of incisive foramina more than 15% of that of upper diastema; temporal foramen present on skull; scar for temporalis muscle extends onto parietal bones; mastoid and bulla inflated, but less than in *Chaetodipus*; no bony flange above orbits. Autapomorphic features: molars greatly decrease in size from M1 to M3; M3 markedly smaller than M2 and circular in occlusal outline.

ETYMOLOGY. — The name is intended to reflect the age of occurrence (Miocene) and the close systematic relationship to *Perognathus*.

DISCUSSION

Mioperognathus n. gen. is clearly referable to the Perognathinae based on the cranial characters used by Wahlert (1985: 14) to distinguish the three extant subfamilies of the Heteromyidae (large optic foramen, non-ossification on orbital wall including ethmoid foramen, inflated auditory bullae with anteroventral processes approaching each other and touching basisphenoid, squamosal bone extending as thin process posteriorly above acoustic meatus, upper incisors grooved). In addition, the brachydont cheek teeth of *Mioperognathus* n. gen. are similar to that of perognathines, and do not attain the mesodonty or hypsodonty of hetermyines or dipodomyines.

Mioperognathus n. gen. differs from *Perognathus* and *Chaetodipus* in lacking a number of derived character states (shorter incisive foramina; loss of temporal foramen; scar for temporalis limited to frontal bone; marked mastoid and bulla inflation; bony flange above orbits). In *Mioperognathus* n. gen., these character states are expressed as: a large, distinct temporal foramen; the length of the incisive foramen is over 20% that of the upper diastema; the scar for the temporalis muscle extends posteriorly for nearly the entire length of the parietal bones; there is some bullar and mastoid inflation, but much less than in *Chaetodipus* (the extant perognathine with the least amount of inflation of this area); and there is no flange of bone above the orbits. The skull of *Mioperognathus* n. gen. is believed to be more primitive because these features are similar to those of mioheteromyines and other geomyoids.

Mioperognathus willardi n. sp.
(Fig. 4; Table 1)

Perognathus minutus – Korth, 1998 (in part).

HOLOTYPE. — FAM 129674, nearly complete cranium with incisors and right M1 (partial)-M3.

OCCURRENCE. — Lower Pojoaque Bluffs, Pojoaque Member, Tesuque Formation, New Mexico.

AGE. — Late Barstovian (middle Miocene).

DIAGNOSIS. — Only species of the genus.

ETYMOLOGY. — Patronym for Willard Korth for his physical and moral support of my research.

DENTAL MEASUREMENTS. — M1, tr = 1.00 mm; M2, a-p = 0.69 mm, tr = 0.89 mm; M3, a-p = 0.43 mm, tr = 0.55 mm (from Korth 1998: table 1). Abbreviations as in Table 2.

DESCRIPTION

The cranium and upper molars of *Mioperognathus* n. gen., FAM 129674, have been previously described in detail as those of *Perognathus minutus* (Korth 1998: 133). Since there is no additional material available, nothing will be added to the original description.

DISCUSSION

Korth (1998) originally referred FAM 129674 to *Perognathus minutus* James, 1963 because of its similar size and time equivalent occurrence to the species from southern California (Lindsay 1972). However, based on dental measurements, the described specimen is distinctly smaller than the Barstovian sample of "*P. minutus*" from California (Lindsay 1972: table 9; Korth 1998: table 1). The only described Tertiary species of *Perognathus* that is similar in size is "*P.*" *trojectioansrum* from the Barstovian of the northern Great Plains.

In addition to overall size, there is another feature that separates FAM 129674 from specimens of *P. minutus*; the relative sizes of the upper molars

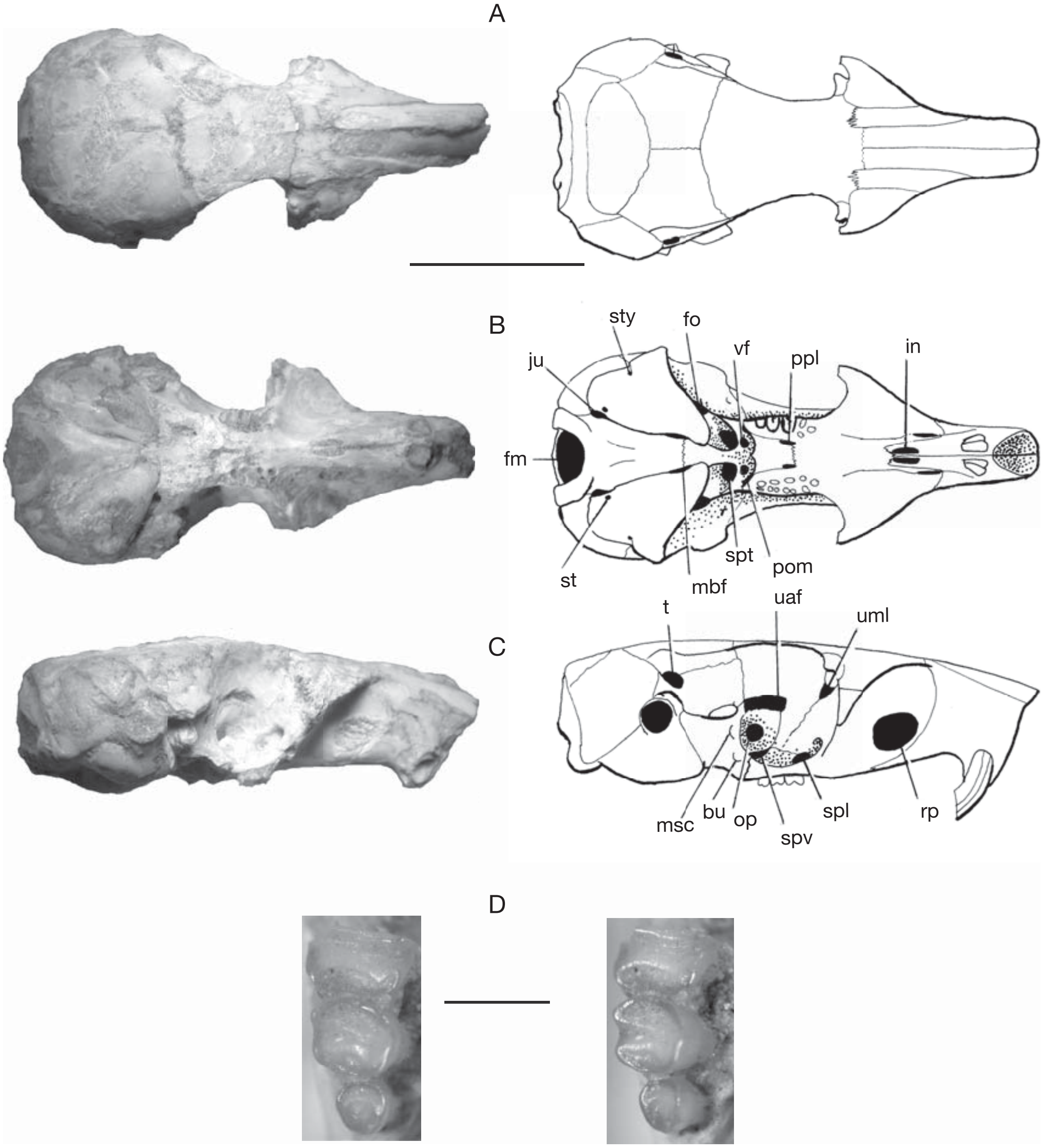

FIG. 4. — Cranium and upper molars of *Mioperognathus willari* n. sp. (FAM 129674) (holotype): **A**-**C**, photographs (left) and line diagrams of the cranium; **A**, dorsal view; **B**, ventral view; **C**, right lateral view (zygomatic arch removed); **D**, right M1(broken)-M3 (stereo pair; anterior toward top). Abbreviations: **bu**, buccinator foramen; **fm**, foramen magnum; **fo**, foramen ovale; **in**, incisive foramen; **ju**, jugular foramen; **mbf**, fissure medial to bulla; **msc**, masticatory foramen; **op**, optic foramen; **pom**, posterior maxillary foramen; **ppl**, posterior palatine foramen; **spl**, sphenopalatine foramen; **spt**, spheopterygoid canal; **spv**, sphenofrontal vacuity; **rp**, rostral perforation (including infraorbital foramen); **st**, stapedial foramen; **sty**, stylomastoid foramen; **t**, temporal foramen; **uaf**, unossified area between alisphenoid and frontal bones; **uml**, unossified area between maxillary and lacrimal bones; **vf**, venous foramen. Scale bars: A-C, 1 cm, D, 1 mm.

TABLE 3. — List of character states used in PAUP analysis.

1. Bony flange above orbit: absent (0), present (1).
2. Length of incisive foramen compared to total length of upper diastema: >23% (0), between 23 and 15% (1), <15% (2).
3. Inflation of auditory bulla and mastoid: absent (0), present (1).
4. Unossified area on orbital wall: absent (0), present (1).
5. More gracile limb bones: absent (0), present (1).
6. Size of optic foramen: <1mm in diameter (0), >1mm in diameter (1).
7. Groove on upper incisor: absent (0), present (1).
8. Stapedial foramen (artery): present (0), absent (1).
9. Loph of p4 united by central loph: absent (0), present (1).
10. Central basin formed on p4: absent (0), present (1).
11. Where premaxillary-maxillary suture crosses the midline of the palate: anterior to the posterior margin of the incisive foramen (0), at the posterior end of the incisive foramen (1).
12. Crown-height of cheek teeth: brachydont (0), mesodont (1).
13. Buccinator and mastecatory foramina: fused (0), separate (1).
14. Accessory foramen ovale on alisphenoid: present and complete (0), present but lacking posterior margin (1), absent (2).
15. Temporal foramen: present (0), absent (1).
16. Length of scar for temporalis muscle: complete to occipital (0), shortened (1).
17. Shape of interparietal bone: triangular (0), oval (1).
18. Depth of parapterygoid fossa: shallow (0), deeper (1), extremely deep (2).
19. Angle of the mandible: straight (0), deflected (1).
20. Bone of the bulla: single lamina (0), trabeculate (1).
21. Squamosal reduced to thin bar posteriorly: absent (0), present (1).

TABLE 4. — Character matrix of taxa used in PAUP analysis.

	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**
Mioheteromyinae	0	0	0/1	0	0	0	0/1	0	0	0	0	0/1	0	0	0	0	0	0	0	0	0
Heteromys/Liomys	1	2	0	0	1	0	0	1	0	1	0	1	0	1	1	0	0	2	0	0	0
Eochaetodipus	0	2	1	?	1	?	0	0	0	0	0	0	1	0	0	0	1	1	0	0	0
Mioperognathus	0	1	1	1	?	1	1	0	0	0	1	0	1	2	0	0	1	1	0	0	0
Perognathus/ Chaetodipus	1	2	1	1	1	1	1	0	1	0	1	0	1	2	1	1	1	2	1	1	1

(Fig. 4D). In all described species of *Perognathus*, M1 and M2 are nearly identical in size, M2 being approximately 95% the width of M1. On the holotype of *M. willardi* n. sp., M2 is less than 90% the size of M1. Even more strikingly, M3 on FAM 129674 is markedly smaller than M2 having a transverse width of only 62% that of M2 (Korth 1998: table 1). On all species of *Perognathus*, M3 is usually smaller than M2 but has over 80% the transverse width of M2. Besides its smaller size, M3 of *M. willardi* n. sp. is circular in occlusal outline, not oval as in species of *Perognathus* and other perognathines. "*Perognathus" trojectioansrum* is similar in size, but it differs from *M. willardi* n. sp. in lacking the difference in proportional size of the upper molars. Although no M2s or M3s of "*P." trojectioansrum* were reported, measurements taken from the figured maxilla with alveoli for these teeth (UNSM 56313; Korth 1979: fig. 3A) demonstrate that the width of M2 is 98% that of M1, M3 has 80% the width of M2, and M3 is wider than long (oval in occlusal outline).

Mioperognathus n. gen. differs from *Eochaetodipus* n. gen. in several features of the skull that are shared with extant *Perognathus*: 1) loss of the accessory foramen ovale; 2) greater inflation of the bulla and

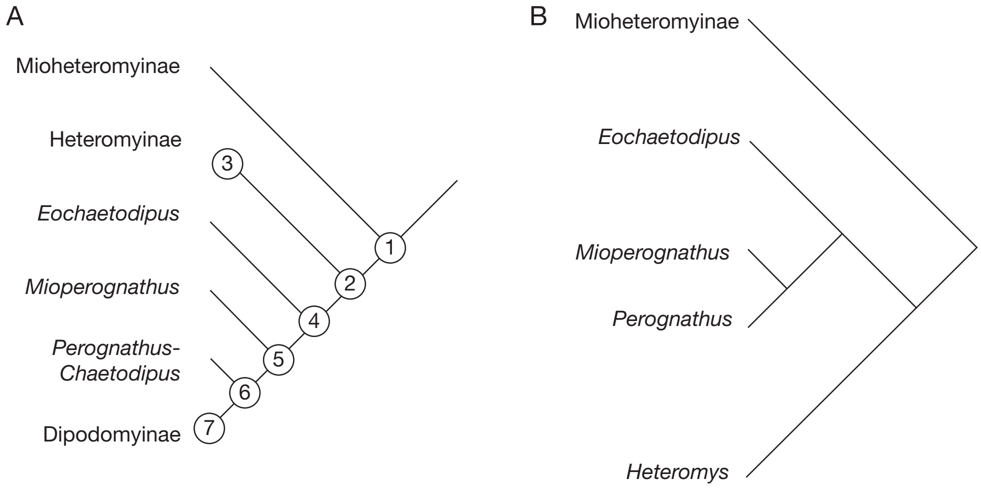

FIG. 5. — Phylogenies of selected heteromyid taxa: **A**, Cladogram of relationships of heteromyids. Explanation of nodes: **1**, Heteromyidae; buccinator and masticatory foramen (fused) separated from accessory foramen ovale; rostral perforation associated with infraorbital foramen. **2**, More gracile skeleton; incisive foramen less than 15% length of upper diastema. **3**, Heteromyinae; bony flange above orbit; loss of stapedial foramen; mesodonty; central basin on lower premolar; deeper parapterygoid fossa; loss of posterior border of accessory foramen ovale. **4**, beginnings of bullar and mastoid inflation; buccinator and masticatory foramina separated; interparietal oval. **5**, presence of unossified area on medial orbital wall; loss of accessory foramen ovale; premaxillary-maxillary suture on palate crosses incisive foramina at their posterior end; greater inflation of bulla and mastoid. **6**, central union of lophs on p4; deeper parapterygoid fossa; loss of temporal foramen; bony flange above orbit; even greater inflation of mastoid and bulla. **7**, Dipodomyinae; bulla enormously inflated; limb proportions for ricochetal locomotion; incisive foramina greatly enlarged; cheek teeth mesodont to hypsodont. **B**, Single most parsimonious tree based on PAUP analysis. Total length = 27 steps. Consistency index = 0.8889. Homoplasy index = 0.1111. Retention index = 0.7500. Multiple derived states for characters 2, 14, and 18 are ordered. See Table 3 for list of character states.

mastoid; 3) shorter posterior extent of the temporalis muscle scar; 4) presence of an unossified area on the orbital wall; 5) squamosal reduced to a thin bar of bone posteriorly; and 6) sulcate upper incisors. The inflation of the mastoid, extent of the temporalis muscle scar, and width of the interparietal bone in *Mioperognathus* n. gen., are not as derived as in Recent *Perognathus* or *Chaetodipus*. *Mioperognathus* n. gen. also retains the temporal foramen as in *Eochaetodipus* n. gen. In one cranial feature, the earlier and generally more primitive *Eochaetodipus* n. gen. is more derived (closer to the morphology of *Perognathus*) than *Mioperognathus* n. gen. The relative length of the incisive foramina compared to the length of the upper diastema in the latter is approximately 23%, whereas in *Eochaetodipus* n. gen. and extant perognathines, it is less than 15%. *Mioperognathus willardi* n. sp. is also much smaller in size than *E. asulcatus* n. sp. *Eochaetodipus* n. gen. also lacks the marked reduction in size of the upper molars present in *Mioperognathus* n. gen.

DISCUSSION

Eochaetodipus n. gen. is referred to the Perognathinae based on several derived characters of the skull and skeleton shared with extant perognathines. *Eochaetodipus* n. gen. has a reduced incisive foramen (length less than 15% that of upper diastema). In mioheteromyines and harrymyines, the ratio of the length of the incisive foramen to the total length of the upper diastema ranges from 24 to 46% (Korth 1997: table 5). Primitively, in mioheteromyines and harrymyines, the buccinator and masticatory foramina are fused into a single foramen. In *Eochaetodipus* n. gen., these foramina are separated as in extant perognathines. The interparietal in harrymyines and mioheteromyines is triangular in shape, similar to extant heteromyines. In *Eochaetodipus* n. gen., the interparietal is oval in shape and very broad. This same broad, oval shape is also present in *Perognathus* and *Chaetodipus*. The bulla and mastoid of *Eochaetodipus* n. gen. show the beginnings of inflation but it is not as marked as in extant perognathines, but is clearly greater than that in heteromyines. One mioheteromyine shows similar inflation of the mastoid and bulla, *Schizodontomys* Rensberger 1973 (Korth *et al*. 1990). The harrymyine genus *Harrymys* also has an inflated bulla and mastoid (Wahlert 1991). It is suggested here that the bullar inflation occurred separately in *Schizodontomys* and *Harrymys* because of the distinctive nature of their cheek teeth (increased crown height, occlusal pattern) and lack of any of the other derived cranial characters of perognathines. Because other mioheteromyines, such as *Balantiomys*, lack this inflation (Gazin 1932; Wood 1935; Korth 1997), it is not likely a primitive condition for that subfamily or for the entire Heteromyidae.

The final feature of *Eochaetodipus* n. gen. that is shared with extant perognathines is the slenderness of the limb bones. The bones of *Eochaetodipus* n. gen. are more delicate than any known for a mioheteromyine.

Eochaetodipus n. gen. cannot be referred to either of the extant genera of perognathines because it lacks a number of derived features: 1) grooved upper incisor; 2) loss of temporal foramen; 3) loss of accessory foramen ovale; 4) unossified area on orbital wall; 5) reduced (shortened) temporalis ridge; 6) greater inflation of mastoid and bulla; 7) angle of mandible deflected laterally; and 8) central union of lophs on p4. The character state of all these features in *Eochaetodipus* n. gen. is primitive, and similar to that of mioheteromyines and harrymyines.

The cranium of *Mioperognathus* n. gen. is markedly similar to the skulls of modern perognathines but retains a large temporal foramen, has less inflation of the mastoids, and has the primitive condition of the temporalis muscle scar (continuous for full length of parietals). However, this skull has several features of extant perognathines that are lacking in *Eochaetodipus* n. gen.: 1) greater inflation of mastoid; 2) grooved upper incisor; 3) loss of accessory foramen ovale; and 4) unossified area on orbital wall. *Mioperognathus* n. gen. is clearly intermediate in morphology between *Eochaetodipus* n. gen. and extant perognathines (Fig. 5A). PAUP analysis was run on the cranial and dental features of the perognathines discussed (Tables 3, 4). The resulting phylogeny (Fig. 5B) shows these same relationships. *Mioperognathus* n. gen. is also temporally intermediate between *Eochaetodipus* n. gen. and perognathines.

The morphocline for many cranial and dental characters in perognathines goes from *Eochaetodipus* n. gen., to *Mioperognathus* n. gen., to *Chaetodipus*, and finally to *Perognathus*. This sequence is also reflected in the fossil occurrence of these genera: *Eochaetodipus* n. gen. is late Arikareean; *Mioperognathus* n. gen. is Barstovian; and all fossil species previously referred to *Perognathus* are Barstovian and younger.

Extant heteromyines have been generally grouped with the perognathines because of several derived characters: flange above the orbit; reduced size of incisive foramen; loss of the temporal foramen; more gracile limb bones; deeper parapterygoid fossa; and loss of the accessory foramen ovale. With the recognition of *Eochaetodipus* n. gen. and *Mioperognathus* n. gen., it appears that several of these features were arrived at independently from the perognathines. Extant heteromyines retain an uninflated bulla and mastoid, and fusion of the buccinator and masticatory foramina. Both these features are derived in both *Eochaetodipus* n. gen. and *Mioperognathus* n. gen., and shared with perognathines. The loss of the accessory foramen ovale in heteromyines is also present in *Mioperognathus* n. gen., suggesting a separate development of this feature. The only feature not present in either *Eochaetodipus* n. gen. or *Mioperognathus* n. gen. is the bony flange above the orbits. Extant heteromyines also have lost the stapedial foramen, a derived feature not present in any other heteromyids, extant or fossil (unknown in *Eochaetodipus* n. gen.).

The Perognathinae could have easily arisen from a primitive mioheteromyine ancestor during the Arikareean. The earliest perognathine is *Eochaetodipus* n. gen., which shares a number of the primitive cranial and dental features of the mioheteromyines. Extant heteromyines represent a different clade that likely arose from a mioheteromyine ancestor as well, but separately from the perognathines.

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