GEOMYOID RODENTS FROM THE EARLY HEMINGFORDIAN (MIocene) OF NEBRASKA

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ABSTRACT

The fauna of geomyoid rodents from the Runningwater Formation of western Nebraska is quite diverse, containing three heteromyids, two geomyids, two florentiamyids and an indeterminate geomyoid. Two new genera, Stratimus (a heteromyid) and Fanimus (a florentiamyid) and five new species are described (Stratimus strobeli, Schizodontomys annectus, Pleurolicus hemingfordensis, Ziamys hugeni, and Fanimus ultimus). The Hemingfordian geomyoid fauna from Nebraska is unique and has little similarity to other rodent faunas of the same age.

A marked increase in the overall diversity of geomyoids in the Hemingfordian is provided by the recognition of the Nebraska species. These species display a diversity intermediate between that of Arikareean faunas that are dominated by geomyids and Barstovian faunas that are dominated by heteromyids.

INTRODUCTION

No geomyoids have been reported previously from the Hemingfordian of Nebraska. Elsewhere in the Great Plains, the described geomyoid fauna has consisted of the geomyids Dikkomys (Galbreath, 1948; Macdonald, 1970; Green and Bjork, 1980) and ?Gregorymys (Martin, 1976), the heteromyids Proheteromys (Wood, 1935; Wilson, 1960; Skwara, 1988), Mookomys (Wilson, 1960), Heliscomys (Skwara, 1988) and Schizodontomys (Rensberger, 1973a; see Wahlert, 1985 for reference to Heteromyidae), and the eomyids Pseudotheridomys (Wilson, 1960; Skwara, 1988), Leptodontomys and ?Paradijdama (Skwara, 1988).

The recovery of a relatively large geomyoid sample from Runningwater deposits in Nebraska was the result of intensive prospecting of Hemingfordian outcrops southeast of Gordon, Nebraska, by Bruce Bailey. Specimens were recovered primarily from surface exposures, although recent screening efforts demonstrate considerable potential for microfossil recovery.

We also include some specimens from UNSM locality Bx-7 (Hemingford Quarry 7B) and from UNSM localities Dw-117 and Dw-118, Runningwater Formation, Box Butte and Dawes counties, Nebraska. Specimens from Bx-7 were collected by UNSM field parties in the late 1930s and early 1940s during quarrying of Runningwater sediments north of the town of Hemingford, Nebraska. Specimens

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from Dw-117 and Dw-118 were screened by R. G. Corner, G. Ostrander, and B. Messenger from Runningwater sediments exposed in roadcuts during realignment of U.S. Highway 385, Dawes County, Nebraska.

Abbreviations used in text are: AMNH, American Museum of Natural History; F:AM, Frick Collections, American Museum; KU, University of Kansas Museum of Natural History; UCMP, University of California Museum of Paleontology; UNSM, University of Nebraska State Museum. Dental terminology used follows Rensberger (1973a, Fig. 6).

**Geology**

The majority of the rodents described in this report were derived from sediments of the Runningwater Formation exposed along the valley of the Niobrara River and its tributaries southeast of Gordon, Nebraska, about 120 km (75 mi) east of the type section of the formation (Cook, 1965). From this area, a number of excellent specimens, including skulls of Schizodontomys and Ziamys, were collected by Bailey together with numerous additional mammalian fossils of Early Hemingfordian age. This eastern extension of the Runningwater Formation in western Cherry County was first reported by Skinner and Johnson (1984), who were aware of the similarity of these sediments south of Gordon to those of the type area of the formation.

Additional Runningwater specimens discussed in this study from the Hemingford Quarries were found 29 km (18 mi) southeast of the type section. The Dw-117 and Dw-118 roadcuts are located within the Niobrara valley 40 km (25 mi) east of the Runningwater type section.

The Runningwater Formation is bracketed by two vitric tuffs, one near the top of the formation in its type area, and the other occurring in the Upper Harrison Beds, the formation underlying the Runningwater Formation over much of its outcrop area. Near the top of the Runningwater Formation, a vitric tuff (SW ¼, NE ¼, NE ¼, section 30, T28N, R51W, Box Butte County, Nebraska) along the south rim of the Niobrara River valley has been fission-track dated using glass shards yielding a minimum age of 16.9 ± 1.7 Ma (Hunt, 1981:276). In Sioux County, Nebraska, a vitric tuff in the Upper Harrison beds (W ½, NW ¼, SW ¼, SE ¼, section 27, T32N, R56W) has been fission-track dated at 19.2 ± 0.5 Ma using zircons (Hunt et al., 1983:366). Consequently, the age of this section based on the dates provided by the two vitric tuffs spans the interval of approximately 19 to 17 Ma. The Runningwater Formation was deposited during the latter part of this interval, from about 18 to 17 Ma.

Hemingford Quarry 7B fossils are from the upper part of the Runningwater Formation and occur near the stratigraphic level of the 16.9 Ma tuff but 16 km (10 mi) east of the tuff locality. The rodents from the Niobrara River valley southeast of Gordon are from the lower part of the Runningwater Formation. On biostratigraphic criteria, the fauna collected from the lower part of the formation (as represented southeast of Gordon) is believed by Hunt to be an older assemblage than that from the Hemingford quarries. The highest faunal levels southeast of Gordon are associated with the Aletomeryx Quarry, worked by parties from Yale University (1914), the American Museum (1934), and Amherst College (1934). From this quarry come the remains of the amphicyonid carnivore Daphoenodon niobarensis, associated with bones of the protolabine camel Michenia, and a large sample of the small ruminant artiodactyl Aletomeryx gracilis. Hunt has been able to compare the stage of evolution of the two artiodactyls and the carnivore with...
similar forms in the Hemingford quarries. The representatives of these three lineages from Aletomeryx Quarry are less advanced than their probable lineal descendants in the Hemingford quarries. Because the Aletomeryx Quarry fauna is derived from the highest stratigraphic level in the Runningwater Formation southeast of Gordon, all of which is the lower part of the formation, the rodents from this level and from beds stratigraphically below it in the Gordon area represent a lower biostratigraphic assemblage within the Runningwater Formation that has been poorly represented in the type area of the formation farther west.

From the lower part of the Runningwater Formation southeast of Gordon there are two heteromyids (Schizodontomys and Proheteromys) and two geomyids (Pleurolicus and Ziamys) described below. Fossil rodents from UNSM localities Dw-117 and Dw-118 are from the Runningwater Formation, hence early Hemingfordian, but the exact stratigraphic level of these sites within the formation is not yet worked out.

SYSTEMATIC PALEONTOLOGY

Order Rodentia Bowdich, 1821
Family Heteromyidae Gray, 1868
Subfamily Perognathinae Coues, 1875
Genus Stratimus, new genus

Type species.—Stratimus strobeli new species.

Range.—Hemingfordian (early Miocene) of Nebraska and Colorado.

Referred species.—None.

Diagnosis.—Small perognathine; P4 with central anteroposteriorly directed loph originating from anterolingual corner of hypoconid and anterobuccal corner of entoconid; small lophules originating from the hypoconid and entoconid on lower molars join anteriorly to form V-shaped hypolophid; upper molars with short anterior cingulum; protocone of P4 circular without accessory cusplets.

Etymology.—Latin, strata, paved road or street; mus, mouse. In reference to the State of Nebraska Department of Roads under whose auspices the topotypic material of Stratimus strobeli was collected.

Discussion.—Stratimus differs from all contemporary heteromyids in the V-shape of the hypolophid of the lower molars and the central lophule of P4. Only two heteromyids are known with a central, anteriorly running loph on P4, Cupidinimus saskatchewanensis from the early late Barstovian of Canada (Storer, 1970, 1975; Barnosky, 1986a), and Proheteromys sp. cf. P. magnus from the Hemingfordian of Colorado (Wilson, 1960). Stratimus is clearly lower crowned than all species of Cupidinimus, and though C. saskatchewanensis is known only from isolated teeth, there are no lower molars of comparable size from the faunas that contain C. saskatchewanensis that share the unique hypolophid of Stratimus. The single isolated specimen referred to Proheteromys sp. cf., P. magnus, KU 10239 (Wilson, 1960), also has this unique loph but is much larger than S. strobeli and much more quadrate. The molars referred to the same species lack the Stratimus-like hypolophid.

The problematical geomyoid Lignimus has lower molars with hypolophids that form the anteriorly pointing V as in Stratimus (Storer, 1970, 1973). It differs from Stratimus in having higher crowned cheek teeth, an anterior cingulum on the lower molars that extends anteriorly encircling and isolating an enamel lake, and a more complex P4, without a central loph.
All other Hemingfordian genera of heteromyids, *Proheteromys* (Wood, 1932, 1935; Wilson, 1960; Lindsay, 1974), *Mookomys* (Lindsay, 1974), *Trogomys* (Whistler, 1984), and *Cupidinimus* (Whistler, 1984; Barnosky, 1986a), have hypolophids on the lower molars that form straight rows of three cusps, the typical geomyoid pattern. Wood (1935: fig. 96a) figured the holotype of *Proheteromys matthewi* from the Hemingfordian Rosebud Formation of South Dakota with a V-shaped hypolophid on M1. However, the hypolophid of this specimen (AMNH 12896a) is thickest at its center (hypoconid) but does not have the sharp anterior apex of *Stratimus*. It is also smaller than *S. strobeli*, and its P4 lacks an anteriorly running loph.

**Stratimus strobeli**, new species
(Fig. 1; Table 1)


*Proheteromys* sp. intermediate species Skwara, 1988:72 (in part).

**Type specimen.** — UNSM 26688, mandible with LP4–M1.

**Horizon and locality.** — Type from UNSM locality Dw-118; referred specimens from UNSM localities Dw-117 and Dw-118, Runningwater Formation, Dawes County, Nebraska.

**Age.** — Early Hemingfordian (early Miocene).

**Referred specimens.** — UNSM 26691 and 26693, partial mandibles with P4 and I1; UNSM 26690 and 26692, partial maxillae with P4–M1; and UNSM 26689, RP4.

**Diagnosis.** — As for genus.

**Etymology.** — Patronym for G. C. Strobel, Director, State of Nebraska Department of Roads, for his support of the Highway Paleontological Salvage Program.

**Description.** — Mandible similar to that of *Proheteromys*; masseteric scar consisting of prominent ventral ridge, rising dorsally below P4, and terminating anteriorly in small anteroposteriorly elongate knob, ventral and anterior to P4, just dorsal to the center of the mandible; mental foramen small, anterior, and slightly ventral to anterior end of masseteric scar, ventral to middle of diastema; diastema shallow and relatively long.

I, narrow, tapering posteriorly; small flattened area on anterior surface; enamel extends about 1/3 depth of tooth on lateral side, just slightly on medial side.

Cheek teeth brachydont, cusps slightly more inflated than in *Proheteromys*; P4 smaller than anterior molars; metalophid consisting of two major cusps (protoconid and metaconid); megacristid slightly larger than protostylid; on UNSM 26691, metalophid cusps connected anteriorly by anterior cingulum (metalophid 1), no connection or anterior cingulum on holotype; metalophid consisting of subequal hypoconid and entoconid; small lophulids extend toward midline of tooth arising from anterolingual corner of hypoconid and anterobuccal corner of entoconid; on UNSM 26691, both lophulids join at midline of tooth and form anteriorly running lophule that terminates anteriorly between cusps of metalophid (not reaching anterior cingulum); on holotype only the lophulid from hypoconid is connected to anterior running lophule which terminates slightly more anterior.

M1 and M2 nearly identical with typical six-cusped, bilophate pattern of geomyoids; protostylid and entoconid nearly identical with typical six-cusped, bilophate pattern of geomyoids; protostylid slightly larger than protostylid; on UNSM 26691, metalophid cusps connected anteriorly by anterior cingulum (metalophid 1), no connection or anterior cingulum on holotype; metalophid consisting of subequal hypoconid and entoconid; small lophulids extend toward midline of tooth arising from anterolingual corner of hypoconid and anterobuccal corner of entoconid; on UNSM 26691, both lophulids join at midline of tooth and form anteriorly running lophule that terminates anteriorly between cusps of metalophid (not reaching anterior cingulum); on holotype only the lophulid from hypoconid is connected to anterior running lophule which terminates slightly more anterior.

Protocone of P4 circular to slightly buccolingually ovate; no accessory cuspules present; metaloph consisting of three major cusps, circular hypocone largest; entoconid anteroposteriorly elongate, extending anterior to remainder of metaloph.

M1 subequal to P4 in size; protoloph and metaloph consisting of parallel rows of three cusps; central transverse valley narrowing between protostyle and entostyle but remaining open lingually; on unworn specimen, UNSM 26692, small anterior cingulum present anterior to protocone, not directly connected to protocone.
Table 1.—Dental measurements of *Stratimus strobeli*. Abbreviations: a-p, anteroposterior length; tra, anterior transverse width; trp, posterior transverse width. Measurements in mm.

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Discussion.—Wilson (1960) identified several isolated teeth and a partial mandible from the Hemingfordian of Colorado as *Mookomys* sp. cf. *M. formicorum*. He distinguished these specimens from those of *Proheteromys* in the same fauna by the more robust cusps of the cheek teeth. Among these specimens, a partial mandible containing P<sub>4</sub>–M<sub>3</sub> (KU 10235) is clearly referable to *S. strobeli*. It is also possible that the other specimens referred to by Wilson are also *S. strobeli*. However, an isolated P<sub>4</sub> (KU 10234) lacks the central loph of *Stratimus*, and may represent a different taxon.

Similarly, Skwara (1988) identified numerous isolated cheek teeth of a heteromyid she referred to "*Proheteromys* sp intermediate species" from the Hemingfordian of Saskatchewan. Many of the figured lower cheek teeth of this species have the characteristic hypolophid of *S. strobeli*. These specimens are also similar in size to those of *S. strobeli*.

Subfamily Heteromyinae Gray, 1868
Genus *Proheteromys* Wood, 1932
*Proheteromys* cf. *P. magnus* Wood, 1932
(Fig. 1b)

Referred specimen.—UNSM 26679, LP<sup>4</sup>.

Horizon and locality.—200 m east of UNSM locality Cr-126, Runningwater Formation, Cherry County, Nebraska.

Age.—Early Hemingfordian (early Miocene).

Description.—UNSM 26679 large for *Proheteromys* (a-p, 1.80 mm; tra, 0.73 mm; trp, 1.80 mm; see Table 1 for abbreviations); heavily worn; brachydont; protoloph consisting of large, ovate protocone and small paracone on buccal slope of protocone; metaloph concave anteriorly; entostyle blocks transverse valley lingually, connecting to hypocone by curving posterolingual cingulum arising from posterior margin of hypocone.

Discussion.—UNSM 26679 is intermediate in size between *Proheteromys magnus* from Florida and *P. sp. cf. P. magnus* from Colorado (Wilson, 1960:79). The wear facet interpreted as the paracone on UNSM 26679 may be homologous to the buccal ridge on the protocone of P<sup>4</sup> from Quarry A (Wilson, 1960: fig. 125). It is very likely that the Nebraska specimen is the same species as that from Quarry A, but its specific reference to *P. magnus* is still questionable, as discussed by Wilson (1960:79–80).
Genus *Schizodontomys* Rensberger, 1973a

*Type species.*—*S. greeni* Rensberger, 1973a.

*Referred species.*—*S. harkseni* (Macdonald, 1970); *S. sulcidens* Rensberger (1973a); and *S. amnicolus* new species.

*Range.*—Medial Hemingfordian of Wyoming, Early Hemingfordian of Oregon, South Dakota, and Nebraska, and latest Arikareean of South Dakota, Nebraska and Wyoming.

*Discussion.*—Rensberger (1973a) originally referred *Schizodontomys* to the subfamily Pleurolicinae of the family Geomyidae. Later, Munthe (1981) described the skull and postcranial skeleton of *Schizodontomys* and concluded that this genus, and possibly all pleurolicines, were distinct from other geomyoids and might constitute a family separate from both the Geomyidae and Heteromyidae.

Most recently, Wahlert (1985) demonstrated that *Schizodontomys*, based on cranial foramina, was referable to the Heteromyidae. He placed *Schizodontomys* questionably in the subfamily Dipodomyinae based on the shared character of an inflated auditory bulla. *Schizodontomys* is here placed in the Heteromyinae based on both dental and cranial features. According to Wood (1935), the heteromyines are distinguishable from other heteromyids by the fusion of the lophs on P₄ which occurs at the buccal and lingual ends of the lophs first, isolating a central enamel lake. In perognathines and dipodomyines the fusion of the lophs on P₄ is central. On all species of *Schizodontomys* the lophs of P₄ fuse as in heteromyines.

Wahlert (1985:14) diagnosed the Heteromyinae as having three derived cranial features: 1) ventral root of anterior-alar fissure rising above M¹; 2) masticatory and buccinator foramina united; and 3) stapedial and sphenofrontal foramina absent. The skulls described by Munthe (1981) and an additional skull, UNSM 26686, clearly possess fused masticatory and buccinator foramina, but do retain a stapedial foramen. This later feature, however, is primitive and would not exclude *Schizodontomys* from the Heteromyinae. On all of the reported skulls of *Schizodontomys*, the medial orbital wall is damaged and the presence or absence of this foramen cannot be determined.

UNSM 26686 preserves slightly more of the medial orbital wall than those skulls described by Munthe (1981) and the ethmoid and sphenopalatine foramina are observable (Fig. 2). An enlarged ethmoid foramen is dorsal to M₂ and oval in outline. The sphenopalatine is dorsal to M¹ and is anteriorly elongate as in Perognathus (see Wahlert, 1985: fig. 3). There is also no evidence of an optic foramen. Bone is lacking on the anterior dorsal corner and the entire posterior edge of the medial orbital wall. This is interpreted on UNSM 26686 to be due to breakage, and not the lack of ossification in these areas as in perognathines and dipodomyines because the bone surrounding these areas in UNSM 26686 has sharp edges and shows no evidence of tapering or thinning.

Unfortunately, breakage has obscured exactly where the root of the anterior-alar fissure arises. Most of the observable features of the cranial foramina of *Schizodontomys* are either primitive, lacking the specializations of perognathines and dipodomyines or are shared with *Heteromyus*.

Wahlert (1985) united *Schizodontomys* with the dipodomyines based on the inflation of the auditory bullae. The inflation of the bulla in dipodomyines is almost entirely dorsal and posterior. The ventral portion of the bulla shows relatively little inflation which makes the anteroventral process of the bulla taper rather quickly with a relatively sharp anterior end (see Wahlert, 1985: fig. 4). The
Fig. 2.—Skull and mandible of *Schizodontomys amnicolus*. A, UNSM 26682, lateral view of skull. B, same as A, ventral view of skull. C, UNSM 26685, lateral view of mandible. Bar scale equals 5 mm. Stippling represents broken areas. Abbreviations for foramina: bu, buccinator; eth, ethmoid; fo, foramen ovale; hy, hypoglossal; ifo, infraorbital; in, incisive; ju, jugular; mbf, fissure medial to bulla; ms, mastoid; msc, masticatory; mt, mental; ppl, posterior palatine; rp, rostral perforation; spl, sphenopalatine; spt, sphenopterygoid canal; st, stapedial; sty, stylomastoid; vf, venous foramen in parapterygoid.
dorsal and especially posterior inflation of the bulla in *Schizodontomys* is less than that even in perognathines. There is no anteroventral process on the bullae of *Schizodontomys* because the entire area is inflated much wider and deeper (dorsoventrally) than that in either perognathines or dipodomyines. Bullar inflation is not rare in rodents. Several other families of rodents develop it independently, such as the Old World Dipodidae. Because the bullar inflation in *Schizodontomys* is only superficially similar to that of other heteromyids, it is viewed here as a parallelism with the perognathines and dipodomyines.

Within the Heteromyinae, *Schizodontomys* represents a unique combination of characters (primitive possession of the stapedial foramen and autapomorphic inflation of auditory bullae) that can ally it with no other genera. Wahlert’s (1985: fig. 6) cladogram would best be redrawn with *Schizodontomys* arising from a node between those for the Heteromyidae and Heteromyinae rather than between the Perognathinae and Dipodomyinae.

**Schizodontomys annicolus** new species
(Fig. 2, 3; Table 2)

*Type specimen.* — UNSM 26682, mandible with L1, P4, and M1.

*Horizon and locality.* — Type from 650 m east by southeast of UNSM locality Cr-23, Runningwater Formation, Cherry County, Nebraska; referred specimens from UNSM localities, Dw-118, Cr-126, Cr-127, Cr-128, Cr-129, Cr-130, Cr-131, Runningwater Formation, Cherry and Dawes counties, Nebraska.

*Age.* — Early Hemingfordian (early Miocene).

*Referred specimens.* — UNSM 26503, 26680, 26681, 26683, and 26684, partial mandibles with cheek teeth; UNSM 26698, isolated LP4; UNSM 26685, fragmentary skull with associated mandibles; and UNSM 26686, complete skull.

*Diagnosis.* — Largest species of the genus (Table 2); P4 with anteroconid and variable other cuspules; enamel on I1 thick (1.5 mm–2.3 mm); I1 with convex anterior surface; ratio of thickness of anterior enamel of hypolophid to posterior enamel of hypolophid on P4 very high (0.73 to 1.11); mental foramen well anterior of P4, as in *S. harkseni*.

*Etymology.* — Latin, *annicolus*, from the river; in reference to the Runningwater Formation.

*Description.* — UNSM 26683 and UNSM 26685 most complete mandibles available; angle convex ventrally, extending ventrally lower than remaining horizontal ramus; shallow ridge running along ventral edge on lateral face; fossa on internal side relatively deep; origin of I1 marked by bulbous lateral expansion level with tooth row (broken on all observable specimens); shallow pit dorsal to this area ventral to coronoid and articular processes; coronoid relatively small, gracile flange, deflecting slightly laterally; masseteric scar marked by prominent ventral and weak dorsal ridges, uniting anteriorly in a V, anterior to P4, dorsal to mid-depth of horizontal ramus; mental foramen single, anterior to terminus of masseteric scar at about middle of diastema, far anterior of P4, diastema fairly deep and shorter than length of tooth row.

I1, similar to those of other species (Rensberger, 1973a); convex anterior surface (no flattened area); enamel thicker than reported for other species (0.15 mm to 0.23 mm; mean = 0.19 mm).

P4, metalophid narrower than hypolophid; metaconid larger than protostylid and D-shaped; small anteroconid always present, connecting to anterobuccal corner of metaconid; other cuspules variable on metalophid (Fig. 3b, c, d); on holotype, second anteroconid present anterior to protostylid; on UNSM 26681, small cuspule attached to posterobuccal corner of protostylid; on UNSM 26698, small cuspule between metaconid and protostylid, along posteriorlingual margin of protostylid (? = protoconid); with wear, metalophid becomes convex anterior arc, eventually joining hypolophid at either lingual or buccal end first, never joining centrally; hypolophid with buccolingually elongate entoconid and hypoconid, circular hypostylid, and small hypoconulid on half of the unworn specimens; ratio of
Table 2.—*Dental measurements of Schizodontomys amnicolus.* Abbreviations: *N,* number of specimens; *M,* mean; *OR,* range; *SD,* standard deviation; *CV,* coefficient of variation; all other abbreviations as in Table 1. Measurements in mm.

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<td>1.60–1.68</td>
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</tr>
<tr>
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<td>tra</td>
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<td>1.72</td>
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<td>P4-M6</td>
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<td>8.22–8.42</td>
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Thickness of anterior enamel to posterior enamel on the hypolophid of P4 very high, ranging from 0.73 to 1.11 (mean = 0.91).

Lower molars six-cusped, bilophate; do not differ from molars described for other species of *Schizodontomys* (Rensberger, 1973a). Similarly, upper cheek teeth do not differ from those described by Rensberger (1973a) for *S. harkseni* except for larger size.

Discussion.—*Schizodontomys amnicolus* is clearly separable from other known species of this genus by its larger size, thick enamel on I1, more complex metalophid of P4, and high ratio of enamel thickness on the anterior and posterior of the hypolophid of P4. *Schizodontomys amnicolus* most closely resembles *S. greeni* from Oregon based on the thickness of the incisor enamel and ratio of enamel on the hypolophid of P4, but has the mental foramen positioned more anteriorly on the mandible as in *S. harkseni* and *S. sulcidens*.

One of the specimens from Wyoming described by Munthe (1981) is considerably larger than the other specimens referred to *S. harkseni* (UCMP 113568) and those listed by Rensberger (1973a). This specimen may well represent *S. amnicolus* which would extend the geographic range of this species to include Wyoming as well as Nebraska.
Family Geomyidae Bonaparte, 1845
Subfamily Entoptychinae Miller and Gidley, 1918
Genus Pleurolicus Cope, 1878

Pleurolicus hemingfordensis new species
(Fig. 4A, D; Table 3)

*Type specimen.*—UNSM 26697, partial mandible with LP₄–M₂.

*Horizon and locality.*—UNSM locality Cr-133, Runningwater Formation, Cherry County, Nebraska.

*Age.*—Early Hemingfordian (early Miocene).

*Referred specimens.*—None.
Table 3.—Dental measurements of Pleurolicus hemingfordensis and Ziamys hugeni. Abbreviations as in Table 1. Measurements in mm.

<table>
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<th>Ziamys hugeni</th>
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</tr>
<tr>
<td>P₄</td>
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<tr>
<td></td>
<td>tra 1.42</td>
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<tr>
<td></td>
<td>trp 1.72</td>
</tr>
<tr>
<td>M₁</td>
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<td>tra 1.68</td>
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<td>trp 1.91</td>
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<tr>
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<td>tra 1.45</td>
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<tr>
<td>P₄–M₃</td>
<td>5.48</td>
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</table>

Diagnosis.—Slightly smaller than P. sulcifrons; P₄ with anteroposteriorly elongate protoconid, separated from metaconid and protostylid by deep valleys; anterior cingulum of P₄ consisting of two small cusps anterior to protostylid; hypolophid of M₃ wider than metalophid; masseteric scar terminus and mental foramen farther anterior than in P. sulcifrons.

Etymology.—Reference to the age of this species.

Description.—Depth of mandible and crown height of cheek teeth similar to that of P. sulcifrons; masseteric fossa marked ventrally by weak ridge rising anterior to a point anterior to P₄ and near the dorsal margin of the diastema; mental foramen at mid-depth of mandible, aligned with center of diastema; diastema shallow and short; I₁ unknown.

P₄ longer anteroposteriorly and narrower buccolingually than M₃; ratio of length of P₄ to M₃ = 1.23; ratio of maximum width of P₄ to M₃ = 0.90; metalophid three-cusped; metaconid large and D-shaped; protostylid small and circular; protoconid distinct from other cusps, separated by deep valleys, and anteroposteriorly elongate; small loph running lingually from anterior end of protoconid; similar loph running buccally from anterior end of protoconid, connecting to two small cusps anterior to protostylid; buccal cuspule larger of the two; hypolophid broad, anteriorly concave loph.

Molars six-cusped and bilophate as in P. sulcifrons; protostylid more anteriorly placed than in P. sulcifrons; metalophid narrower (buccolingually) than hypolophid on M₃, (Table 3).

Discussion.—Pleurolicus hemingfordensis is clearly distinguishable from other species of this genus by the morphology of P₄ and position of the mental foramen and masseteric fossa on the mandible. The anterior cusps, possibly homologous to an anterior cingulum, are more characteristic of Gregorymys or Entoptychus (Wood, 1936a; Rensberger, 1971), but the crown height of P. hemingfordensis is the same as in Pleurolicus, and lower than that of Gregorymys. The very short diastema of the mandible of P. hemingfordensis is also characteristic of Pleurolicus and drastically different from the lengthened diastema in Entoptychus. The protoconid of P. dakotensis is characterized as being anteroposteriorly elongate as in P. hemingfordensis, but is very close to the other cusps of the metalophid, and in the two known specimens of P. dakotensis, a moderate amount of wear has fused

it with them. The valleys that separate the protoconid on P₄ of *P. hemingfordensis* are deep and would not be obliterated until the tooth is very heavily worn. The protoconid on P₄ in *P. dakotensis* also extends to a point posterior to the other metalophid cusps. In *P. hemingfordensis*, the posterior margin of the protoconid on P₄ is even with that of the metaconid and protostylid. *Pleurolicus hemingfordensis* also differs from *P. dakotensis* in the ratio of length and width of P₄ to M₁. These ratios are much higher for *P. dakotensis* than *P. sulcifrons* (Rensberger, 1973a: fig. 25), and these ratios for *P. hemingfordensis* fall within the range of *P. sulcifrons*.

*Pleurolicus hemingfordensis* is the youngest species of the genus yet described.
Gawne (1975) referred several specimens from the early Hemingfordian of New Mexico to Pleurolicus sp. The New Mexico material is slightly larger than the holotype of P. hemingfordensis. The metalophid of M₁ of the New Mexico specimen is slightly narrower than the hypolophid in P. hemingfordensis, but the difference is much less than that in P. hemingfordensis. No P₄ is known for the New Mexico species, so a reference to P. hemingfordensis is not currently possible.

Ziamys Gawne, 1975

**Ziamys hugeni**, new species

(Fig. 4B, C, 5; Table 3)

*Type specimen.* — UNSM 26694, rostrum of skull with both upper incisors and LP₄–M₁.

*Horizon and locality.* — Type from UNSM locality Cr-134; from either Runningwater Formation or subjacent late Arikareean unit; referred specimen from UNSM locality Cr-135, Runningwater Formation, Cherry County, Nebraska.

*Age.* — Early Hemingfordian (early Miocene).

*Referred specimens.* — UNSM 26695, mandible with LI₁, P₄–M₃.

*Diagnosis.* — Smaller than Z. tedfordi; upper incisors relatively reduced in size compared to cheek teeth; rostrum tapers anteriorly; cheek teeth more lophate than in Z. tedfordi; protoloph joins metaloph of P₄ lingually at earlier stage of wear than in Z. tedfordi.

*Etymology.* — Patronym for Benny Hugen for his cooperation and assistance in the collection of fossil materials on his property.

*Description.* — UNSM 26694 consists of anterior portion of rostrum (premaxilla and part of maxilla only); laterally, rostrum tapers anteriorly as in Z. tedfordi; length of diastema = 10.7 mm; incisive foramen small (15% of diastemal length), midway between incisors and P₄; anterior portion of palate and remainder of rostrum as in Z. tedfordi (Gawne, 1975:19); dorsally, rostrum tapers slightly anteriorly; I₁ with central and medial groove; I₁ originating posteriorly above P₄.

P₄ and M₁ moderately worn; no individual cusps distinguishable; protoloph and metaloph fuse lingually; all lophs anteroposteriorly compressed; anterior slope of P₄ a flat surface; protoloph of P₁ gently convex anteriorly.

Mandible as described for Z. tedfordi; pulp cavity for I₁, exposed high on ascending ramus, dorsal to tooth row, circular in outline; condyle highest point on ascending ramus; no coronoid process present (very little breakage in this area may indicate a minute process was lost). I₁, triangular in cross-section, flattened medial, anterior, and lateral sides; enamel only extending slightly onto lateral and medial sides of teeth (less than 20% of depth of tooth).

P₁, metalophid with two main cusps; metaconid roughly circular in outline and nearly twice as large as protostyloid, small obliquely compressed, elongate anteroconid present, anterior to protostyloid; hypolophid straight, loph with no distinguishable cusps.

Molars bilophate with no distinguishable cusps at present stage of wear; central swelling at center of both lophs (protoconid and hypoconid); transverse valley fuses centrally; no visible anterior cingulum; metalophid wider than hypolophid at buccal end.

*Discussion.* — The characters that separate Ziamys hugeni from the type species Z. tedfordi from New Mexico are: 1) size; 2) degree of lophodonty of upper cheek teeth; and 3) morphology of the rostrum. All of the measurements of the cheek teeth of Z. hugeni range from 10% to 15% smaller than those of Z. tedfordi (Gawne, 1975: table 2; Table 3, this paper). The upper incisors of Z. hugeni, however, are

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Fig. 5.—Rostrum and mandible of Ziamys hugeni. A, UNSM 26694, dorsal view of rostrum. B, same as A, lateral view. C, UNSM 26695, lateral view of mandible. Bar scale equals 2 mm. Stippling represents matrix.
nearly 30% smaller. This relative reduction in the incisors is likely related to the differences between these species in the shape of the rostrum. Dorsally, the snout of *Z. tedfordi* widens or remains the same width anteriorly, while in *Z. hugeni* there is a definite tapering of the snout anteriorly.

The degree of lophodonty is greater in *Z. hugeni* than in the type species. In the Nebraska species, the lophs of the upper cheek teeth are straight sided with no swellings or other indication of cusps. The upper molars of the holotype of *Z. tedfordi* (F:AM 51264) have lophs that are irregular, expanding at each cusp and constricted between them. The protoloph of P₄ is oval with a convex anterior surface, and though the tooth is moderately worn, it is not connected to the metaloph. The anterior slope of the protocone is flat on P₄ of the holotype of *Z. hugeni*, and the metaloph and protoloph are connected buccally even though the specimen is at about the same state of wear as in the New Mexico specimen.

Family Florentiamyidae Wood, 1936b

Genus *Fanimus* new genus

*Type species.* — *F. ultimus* new species.

*Range.* — Arikareean (late Oligocene) of South Dakota, Early Hemingfordian (early Miocene) of Nebraska.


*Diagnosis.* — P₄ lacking protostyle; P₄ with protostylid single and more posterior than in other florentiamyids; relatively large anteroconid on P₄.


*Discussion.* — Among geomyoids, *Fanimus* agrees with the Arikareean genera *Sanctimus* and *Florentimys* in its relatively large size, brachydont cheek teeth with large bulbous cusps, convex anterior surface of I₁, and continuous lingual cingulum on the upper molars. Therefore it can readily be referred to the Florentiamyidae. It differs from these Arikareean genera in the lack of a protostyle on P₄, presence of an anteroconid and posterior position of the protostylid on P₄.

The only other species with the diagnostic dental morphology of *Fanimus* is *Pleurolicus clasoni* Macdonald (1963) from the early Arikareean Sharps Formation of South Dakota. After its initial description, Macdonald (1970) later referred this species to his new genus *Sanctimus*. In a review of the genus *Sanctimus*, Rensberger (1973b) noted the difference between the P₄ of *S. clasoni* and other species of the genus, but maintained it in *Sanctimus*. Most recently, Wahlert (1983:12) questioned this species’ inclusion in *Sanctimus*, again noting the unique features of P₄. The features of P₄ noted by Wahlert (posterior protostylid, anteroconid) are diagnostic of *Fanimus*, hence, this species should be included in the new genus. It is also possible that another problematical species, *Florentiamys agnem*, also from the Sharps Formation (Macdonald, 1963), is synonymous with *F. clasoni*. The large anteroconid and posterior position of the protostylid of P₄ of *Fanimus* is present on the holotype and only known specimen of *F. agnem* (SDSM 55120). This specimen is also the same size as specimens of *F. clasoni*. The only difference between SDSM 55120 and specimens of *F. clasoni* is the more posterior position of the protostylid on M₁, which allows the buccal cingulum to be continuous rather than interrupted by a narrow valley between the hypostylid and protostylid (as in all other florentiamyids). It is quite possible that this morphology is anomalous on SDSM 55120, which would allow it to be considered as a referred specimen of *F. clasoni*.

Similarly, *Tenudomys titanus* from the Gering Formation of Nebraska (Martin,
Table 4. — Dental measurements of Fanimus ultimus. Abbreviations as in Table 1. Measurements in mm.

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<table>
<thead>
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1974) may also be synonymous with *F. clasoni*. The former species is characterized by its larger size and more robust, bulbous cusps, characters of florentiamyids which are drastically different from species of *Tenudomys* (see Rensberger, 1973a). The holotype of *T. titanus*, a P⁴ (UNSM 11531), lacks a protostyle, a diagnostic feature of *Fanimus*. The only referred specimen (UNSM 11504) was identified as an upper molar by Martin (1974) but is clearly a lower molar. The protostylid on UNSM 11504 is positioned at the center of the transverse valley of the tooth, similar in position to that of *F. clasoni*. *Tenudomys titanus* is also from approximately the same age as the holotype of *F. clasoni*, making its synonymy with the latter quite likely.

The holotype of one species of *Florentiamys* described by Wahlert (1983), *F. kennethi*, has only two lingual stylar cusps on P⁴ as in *Fanimus*, which is interpreted by Wahlert as the fusion of the protostyle and entostyle. This species is not referred to *Fanimus* because the holotype (F:AM 103382) contains associated mandibles with all cheek teeth, and the P₄ has the diagnostic doubled protostylid of *Florentiamys* and lacks the large anteroconid of *Fanimus*.

**Fanimus ultimus**, new species

(Fig. 6; Table 4)

*Type specimen.* — UNSM 26504, mandible with LI₁, P₄-M₂.

*Horizon and locality.* — Type and most referred specimens from UNSM locality Bx-7; UNSM 26696 from UNSM locality Cr-136, ?Runningwater Formation, Box Butte and Cherry counties, Nebraska.

*Age.* — Early Hemingfordian (early Miocene).

*Referenced specimens.* — UNSM 26696, mandible with LI₁, P₄-M₃; UNSM 26506 and 26515, isolated P₄s; UNSM 26508, 26509, 26510, 26512 and 26513, isolated P⁴s; UNSM 25607, 26511, 26514, and 26516, isolated upper molars.

*Diagnosis.* — Larger than *F. clasoni*; protoconid or homologous lophule present on P₄.

*Etymology.* — Latin, ultimus, latest.
Description.—Mandible slightly more robust than that previously figured for Florentiamys and approximately equal to that of Sanctimus (Wood, 1936b: fig. 3; Wahlert, 1983: fig. 5, 6); otherwise, only difference from Florentiamys is presence of short, strong ridge posterior to the pulp cavity for I, forming small shelf continuous to posterior margin of mandible. I, with convex anterior and lateral surfaces, flat medial surface; enamel extending about ½ depth of tooth on lateral side and only slightly onto medial side.

Cheek teeth low crowned with bulbous cusps as in other florentiamyids; metaconid largest cusp on metalophid of P3; protostylist small and more posterior than metaconid; small anteroconid present anterior to protostylist, separated from metaconid by deep valley; small anterior cingulum anterior to metaconid on holotype, absent on others; protoconid distinct, transversely compressed cusp on UNSM 26506, connecting posteriorly with the protostylist; on holotype and UNSM 26515, loph originating at posterolingual corner of protostylist running anteriorly, terminating posterior to anteroconid; transverse valley between metalophid and hypolophid deep, lophs not joining even at latest stages of wear; entoconid and hypoconid anteroposteriorly compressed, wearing to thick, straight loph; hypostylist small, round.

M1 and M nearly identical; bilophate; protostylist posterior to protoconid and metaconid, attached to short anterior cingulum arising from anterobuccal margin of protoconid; metalophid much more anteroposteriorly broad than hypolophid; all major cusps (metaconid, protoconid, entoconid, hypoconid) anteroposteriorly compressed.

M only preserved on UNSM 26696 and heavily worn; narrower buccolingually but longer than anterior molars; outline of cusps distinguishable on lophs; protoconid and hypoconid largest cusps; lophs will unite buccally as in anterior molars with a little more wear.

Protoloph of P3 consisting of two cusps (paracone, protocone); paracone on buccal slope of protocone and smaller; metacone and hypocone subequal in size; hypostyle circular, smaller than hypocone; entostyle large, transversely compressed; no protostyle present; on UNSM 26512 minute cuspule present between entostyle and protocone, possibly twinning of elongate entostyle.

Upper molars typical florentiamyid pattern; four major cusps (paracone, metacone, protocone, hypocone) and continuous cingulum running from lingual margin of paracone to base of hypocone blocking central transverse valley lingually; entostyle and protocone distinguishable on lingual cingulum; narrow valley separates entostyle and protostyle on UNSM 26516.

Discussion.—Fanimus ultimus and the species of Florentiamys described below are not the latest known florentiamyids. Voorhies (in press) reported several isolated cheek teeth of an indeterminate florentiamyid from the Barstovian Valentine Formation of Nebraska. The presence of these two florentiamyids from the Hemingfordian shows that the family continues from the Arikareean (Wahlert, 1983) through the Hemingfordian, and into the Barstovian probably without interruption.

Genus Florentiamys Wood, 1936b
Florentiamys sp.
(Fig. 6E)

Referred specimen.—UNSM 26505, LP4.
Horizon and locality.—UNSM locality Bx-7, Runningwater Formation, Box Butte County, Nebraska.
Age.—Early Hemingfordian (early Miocene).

Description.—Larger than any previously described florentiamyid (a-p, 4.33 mm; tra, 2.88 mm; trp, 3.58 mm) major cusps as in other Florentiamys (Wahlert, 1983: fig. 3); hypostyle obliquely compressed.
and small; entostyle and protostyle small and subequal in size; protostyle separated only by shallow valley from protocone; minute spurs originating from metaloph running into central transverse valley between protoloph and metaloph; minute cuspule on anterolingual slope of protocone.

**Discussion.** — UNSM 26505 has the protostyle continuous with the entostyle diagnostic of *Florentiamys*, so it can easily be referred to this genus. The minute cuspule on the anterior slope of the protocone of UNSM 26505 is not unique among species of *Florentiamys*. It has been figured in specimens of *F. kinseyi* (Wahlert, 1983: fig. 3d). UNSM 26505 is distinguishable from all other species of *Florentiamys* by its much larger size (see Wahlert, 1983: table 2) and minute lophules running from the metaloph into the central transverse valley. It is also the youngest species of the genus.

**Geomyoindeterminate**

(Fig. 6F)

**Referred specimen.** — UNSM 26517, LP4.

**Horizon and locality.** — UNSM locality Bx-7, Runningwater Formation, Box Butte County, Nebraska.

**Age.** — Early Hemingfordian (early Miocene).

**Description.** — Relatively large (a-p, 2.50 mm; tra, 1.85 mm; trp, 2.40 mm), brachydont tooth; all cusps round and bulbous; protostylid and metaconid nearly equal in size; metaconid flattened buccally; protoconid large, slightly smaller than protostylid, posterior to metaconid and protostylid; protoconid separated from metaconid by deep valley, and protostylid by narrow, shallow valley; hypolophid cusps not compressed; hypostylid as large as hypoconid and entoconid; entoconid and hypoconid separated by narrow, shallow valley; hypostylid separated from hypoconid by deep valley.

**Discussion.** — The size, crown height and bulbous cusps of UNSM 26517 are similar to cheek teeth of florentiamyids. However, the unique position and shape of the protoconid, the lack of compression of the hypolophid cusps, and the relatively large size of the hypostylid (large as hypoconid) are unique among geomyids and florentiamyids. It is very unlikely that UNSM 26517 belongs to the species of *Florentiamys* described above because of its smaller size and lack of a doubled protostylid characteristic of *Florentiamys*.

**Conclusions**

The Hemingfordian geomyoid rodent fauna from Nebraska is much more diverse than any other known Hemingfordian fauna from North America. The composition of the fauna does not ally it with any other known Hemingfordian fauna. The presence of *Stratimus strobeli* and *Proheteromys* cf. *P. magnus* are known elsewhere only from the Quarry A fauna of Colorado (Wilson, 1960) and Toham Ranch local fauna of Saskatchewan (Skwara, 1988), both of which lack any geomyids or florentiamyids. Similar species of *Schizodontomys* are known from South Dakota and Wyoming (Rensberger, 1973a; Munthe, 1981), but these areas lack other heteromyids and florentiamyids found in Nebraska. The presence of *Pleurolicus* and *Ziamys* in the Hemingfordian is known only from New Mexico (Gawne, 1975) which also lacks any florentiamyids and similar species of heteromyids. The Nebraska Hemingfordian fauna thus far lacks comyids and smaller species of heteromyids known from other areas of the Great Plains (Wood, 1935; Wilson, 1960).

Arikareean geomyoids are dominated by 22 species of geomyids, mainly the entoptychines *Gregorymys* and *Entoptycus* (Wood, 1936a; Rensberger, 1971). Florentiamyids are also diverse in the Arikareean, being represented by as many
as 12 species (Wahlert, 1983). Heteromyids are limited to ten species in the Arikareean. Only one species of eomyid has been reported (L. Macdonald, 1972).

In the Barstovian, the geomyoid fauna is dominated by heteromyids (16 species), Cupidinimus being the most abundant genus (Klingener, 1968; Lindsay, 1972; Storer, 1975; Korth, 1979; Barnosky, 1986a, 1986b). Geomyids are reduced to only seven species and florantiamyids are represented only by several isolated teeth of a single taxon (Voorhies, in press). Eomyids are represented by four species in the Barstovian (Shotwell, 1967; Lindsay, 1972).

Previously, nine heteromyids, three geomyids, three eomyids, and no florantiamyds were known from the Hemingfordian. With the addition of the Nebraska species, the diversity of each group of geomyoids is intermediate, or nearly so, between that of the Arikareean and Barstovian. This is particularly evident in the geomyids (two additional species) and florantiamyids (two species). The geomyids go from a diversity of 22 species in the Arikareean to five in the Hemingfordian to seven in the Barstovian. Florantiamyids also show a decrease from 12 to two to one. The Nebraska heteromyids allow for a gradual increase in the number of species from the Arikareean to Barstovian. Ten species are known from the Arikareean, 11 from the Hemingfordian, and 16 from the Barstovian.

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