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A NEW GENUS OF HELISCOMYID RODENT (RODENTIA, GEOMYOIDEA, HELISCOMYIDAE) BASED ON CRANIAL MORPHOLOGY

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ABSTRACT

The cranium of *Heliscomys mcgrewi* Korth is described. It differs from previously described skulls of *Heliscomys* in its larger size, the presence of a rostral perforation (elsewhere only known in Hetermyidae), shortening of the nasal bones posteriorly (typical of all other geomyoids), presence of a foramen on the alisphenoid anterior to the accessory foramen ovale (present in early heteromyids), and having the posterior palatine foramina within the maxillary-palatine suture. These more advanced features of the cranium, along with the much larger size of the species, are the basis for the establishment of the new genus *Megaheliscomys* containing only the type species *M. mcgrewi*. The presence of these otherwise heteromyid-like cranial features of *M. mcgrewi* may suggest that the Heteromyidae originated with a heliscomyid ancestor. However, the specialization of the dentition of *M. mcgrewi* (marked reduction of P4) bars this species from any direct ancestry of heteromyids.

INTRODUCTION

Setoguchi (1978:fig. 23a, b) was the first to figure the skull of the early geomyoid rodent *Heliscomys* Cope, 1873, from the Orellan of Wyoming, but he did not offer a description. The specimen consisted only of the rostrum and a small portion of the maxilla. The skull of *Heliscomys* was first described in detail by Korth et al. (1991). The specimen described was from the Chadronian of Wyoming, and consisted of the anterior half of the cranium. It was demonstrated that the morphology of the skull was sufficiently distinct from all other geomyoids that a new family, the Heliscomyidae, was established. Later, a partial skull of an Orellan species, *H. senex* Wood, 1935, from South Dakota was briefly described (Korth, 1995). The distinctive morphologies of the Chadronian skull were also present in the Orellan skull, giving support to the recognition of the Heliscomyidae as distinct from other geomyoid families. However, the neurocranium and basicranial area of *Heliscomys* have never been described. A specimen of a nearly complete skull of a heliscomyid from the Orellan of Montana has allowed for the description of the remainder of the cranium not previously known for this genus (and family), and for the recognition of a new genus.

Terminology—Dental terminology follows that of Korth (1994:fig. 15.2). Terminology for cranial foramina follows that used elsewhere for geomyoid rodents (Wahlert, 1978, 1983, 1985, 1991; Wahlert and Souza, 1988; Korth et al., 1991). Upper teeth indicated by capital letters (e.g. M1, M2). Abbreviations for institutions: KU, University of Kansas Natural History Museum; USNM, National Museum of Natural History, Smithsonian.

SYSTEMATIC PALEONTOLOGY

Order Rodentia Bowdich, 1821
Family Heliscomyidae Korth, Wahlert, and Emry, 1991
Genus *Megaheliscomys* n. gen.

Type and Only Species—*Heliscomys mcgrewi* Korth, 1989.

Range—Orellan (Oligocene) of Nebraska and Montana.

Diagnosis—Primitive geomyoid feartures as in *Heliscomys*: cheek teeth brachydont and weakly bilophate with rudimentary stylar cusps; posterior maxillary notch present (rather than foramen); auditory bulla uninflated; sphenopterygoid canal lacking; incisive foramina enlarged and recessed into rostrum. Derived heteromyid features: large perforation on lateral side of rostrum; posterior palatine foramen within maxillary-palatine suture (more anterior than in *Heliscomys*); nasal and premaxillary bones end posteriorly on skull roof anterior to orbits (shorter than in *Heliscomys*); additional foramen anterior to accessory foramen ovale on alisphenoid (likely combined masticatory and buccinator foramina as in early heteromyids). Derived features: dental measurements approximately 25-30% larger than species of *Heliscomys*; P4 greatly reduced relative to M1 as in *Heliscomys* (*Heliscomys*), with one large, central cusp (hypocone) and three greatly reduced cusps (paracone, protocone, entostyle); lingual cingulum on upper molars continuous; hypostyle only recognizable cuspule on lingual cingulum (M1 only).

Etymology—Greek, *megas*, large; and *Heliscomys*, a closely related rodent.

Megaheliscomys mcgrewi (Korth, 1989)

Heliscomys mcgrewi Korth, 1989

Type Specimen—KU 68466, maxilla with P4-M2.

Additional Specimen—USNM 243576, cranium with complete dentition, lacking nasals, occipital, parietal bones and zygomatic arches.

Horizon and Locality—Holotype and topotypic material from late Orellan (Orella D), Orella Member, Brule Formation, Sioux County, Nebraska (Korth, 1989:34). Referred cranium from USNM locality D 402, listed as "Dry Hollow, Chris Miller Ranch; 8 mi. SE of Townsend. SW ¼ and S ½, NW ¼, Sec. 6, NW ¼, Sec. 7, T. 5 N., R. 3 E, Broadwater County, Montana, collected by H. Morton Sperry in 1957" (USNM records). The fossil collection from D 402 consists mostly of Orellan taxa (largely *Palaeolagus burkei* and *Eumys cricetodontoides*) but also includes two jaws of *Pipestoneomys* (a genus generally considered Chadronian but has been previously reported from the Orellan [West and Korth, 1994]) and one of *Aulolithomys* (elsewhere only known from the Chadronian [Korth, 1994]). It is believed that the specimen described below is from an Orellan horizon.

Description—In dorsal view, much of the cranium is missing (Figure 1A). The frontals and parietals are represented only by small fragments, and the occipital and nasals are completely lacking. It is evident that the premaxillary and nasal bones extended posteriorly to the same point, level with the anterior margin of the zygmatic arch. In *Heliscomys* the nasals extend much farther posteriorly (Korth et al., 1991). From the outline of the nasals, it appears that they are parallel sided with very little flaring anteriorly. In overall proportions, the skull appears short and broad with lateral expansion and dorsoventral flattening of the neurocranium.

The lateral side of the rostrum is damaged on both sides of the skull, but better preserved and undistorted on the right side (Figure 1C, 2). The skull is clearly sciuromorphous with the masseteric scar extending well onto the premaxillaries. The premaxillary-maxillary suture descends down the side of the rostrum near the anterior end of the masseteric scar, more anterior than in that of the previously described crania of *Heliscomys* (Setoguchi, 1978:fig. 23b; Korth, et al., 1991; Korth, 1995:fig. 1.4). It curves anteriorly to a point approximately 1 mm posterior to the posterior margin of the incisor alveolus (Figure 2). This too, is more anterior than in *Heliscomys*, where the suture is nearly twice as far posterior relative to the incisor alveolus. The suture then curves posteriorly and crosses the ventral surface of the palate near the center of the upper diastema. Posterior to the suture is a large, oval rostral perforation, typical of heteromyids and not present in other skulls of *Heliscomys*. There is some breakage which suggests that the size of the perforation has been at least somewhat expanded from its original size, but the edges surrounding most of the opening do not appear to be broken.

The orbital wall is badly damaged on both sides of the specimen, so little of the position of the sutures or foramina can be determined. On the left side (Figure 1D), a small, oval nasolacrimal foramen is present at the anterodorsal corner of the orbital wall. On the floor of the orbit, a sphenopalatine foramen is present dorsal to M1. A dorsal palatine foramen is also present posterior to the tooth row. At the posteroventral side of the alisphenoid is a small, circular accessory foramen ovale, similar to that of *Heliscomys*. Anterior to the latter is a minute foramen which likely contains the buccinator and masticatory foramina as in some heteromyids *Heliscomys*.

An oval postglenoid foramen is preserved in a fragment of the parietal bone on the left side of the cranium. The bulla is only preserved on the left side (Figure 1D). There is very little inflation. It is almost entirely limited to the lateral side of the skull and is roughly circular in outline. The external acoustic meatus is a small circle near the dorsal margin of the bulla.

Ventrally, the rostrum is narrow and nearly parallel-sided for its entire length (Figure 1B). The incisive foramina are large (3.01 mm) and recessed into the palate, making up over 46% of the total length of the upper diastema (6.47 mm). This is slightly less than the relative length of the incisive foramina of *H. ostranderi* (59%), but greater than most other geomyoids excluding dipodomyine heteromyids. The maxillary-premaxillary suture crosses the palate at the center of the incisive foramina, cutting through the small swellings ventral to the rostral perforation for the attachment of the superficial masseter muscle.

The palatal surface of the maxilla is gently concave between the tooth rows. The maxillary-palatine suture starts posterior to M3 and runs anteriorly along the inside of the tooth row, crossing the midline of the palate even with the anterior margin of M1. The posterior palatine foramina are within the maxillary-palatine suture, medial to M1. In *H. ostranderi* they are entirely within the palatine bones. On the right side, there are secondary posterior palatine foramina, posterior to the principal one. Posterior to M3 is a large posterior maxillary notch that is open laterally.

The pterygoid fossa is posterior to the tooth row. There is no sphenopterygoid canal on the skull of *H. ostranderi* (Korth et al., 1991). On the specimen of *M. mcgrewi* there are openings in this area, but they

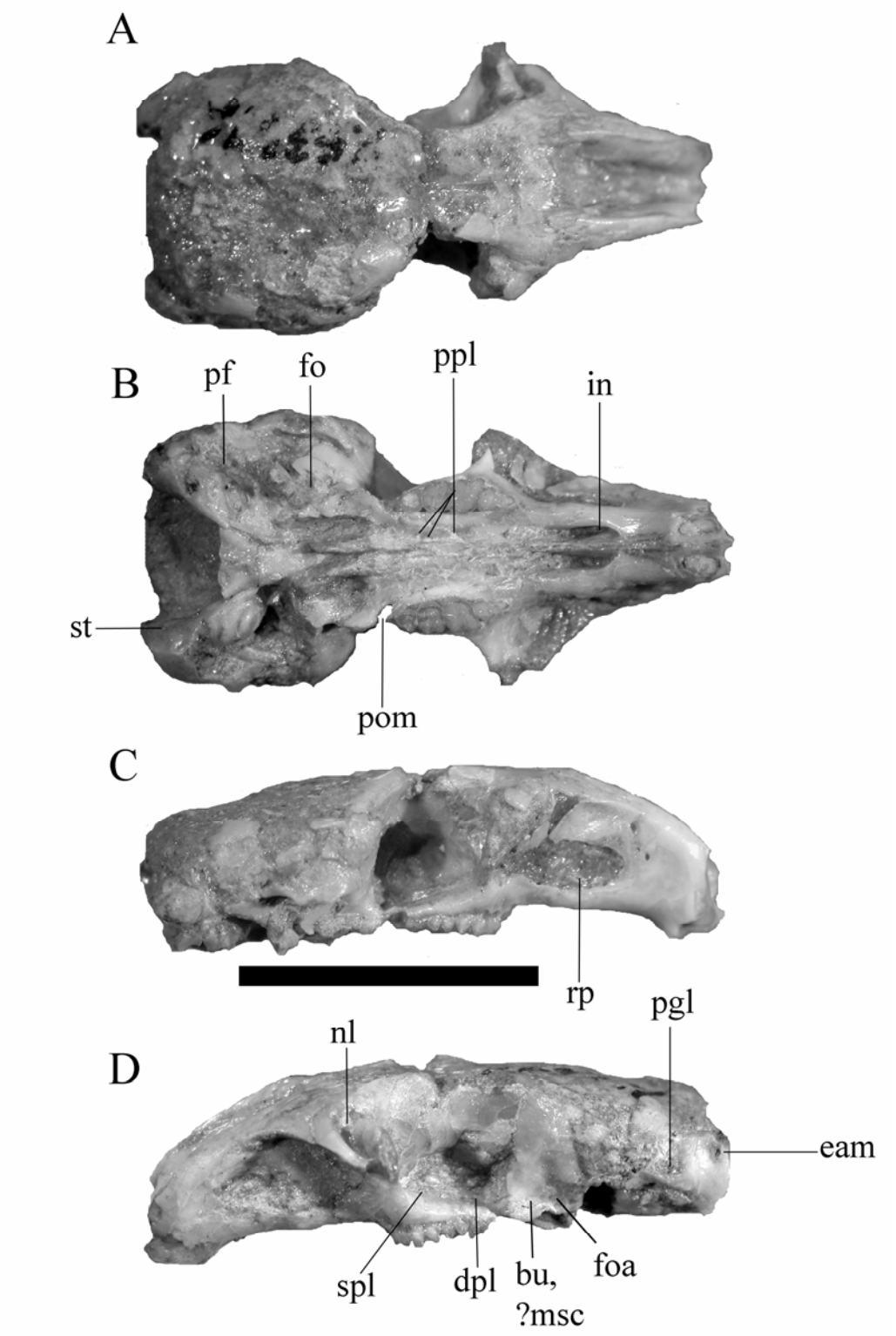

FIGURE 1. Cranium of *Megaheliscomys mcgrewi*, USNM 243576. A, Dorsal view. B, Ventral view. C. Left lateral view. D. Right lateral view. Abbreviations: bu, buccinator foramen; dpl, dorsal palainte foramen; eam, external acoustic meatus; fo, foramen ovale; foa, accessory foramen ovale; in, incisive foramen; msc, mastecatory foramen; nl, nasolacrimal foramen; pf, piriform fenestra; pgl, postglenoid foramen; pom, posterior maxillary notch; ppl, posterior palatine foramen; rp, rostral perforation; st, stapedial foramen; spl, sphenopalatine foramen. Bar scale = 1 cm.

appear to be due to breakage evidenced by the rough edges of the sides of the openings and the fact that they are markedly different in shape on either side of the skull. The only piece of the occipital bone is a small fragment of the basioccipital that is not yet fused to the basisphenoid. The ventral part of the auditory bulla extends anteriorly from the posterolateral corner of the skull, but is not at all inflated, appearing as a thin layer of bone covering the middle ear. Anterior to the cochlea is a large, obliquely oriented, and oval piriform fentestra. The foramen ovale is circular in outline anterior to the piriform fenestra, confluent with the accessory foramen ovale. A minute stapedial foramen is present on the bulla along its medial side, presumably along the suture with the occipital (missing). No other foramina are preserved in the basicranial area.

The P4-M2 of *Megaheliscomys mcgrewi* have been fully described elsewhere (Korth, 1989). The incisors and M3, preserved in USNM 243576, have not been described previously. The incisors are very narrow, being more than twice as long as wide. The medial and lateral sides are nearly parallel and the anterior enamel surface is very gently convex. Enamel is mostly restricted to the anterior surface, extending a quarter of the way onto the lateral side. There is no longitudinal groove anteriorly in the enamel.

M3 is smaller than M1 and M2, wider than long, and more nearly circular in occlulsal outline than M1 or M2. There are only two distinct cusps, the paracone and protocone, which are connected by a loph (protoloph). The protocone is isolated, just anterior to the center of the occlusal surface. The anterior cingulum originates at the buccal side of the paracone, and continues along the anterior margin of the tooth, and is continuous with the lingual and posterior cingula. The posterior cingulum ends buccally at the metacone, which has been reduced to small cuspule. The posterior cingulum is broadened (anteroposteriorly) at its center, lingual to the metacone.

Discussion—The species identification of USNM 243576 is based on dental morphology (see Korth, 1989, 1995). The width of P4 is 61-62% that of M1, and the occlusal morphology of the premolar consists of only one major cusp, the hypocone, minute paracone and protocone, and a slightl swelling on the lingual side of the hypocone homologous with the entostlye (Figure 3). In size, the dental measurements of the specimen are larger than any species of *Heliscomys* (Table 1; also see Korth, 1989:table 1 for comparative measurements). The relative size and morphology of P4 and the overall size of the dentition indicate that this specimen is referable to "*Heliscomys" mcgrewi* Korth, 1989.

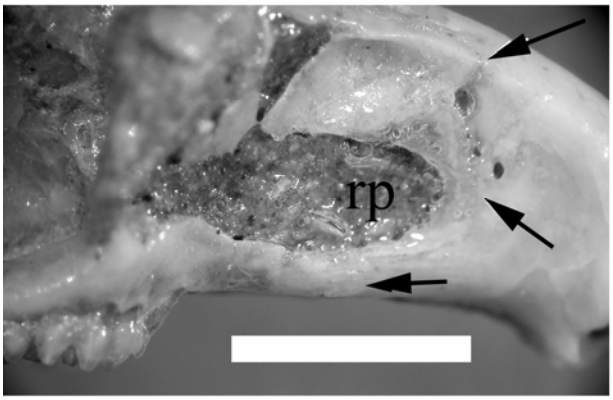

FIGURE 2. Right side of rostrum of *Megaheliscomys mcgrewi*, USNM 243576. Arrows point to premaxillary-maxillary suture anterior to rostral perforation (rp). Bar scale = 5 mm.

The newly described cranium of *Megaheliscomys* allows for observation on the posterior portion of the skull not previously known for heliscomyids. Among the features present are several that are considered primitive for geomyoids: 1) auditory bulla uninflated; 2) stapedial foramen (and artery) present in bulla; and 3) postglenoid foramen present. This is not surprising considering that the basic cranial morphology of *Heliscomys* is primitive for geomyoids (Korth, et al., 1991).

There are four features of the cranium of *M. mcgrewi* that are different from the previously described skulls of *Heliscomys*, which appear to be advanced, and more like that of heteromyids. First is the presence of a rostral perforation. This feature is diagnostic of Heteromyidae (Wahlert, 1984) and is not present in the previously described crania of *Heliscomys* (Setoguchi, 1978:fig. 23a; Korth, et al., 1991:fig. 1; Korth, 1995:fig. 1). Whereas there is some damage to the bone on the side of the rostrum of USNM 243576 that may have enlarged the foramen, the position of the premaxillary-maxillary suture on the side of the rostrum is far more anterior on the *M. mcgrewi* specimen than on species of *Heliscomys* (Figure 2). The more anterior position of the suture is to accommodate a larger foramen.

The second feature is the position of the posterior palatine foramen. In the skull of *H. ostranderi* it is near the maxillary-palatine suture, but is entirely within the palatine bone (Korth et al., 1991). In *M. mcgrewi* it is more anterior, within the suture. This same feature was noted also in the skull of *H. senex* (Korth, 1995). The position of the foramina within the suture is considered more derived and entirely within the palatine bone to be primitive for geomyoids, however,

it does occur entirely within the palatine in extant *Microdipodops* (Wahlert, 1985; Korth et al., 1991).

The third feature is the posterior extent of the nasals on the skull roof. In *Heliscomys* the nasals, as well as the premaxillaries, extend posterior to the anterior root of the zygomatic arches. In the skull of *Megaheliscomys*, the nasals end posteriorly even with the anterior margin of the zygmatic arches. The longer nasals in *Heliscomys* are viewed as primitive for geomyoids, whereas the shortening of the nasals is derived and present in all other geomyoids (Korth et al., 1991).

The final feature is the presence of a foramen on the alisphenoid bone separate from the accessory foramen ovale. In other crania of *Heliscomys* the only foramen on the ventral part of the alisphenoid is the accessory foramen ovale. On the skull of *M. mcgrewi*, there is a minute foramen anterior to it. Some earlier heteromyids such as *Schizodontomys*, *Harrymys*, and *Mioheteromys*, as well as in extant heteormyines (Wahlert, 1991; Korth, 1997) have this same arrangement where there is a smaller foramen anterior to the accessory foramen ovale that is the fused buccinator and masticatory foramina.

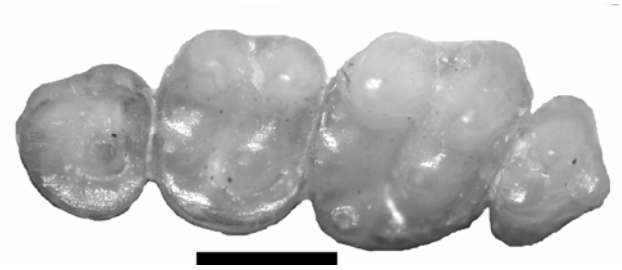

FIGURE 3. Upper cheek teeth of *Megaheliscomys mcgrewi*, USNM 243576. Right P4-M3. Anterior to the right. Bar scale = 1 mm.

CONCLUSIONS

As early as the 1930s, *Heliscomys* was considered the basal geomyoid and likely ancestral to all later geomyoids (Wood, 1931, 1935). In the original description of the Heliscomyidae, Korth et al. (1991) listed several derived features of the skull of *Heliscomys* that barred it from this ancestral condition: 1) enlarged incisive foramen; 2) accessory foramen ovale contains both the masseter and buccinator foramina, and 3) the morphology and the masseteric scar and mental foramen on the mandible. In the caption of their cladogram (Korth et al., 1991:fig 3) they also list the extreme brachydonty and rudimentary stylar cusps on the molars as derived features. However, it appears that these may not all be derived characters. The presence of a single accessory foramen ovale containing both the masticatory and buccinator foramina has been demonstrated to be primitive for geomyoids rather than derived, and having separate mastecatory and buccinator foramina is the advanced condition (Korth, 1997). Similarly, the brachydonty and rudimentary (or lack of) stylar cusps on the molars is also likely the primitive condition because of its occurrence in the earliest (Duchesnean) heliscomyids (Korth and Eaton, 2004).

It is also possible that the large size of the incisive foramen is primitive for geomyoids as well. In eomyids, the length of the incisive foramen to the length of the upper diastema is much shorter (24-40%; Wahlert, 1978) than in *Heliscomys* (51-59%; Setoguchi, 1978; Korth et al., 1991; Korth, 1995). However, in the earlier heteromyids (mioheteromyines, harrymyines) the incisive foramen is much larger than in extant heteromyids (Wahlert, 1991; Korth, 1997), intermediate between that of heliscomyids and extant heteromyids. The incisive foramen in *Megaheliscomys* is slightly smaller relative to the length of the upper diastema (46%) than in *Heliscomys*, which is intermediate between the latter and mioheteromyines (24-41%; Korth, 1997), and nearly the same size as in *Harrymys* (45-46%; Wahlert, 1991:4). This suggests that perhaps the primitive condition for geomyoids was a large incisive foramen that tends to become smaller through time. This leaves only the morphology of the masseteric scar and position of the mental foramen on the mandible as derived characters for the Heliscomyidae, which is not known for *Megheliscomys*.

Table 1. Cranial and dental measurements of *Megaheliscomys mcgrewi*, USNM 243576. Abbreviations for dental measurements: L, anteroposterior length; W, transverse width. Measurements in mm.

Total length of cranium		20.54
Maximum width of rostrum		5.18
Minimum width (postorbital constriction)		4.16
Maximum width of neurocranium		10.08
Length of upper diastema		6.47
Length of incisive foramen		3.01
Depth of skull at M2		5.43

		Right	Left
I1	L	1.22	1.17
	W	0.54	0.59
P4	L	0.68	0.75
	W	0.80	0.82
M1	L	1.11	1.17
	W	1.30	1.34
M2	L	0.94	0.89
	W	1.18	1.19
M3	L	0.72	0.73
	W	0.90	0.89
P4-M3		4.00	3.99

The skull of *Megaheliscomys* cannot be generically separated from *Heliscomys* based on dental criteria other than size, but the cranial features show derived features that may ally it with the Heteromyidae. The presence of a rostral perforation, shortening of the nasals, presence of a second foramen on the alisphenoid, and the position of the posterior palatine foramina are all derived features in *Megaheliscomys* that are also present in heteromyids. The rostral perforation is exclusive to, and diagnostic of, the Heteromyidae (Wahlert, 1985). Unfortunately, the mandible of *Megaheliscomys* is unknown, so the mandiblular features distinctive to heliscomyids cannot be confirmed.

The presence of these derived heteromyid cranial morphologies in *Megaheliscomys* may suggest that the origin of at least the heteromyids may have been from within the Heliscomyidae. The earliest reported rodents referred to the Heteromyidae are Arikareean (Korth, 1994), and the earliest previously reported skull is Hemingfordian (Gawne, 1975). The extended time gap between the occurrence of *Megaheliscomys* and these earliest heteromyids could allow for the modification into the heteromyid morphology. The only morphology of *Megaheliscomys* that would bar it from the ancestry of the earliest heteromyid (*Proheteromys*) is the small size of P4.

Alternatively, the presence of these advanced features in *Megaheliscomys* may be due to parallelism with the heteromyids, possibly related to the increased size of *Megaheliscomys* compared to all other heliscomyids. Another interpretation would be that *Megaheliscomys* belongs to the Heteromyidae, and is not a heliscomyid. It has been suggested that the ancestry of the Heteromyidae could more likely be found in Mexico and Central America where there is a much poorer fossil record (Wahlert and Souza, 1988; Wahlert, 1993), thus the North American development of heliscomyids was independent of the earliest heteromyid radiation.

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