

A NEW SPECIES OF BEAVER (RODENTIA, CASTORIDAE) FROM THE EARLY BARSTOVIAN (MIOCENE) OF NEBRASKA

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ABSTRACT

A new species of the early castoroidine beaver *Euroxenomys* Samson and Radulesco, *E. galushai*, is named from the early Barstovian of western Nebraska. It is distinguished from other species by its larger size, low crowned cheek teeth, and the posterior maxillary foramen opening laterally to form a notch. It is the third species of *Euroxenomys* recognized from North America.

INTRODUCTION

Sutton and Korth (1995) first recognized *Euroxenomys* from North America. The species, *E. inconnexus*, was from the early Barstovian of Montana. Previously, this genus was only known from the Miocene of Europe (Samson and Radulesco, 1973; Engesser, 1972; Huegeney, 1999). Later, Korth (2001a) named a second species from North America, from the early Hemingfordian of Colorado, *E. wilsoni*. The species of *Euroxenomys* were distinguished from the contemporaneous castoroidine *Monosaulax* by the lower crowned cheek teeth with shallower lingual striids on the lower premolar and by the slight elongation of M³. The material described below is from the early Barstovian of Nebraska, the easternmost occurrence of this genus in North America. It is represented also by a specimen of the anterior half of the skull. The previously described skull of *Euroxenomys* from North America is badly distorted, so little of the details of the morphology can be determined (Korth, 2001a). However, the new specimen is not crushed or distorted, so much more detail of the skull can be determined.

Dental terminology used follows that of Stirton (1935:figs. 1-12) and Korth (1994:fig. 13.2). Fossettes (-ids) and flexi (-ids) are features of the occlusal surface of the cheek teeth; striae (-ids) are features of the medial and lateral sides of the cheek teeth. Measurements taken on the height of the premolars and abbreviations follow those presented by Korth (2001a:fig. 1). The identification of cranial foramina is based on Wahlert (1974, 1977). Abbreviations for institutions used: FAM, Frick Collections, American Museum of Natural History.

SYSTEMATIC PALEONTOLOGY

Order Rodentia Bowdich, 1821

Family Castoridae Hemprich, 1820

Subfamily Castoroidinae Allen, 1877

Euroxenomys Samson and Radulesco, 1973

Euroxenomys galushai new species

Type Specimen—FAM 64274, right mandible with P₄-M₃ (Figure 1A).

Referred Specimens—FAM 22068, 64272, 64273, 64275, 64276, 64277, 64278, 64279, 64280, 64281, 64282, 64283, 64284, 64285, 64286, 64287, 64288, all mandibles with cheek teeth; FAM 64270, isolated right P⁴; and FAM 64269, anterior half of a cranium with both incisors and premolars.

Horizon and Locality—Holotype and several referred specimens from Version Quarry, remainder of specimens from Boulder, East Surface, West Sinclair Draw, and East Sand Draw quarries. All quarries are in the Olcott Formation, Sioux County, Nebraska (see Skinner et al., 1977, for precise locality data).

Age—Early Barstovian (middle Miocene).

Diagnosis—Largest species of the genus; cheek teeth low crowned, lingual striids on P₄ very short, similar to *E. wilsoni*, shorter than *E. inconnexus*; posterior maxillary foramen open laterally (forming notch).

Etymology—Patronym for Ted Galusha in recognition of his contributions to the Frick Collections at the American Museum of Natural History.

Description—The cheek teeth are mesodont and rooted. Species of *Euroxenomys* have been diagnosed based on the crown-height of the lower premolar and the depth of the lingual striids on that tooth (Korth,

2001a). Unfortunately, none of the specimens referred here to *E. galushai* are completely unworn, so the indices for crown height cannot be determined precisely. However, the holotype, FAM 64274 is in the early stages of wear. The indices for crown height (H/L, height/ length; B/H, height of crown below mesostriid/crown height) calculated for this specimen are 1.14 and 0.69, respectively. If the measured P₄ was totally unworn, both the H/L and B/H indices would be slightly higher. These numbers are compatible with species of *Euroxenomys* (Korth, 2001a:table 2) and markedly lower crowned premolar with a shorter mesostriid than any species of the *Monosaulax* (Korth, 1999:table 2; CHI = H/L; SHI = B/H). The premolar is largest at its base, so all of the measurements increase with wear. Thus, the measurements listed in Table 1 are taken at the base of the crown.

TABLE 1. Dental measurements of *Euroxenomys galushai*. Abbreviations: N, number of specimens measured; M, mean; OR, range of variation; SD, standard deviation; CV, coefficient of variation. Measurements in mm.

	N	M	OR	SD	CV
P ₄ -M ₃	14	16.21	14.97-17.54	0.77	4.77
P ₄ L	14	5.71	4.86-6.21	0.35	6.05
W	12	4.53	4.18-4.92	0.26	5.70
I ₁ L	8	4.12	3.75-4.49	0.26	6.43
W	11	3.72	3.43-3.98	0.15	4.06

The occlusal pattern of the lower premolars consists of a hypoflexid (which remains open on all specimens except the most worn, FAM 64288), a parafossettid, a metafossettid, and a mesofossettid. On less worn individuals, the mesoflexid is open lingually (Figure 1A, B, C). The only exception to this pattern is on the holotype (least worn) where the parafossettid is slightly open laterally (Figure 1A). However, the parastriid is extremely short (less than 0.5 mm) and the fossettid will form after only minor additional wear. Generally, the three fossettids are elongated and oriented obliquely. On nine of the 18 specimens, the parafossettid is concave anteriorly, in the remainder the parafossettid is straight (Figure 1D). There is no indication of the short loph within the parafossettid of unworn specimens as in those of *E. wilsoni* (Korth, 2001:fig. 2B, E). However, the degree of curvature is similar to that in the European species (Hugueney, 1999:fig. 28.7). In some of the heavily worn specimens, the mesofossettid is also curved as in the parafossettid. Three of the P₄s have an accessory fossettid anterior to the parafossettid (Figure 1C). It is minute and circular in shape. This has also been figured for specimens of *E. minutus* (Hugueney, 1999:fig. 28.7A).

M₁ and M₂ are nearly identical in occlusal morphology, but M₁ always shows a greater amount of wear. The molars are nearly square in outline, but change shape as they wear and become markedly shortened anteroposteriorly. The least worn molars have an open hypoflexid and mesoflexid with a para- and metafossettid formed (Figure 1A, B, C). After moderate wear, the mesofossettid is formed (Figure 1D). FAM 64272 is little worn, and has a minute accessory fossettid on M₂ lingual to the end of the metafossettid (Figure 1B). In later stages of wear, as the tooth shortens, the enamel is removed from the anterior edge by interdental wear and the fossettids become compressed. The largest of the fossettids, the mesofossettid, is the most persistent. The para- and metafossettids are sometimes completely lost on senile individuals (Figure 1E).

M₃ is narrower (buccolingually) than M₁ and M₂, but is usually as long or longer (anteroposteriorly). M₃ is not tapered ventrally, so it retains its squared shape even in very heavily worn specimens. The occlusal pattern of the last molar is similar to that of the anterior molars except that the parafossettid is usually the longest of the lingual fossettids, rather than the mesofossettid. On the holotype, there are two small, circular fossettids anterior to the parafossettid (Figure 1A). It appears that these will be eliminated after minor additional wear.

The lower incisors have a smooth anterior enamel surface and are nearly as wide as they are long (anteroposteriorly). The anterior surface is strongly rounded. The upper incisors are nearly identical in cross-sectional shape with a smooth rounded anterior surface.

The only upper cheek tooth known is P⁴ (Figure 1F). Based on the alveoli present on the partial cranium FAM 64269, it is the largest of the cheek teeth. The hypoflexus is open on all specimens and extends anterobuccally for about half the width of the tooth. The paraflexus is open lingually on the premolars of FAM 64269, but the parastria is only 0.6 mm deep, so it will close after a little more attrition. The parafossette has already formed on FAM 64270 which shows only a little more wear than the premolars of the skull. The mesofossette originates at the center of the buccal border of the tooth and bends posteriorly, ending at the center of the posterior border of the tooth. The metafossette is the smallest. It is slightly elongated (buccolingually) and oriented slightly obliquely. Based on the alveoli, M³ is not markedly larger than M².

The cranium of *E. galushai* is well preserved in FAM 64269, which is not crushed or distorted, and preserves the entire skull anterior to the parietal bones. In dorsal view (Figure 2A), the rostrum is parallel-sided. The nasals widen slightly anteriorly and end

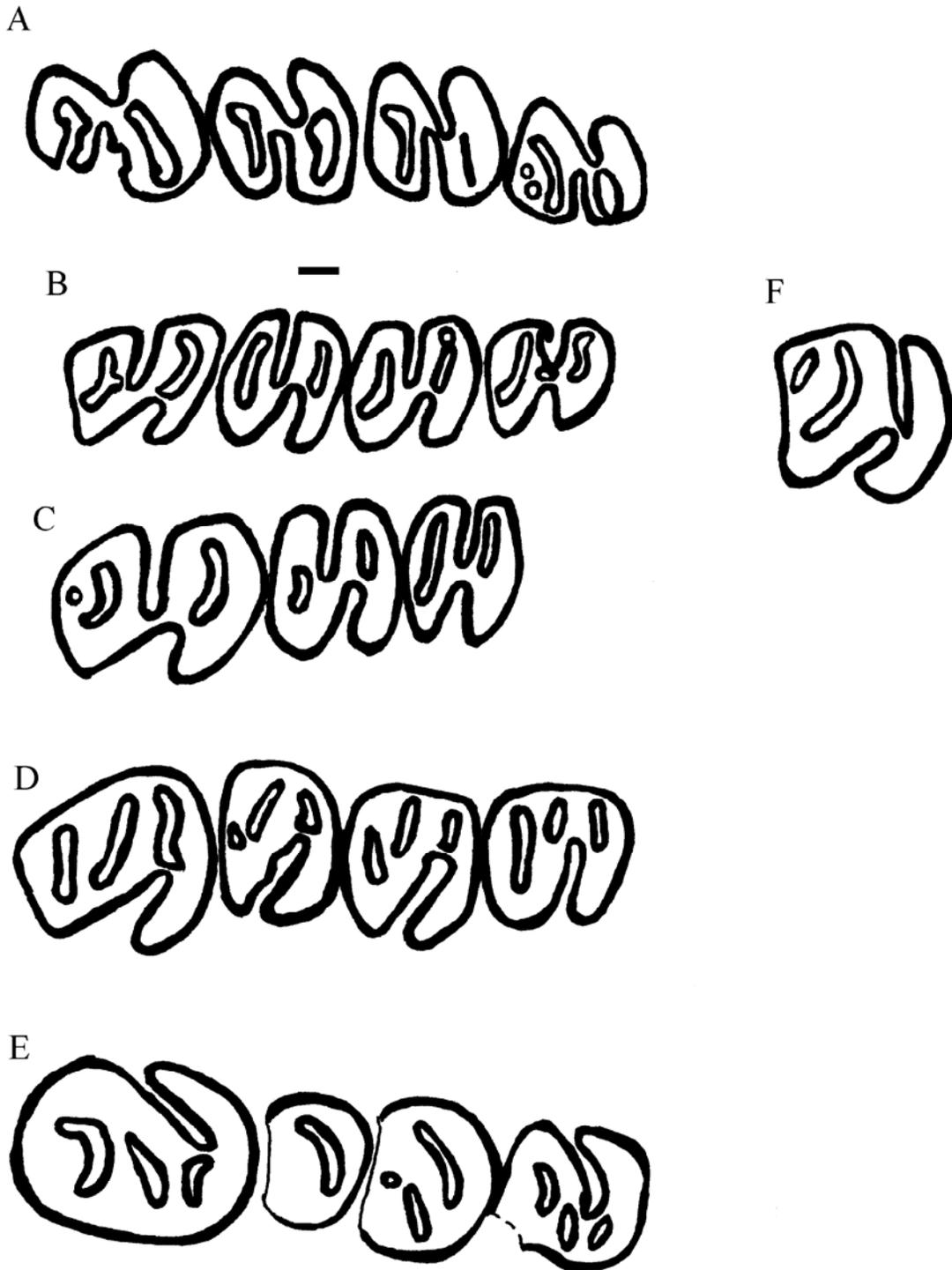


FIGURE 1. Occlusal patterns of dentitions of *Euroxenomys galushai*. A, Holotype, FAM 64274, right P₄-M₃. B, FAM 64272, left P₄-M₃. C, FAM 64278, left P₄-M₂. D, FAM 64281, left P₄-M₃. E, FAM 64283, right P₄-M₃. F, FAM 64269, right P⁴. Anterior is to the left on Figures A-E. Anterior to the right on Figure F. Bar scale = 1 mm.

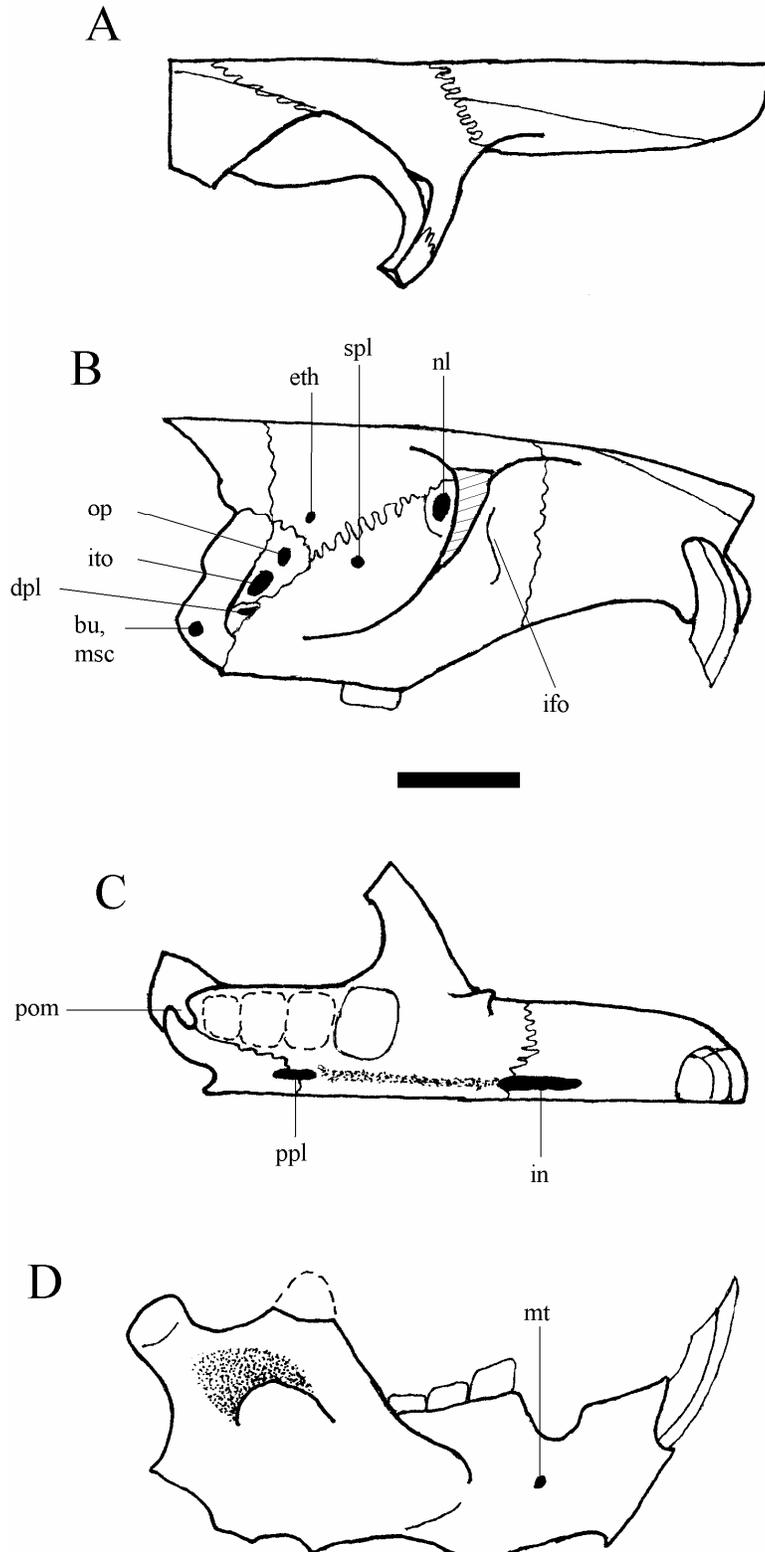


FIGURE 2. Skull and mandible of *Euroxenomys galushai*. A-C, FAM 64269, right half of cranium. A, dorsal view. B, lateral view. C, ventral view. D, Right lateral view of mandible (based on FAM 64283 and FAM 64287). Abbreviations for foramina: bu, buccinator; dpl, dorsal palatine; eth, ethmoid; ifo, infraorbital; in, incisive; ito, interorbital; msc, masticatory; mt, mental; op, optic; pom, posterior maxillary; ppl, posterior palatine; spl, sphenopalatine. Bar scale = 1 cm.

posteriorly at the anterior margin of the anterior root of the zygoma. The frontal-nasal suture is continuous with the frontal-premaxillary suture, but the nasals extend slightly more posterior. There is only a minute contribution to the skull roof by the lacrimal. Enough of the zygomatic arch is preserved on both sides of the skull that the anterior end of the jugal is preserved. It does not contact the lacrimal, but nearly so, falling short by approximately 2 mm. The posterior margin of the frontals at the frontal-parietal suture originates at the postorbital constriction and forms a V posteriorly. Just a small portion of the parietals remain, but it is evident that they have the rugose textured surface typical of all castorids. Above each orbit, on the frontals, are low ridges that converge posteriorly. These ridges are coincident with the frontal-parietal suture but do not completely fuse as far as the cranial bones that are preserved.

In lateral view (Figure 2B), the skull is clearly sciuriform. The rostrum tapers slightly anteriorly and is gently arched. The premaxillary-maxillary suture extends ventrally down the side of the rostrum, originating at the anterior margin of the zygomatic plate. The infraorbital foramen is a slit that opens anteriorly, just anterior to the zygomatic plate at about mid-depth of the rostrum. There is a distinct area for a muscular attachment at the ventral end of the lip of the infraorbital foramen.

The orbital wall is well preserved. The nasolacrimal foramen is large and opens dorsally in the anterodorsal corner of the orbital wall. The optic foramen is a small oval near the center of the orbital wall, within the orbitosphenoid bone, dorsal to the second upper molar. Almost directly anterior to it is the sphenopalatine foramen, entirely within the maxillary bone. A small ethmoid foramen is anterior and dorsal to the optic foramen within the frontal. Just posterior and ventral to the optic foramen is a large oval interorbital foramen. Ventral to the latter is a small dorsal palatine foramen. There is a single, circular foramen on the posteroventral corner of the alisphenoid which appears to be the opening for the buccinator and masticatory foramina.

The incisive foramina are typically small and slit-like, near the center of the upper diastema (Figure 2C). On the palatal surface, the premaxillary-maxillary suture bends posteriorly and crosses the mid-line at the posterior end of the incisive foramina. There are two distinct but shallow grooves extending posteriorly from the incisive foramina into the maxilla and end at the

posterior palatine foramina. The tooth rows diverge posteriorly. The maxillary-palatine suture originates posterior to the tooth row, runs along the medial side of the cheek teeth and ends anteriorly where it crosses the mid-line of the palate even with the alveoli for the first molars. The posterior palatine foramina are large ovals that penetrate the maxillary-palatine suture lateral to its anterior extent. The only other foramen visible on the cranium is the posterior maxillary, which is posterior to the tooth rows on both sides of the palate. It is large and oval, and is not closed laterally, forming a large notch.

Table 2. Cranial measurements of *Euroxenomys galushai*, FAM 64269. Measurements in mm.

Upper diastema length	21.60
Alveolar length P ⁴ -M ³	14.90
Maximum rostral width	13.98
Width of postorbital constriction	10.13
Length of incisive foramen	6.02

The mandible is robust and the diastema deep and relatively short (shorter than the tooth row). The digastric process is present but very small. The masseteric scar ends anteriorly below the premolar. Just anterior to it is a single, small mental foramen, below the anterior margin of P₄. The ascending ramus blocks the last molar from lateral view. The angle of the mandible is not completely preserved on any specimen, but enough of it is present on FAM 64288 and FAM 74283 to show that it was flattened ventrally. Only the base of the coronoid preserved. It was wide and clearly lateral to the condyle, completing the zigzag pattern of the mandibular processes, typical of castoroidines. There is a deep, wide valley separating the ascending ramus from the tooth row. On the lateral side of the ascending ramus is a large knob that houses the base of the lower incisor. Medial to it is a large depression.

Discussion—Dentally, *Euroxenomys galushai* clearly belongs to this genus based on the emended diagnosis (Hugueney, 1999:291; Korth, 2001a:73). The cheek teeth are lower crowned with shorter striids than any contemporaneous species of *Monosaulax* or *Eucastor* (Korth, 1999:table 2), but comparable with those of North American species of *Euroxenomys* (Korth, 2001a:table 2).

The skull is similar in overall shape and proportions of that described for *E. inconnexus* (Korth, 2001a). It has a relatively short and

broad rostrum. There are three peculiarities of the skull of *Euroxenomys galushai*. *Eutypomys* and nearly all reported castorids have an interorbital foramen anterior to the optic foramen in the cranium. Wahlert (1977) used this as one of the diagnostic characters of Castoroidea. The buccinator and masticatory foramina in *Eutypomys* and many other castorids are separate from one another (Wahlert, 1977). They appear to be fused in *E. galushai*. However, this is also the condition in the Hemphillian *Dipoides* (Wagner, 1983). Unfortunately, these features cannot be observed on the only previously described skull of *Euroxenomys* (Korth, 2001a).

The most unusual feature is that of the posterior maxillary foramen. In *E. galushai* it is open laterally, forming a notch. In the skull of *E. inconnexus* the posterior maxillary foramen is laterally closed off (Korth, 2001a). Wahlert (1977) viewed the lateral closure of the posterior maxillary foramen as a derived one for castoroids. The only other castorids with a posterior maxillary notch are the anchitheriomysines *Anchitheriomys* and *Oligotheriomys* (Korth, 1998; Korth and Emry, 1997), clearly not closely related to the castoroidines (Korth and Martin, in press).

CONCLUSIONS

In the most recent review of European castorids, Huegeney (1999) included *Euroxenomys* as a subgenus of *Trogontherium* and recognized only one species that included two subspecies, *T. (E.) minutum minutum* and *T. (E.) minutum rhenanum*. Korth (2001b) noted significant differences between *Euroxenomys* and *Trogontherium* and recognized them as separate genera. The only difference between the subspecies of *E. minutum* is the elongation of M^3 . In *E. m. minutum* the M^3 is similar in size to M^2 , but in *E. m. rhenanum* the M^3 is elongated with an accessory fossette, more closely approaching the elongation of M^3 in *Trogontherium*. None of the recognized species of *Euroxenomys* from North America has the elongation of M^3 as in *E. m. rhenanum*, but instead are very similar to *E. m. minutum* in this character (Huegeney, 1999:fig. 28.7 E₁, F₁).

The earliest occurrence of *Euroxenomys* is nearly contemporaneous in both Europe and North America. Korth (2001a, 2001b) suggested that the genus originated in North America because of its earlier occurrence there. However, the earliest occurrence of *Euroxenomys* in Europe is Orleanian (MN4, Huegeney, 1999:fig.

2809), contemporaneous with the early Hemingfordian occurrence of *Euroxenomys* in North America (Korth, 2001a, 2004). The origin of *Euroxenomys* and the remainder of the Trogontheriini is uncertain at this time.

In North America, the genus is short-lived, existing only through the early Barstovian, whereas in Europe it continues until Turolian (MN13, roughly equivalent to the late Hemphillian). Although only one species with two subspecies of *Euroxenomys* is recognized in Europe, the tribe Trogontheriini is more diverse in the Old World including the greatly derived *Trogontherium* and several other European and Asian genera that continue into the Pleistocene (Xu, 1994; Korth, 2001b). In North America, there are three distinct species from the late Hemingfordian to early Barstovian, but no other species referable to the Trogontheriini are known.

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