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Author: Korth, William W.

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Cranial morphology, systematics and succession of beavers from the middle Miocene Valentine Formation of Nebraska, USA

WILLIAM W. KORTH

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Previously, it was believed that there was a dramatic turn-over in the fauna of beavers (Rodentia, Castoridae) from the Barstovian to the Clarendonian from Nebraska. Stratigraphically controlled collections of fossil castorids from the Valentine Formation, which cross this boundary, now indicate that a complete change in the castorid fauna did not occur, but instead a more gradual change and replacement of earlier taxa with more advanced taxa occurred. The range of *Eucastor tortus* and *Monosaulax skinneri* is extended from late Barstovian into the latest Barstovian Devil's Gulch Member and the range of the otherwise Clarendonian species of *Prodipoides* is extended downward into the late Barstovian Crookston Bridge Member. The skulls of *Monosaulax skinneri* and *Eucastor valentinensis* are described in detail for the first time. The cranial morphology of *M. skinneri* is primitive for Castoroidini and that of *E. valentinensis* is specialized for tooth-digging behavior as in the Nothodipoidini. A new genus, *Temperocastor*, is proposed for *E. valentinensis* based on its primitive morphology of the cheek teeth and derived cranial morphology. *Temperocastor* represents the most primitive nothodipoidine.

Key words: Castoridae, faunal succession, Barstovian, Clarendonian, Valentine Formation.

William W. Korth [wwkorth@frontiernet.net], Rochester Institute of Vertebrate Paleontology, 265 Carling Road Rochester, New York 14610, USA.

Introduction

Beavers (Castoridae) are a diverse family of rodents throughout the late Paleogene and Neogene of North America. The most diverse subfamily is the Castoroidinae which had its greatest diversity in the Miocene (Barstovian to Hemphillian), culminating in the giant beaver *Castoroides* which became extinct in the Pleistocene (Stirton 1935; Korth 1994). Stirton (1935) viewed the phylogeny of this subfamily to be represented by the most primitive genus *Monosaulax* during the Barstovian, followed by the more derived *Eucastor* in the late Barstovian through the Clarendonian, which then gave rise to *Dipoides* in the Hemphillian. This sequence of genera was followed by nearly all later authors (Korth 2001). More recently, it has been demonstrated that the Castoroidinae in North America during the Miocene were recognizable into two tribes, Castoroidini and Nothodipoidini (Korth 2007a, b). Each of these tribes was represented by a different phylogenetic sequence: *Monosaulax–Prodipoides–Dipoides* in the Castoroidini and *Eucastor–Nothodipoides* in the Nothodipoidini (Korth 2007a, b). The generic changes in these lineages were coincident with the provincial ages: *Eucastor* and *Monosaulax* in the Barstovian, *Nothodipoides* and *Prodipoides* in the Clarendonian.

The Valentine Formation of northern Nebraska represents the time from the middle Barstovian through the Clarendonian and is therefore, ideal for demonstrating any phylogenetic change present in each of these lineages. Due to the extensive and stratigraphically controlled collections made by the field parties of the American Museum of Natural History (Frick Collections) and the University of Nebraska State Museum in the Valentine Formation of Nebraska, a nearly continuous sequence of faunas can be reconstructed. A reexamination of castorid specimens from this section on the species level suggests that the change in the castorids over the time represented by these strata was not as simple and dramatic as previously believed.

Leidy (1858) described the first beaver, *Eucastor tortus*, from what is now known as the Barstovian (middle Miocene) Valentine Formation in northcentral Nebraska. In all, three species of castoroidine beavers have been identified from the Barstovian section of the Valentine Formation in this area: *Eucastor tortus*, *Monosaulax skinneri* Stout, 1999, and *E. valentinensis* Stout, 1999 (see Stirton 1935; Voorhies 1990a, b; Evander 1999; Korth 1999, 2006). The castorodines reported from the superjacent Clarendonian Burge Member of the Valentine Formation were *Eucastor burgensis* Korth, 2002, *E. dividerus* Stirton,1935 (both species later referred to *Prodipoides* Korth, 2007), and *Nothodipoides stritoni* Korth, 2002. From this record, it appears that there is a dramatic change in the castoroidine castorids through the time spanned by the Valentine Formation: the Barstovian is represented by three species referred to *Eucastor* or *Monosaulax* (Leidy 1858; Stirton 1935), whereas the early Clarendonian is represented by three species referred to either *Nothodopoides* or *Prodipoides* (Korth 2002a, 2007a).

The cranial morphology of *Eucastor tortus*, *Nothodipoides*, and species of *Prodipoides* from the Valentine Formation has been described in detail elsewhere (Korth 2007a, b). On the basis of the cranial differences between these genera, the North American Castoroidinae were divided into two, the Castoroidini and Nothodipoidini. However, only fragmentary crania of *Monosaulax* species have been previously described (Korth 1999, 2001b). The skull of "*Eucastor*" *valentinensis* was described by Korth (2005), but the specimen was later referred to *E. tortus* (Korth 2006, 2007a), so the cranial morphology of "*Eucastor*" *valentinensis* is not known. Two nearly complete crania of *Monsaulax skinneri* and a partial skull of "*Eucastor*" *valentinensis* from the Valentine Formation are described below, and allow for a better understanding of the systematic position of these species.

Cranial terminology follows that of Wahlert (1977) and Wible et al. (2005); dental terminology follows that of Stirton (1935). Procumbency indices for upper incisors follow Korth and Rybczynski (2003: fig. 7).

Institutional abbreviations.—CM, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania USA; FAM, Frick Collections, American Museum of Natural History, New York, New York USA; UCMP, University of California Museum of Paleontology, Berkeley, California USA; UNSM, University of Nebraska State Museum, Lincoln, Nebraska USA; USNM, U.S. National Museum of Natural History, Smithsonian, Washington D.C., USA.

Geological setting

The Valentine Formation is exposed throughout the north-central part of Nebraska and is the lowest part of the Ogallala Group in this area (Skinner et al. 1968; Skinner and Johnson 1984). This formation has been divided into four superposed members (Fig. 1): Cornell Dam (lowest), Crookston Bridge, Devil's Gulch, and Burge (highest) (Skinner and Johnson 1984). The entire section is estimated to represent two million years from approximately 14 Ma to 12 Ma based on dated volcanic ash beds in the area (Tedford et al. 2004). Unconformities are present between the lower two members, Cornell Dam and Crookston Bridge, and also between the Devil's Gulch and Burge Members (Skinner and Johnson 1984). The latter is believed to represent a greater hiatus (Skinner et al. 1968).

Precise locality data for the cited quarries are presented in Skinner and Johnson (1984) and Voorhies (1990a, b).

Voorhies (1990a) compiled faunal lists of quarries throughout the Barstovian in Nebraska and determined the age of each of these members. He concluded that faunas from the Cornell Dam Member were medial Barstovian, those from the Crookston Bridge Member were late Barstovian, and those from the Burge Member were earliest Clarendonian (Voorhies 1990a: fig. 4). Voorhies did not list any quarries from the Devil's Gulch Member. Most recently, Tedford et al. (2004) followed Voorhies's (1990a) sequence, but considered the Cornell Dam faunas as early–late Barstovian instead of medial Barstovian, and placed the Devil's Gulch Member in the latest Barstovian just above the Crookston Bridge faunas. Tedford et al. (2004: fig. 6.2) also indicated a significant time gap, represented by the unconformity, between Devil's Gulch Member and Burge Member, but not between the Cornell Dam and Crookston Bridge members. Voorhies (1990a) also noted several fossil quarries along the Republican River in southcentral Nebraska. These quarries were not assigned to the Valentine Formation, but represent basal sediments of the Ogallala Group that are of equivalent age to the Barstovian Crookston Bridge Member quarries in the north. Several specimens cited below are from this area.

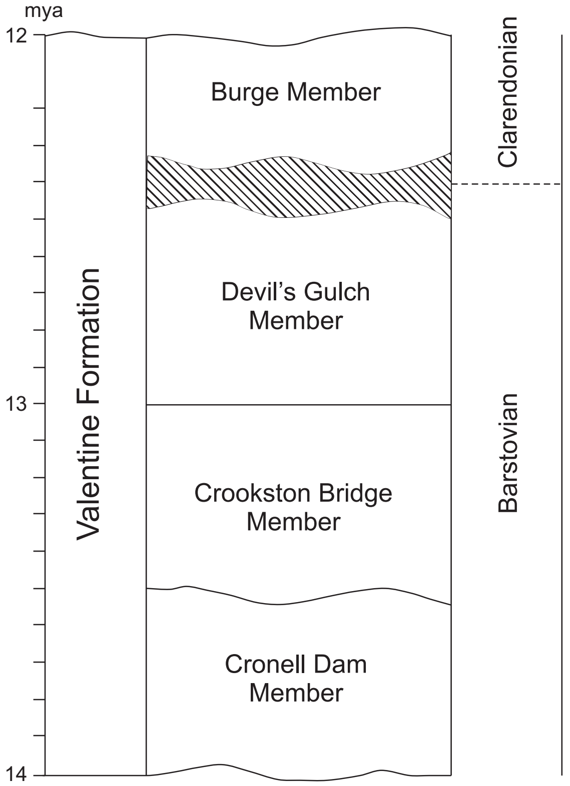

Fig. 1. Generalized stratigraphic section of the middle Miocene Valentine Formation in northern Nebraska (modified after Skinner and Johnson 1984: fig. 4 and Tedford et al. 2004: fig. 6.2). Striped area represents time gap of unconformity between members.

Systematic paleontology

Family Castoridae Hemprich, 1820

Subfamily Castoroidinae Allen, 1877

Tribe Castoroidini Allen, 1877

Genus *Monosaulax* Stirton, 1935

Type species: *Steneofiber pansus* Cope, 1874; Barstovian (Miocene), New Mexico, USA.

Monosaulax skinneri Stout, 1999

Figs. 2, 3, 4A–D.

1935 *Monosaulax pansus* (Cope, 1874); Stirton 1935 (in part): 416.
1990 *Monosaulax pansus* (Cope, 1874); Voorhies 1990a (in part): tables 1, 2.
1990 "*Monosaulax*" sp.; Voorhies 1990b: A94–A95.
1999 *Monosaulax skinneri* sp. nov.; Stout 1999 in Evander 1999: 246, fig. 7.

Holotype: UNSM 67241, left mandible with p4–m3.

Type locality: Railway Quarry (UNSM locality Cr 12), Cherry County, Nebraska, USA.

Type horizon: Late Barstovian (middle Miocene) Crookston Bridge Member, Valentine Formation.

Material.—UNSM 49027 and 49028, nearly complete crania; UNSM 49030 and 49031, mandibles with cheek teeth; FAM 64292, 64317, 64315, 64956, partial mandibles with incisor and cheek teeth; FAM 64322, isolated (unworn) p4.

Emended diagnosis.—Largest species of the genus; cheek teeth lower-crowned than other species; p4 three-rooted (two-rooted in other species); parafossettid curved and accessory fossettids common on p4.

Description.—The two crania of *Monosaulax skinneri* are the most complete ever described for the genus. UNSM 49027 is an undistorted skull lacking only the zygomatic arches and the basicranium, with complete dentition. UNSM 49028 has a complete dentition and lacks only the zygomatic arches. However, the latter cranium is laterally crushed, with only the palate between the tooth rows not distorted, but the basicranial area is intact, allowing for a description of the complete cranium. UNSM 49027 is slightly larger than UNSM 49028 (Table 1).

In dorsal view (Fig. 2A), the rostrum is parallel sided and longer relative to the length of the entire skull compared to that of *Castor*, but less so than in contemporaneous *Eucastor* (Korth 2007a). The nasals extend posteriorly to a point even with the center of the anterior root of the zygomatic arches, just slightly posterior to the end of the premaxillaries. The nasals widen anteriorly, making up the entire width of the rostrum at its anterior end. The lacrimal bones are missing on both specimens, but it is evident that the anterior extent of the jugal bone does not contact it on the zygomatic arch, a character diagnostic of castoroidines (Xu 1995; Korth 2001). The frontal bones are dorsally flat and extend together onto the neurocranium in a posteriorly pointing V-shape. The postorbital constriction occurs at the posterior end of the orbits and is nearly as great as in *Eucastor* (Table 1; Korth 2007a: tables 1, 3). The surface of the parietals is rugose, typical of castorids. The temporal crests are very low and originate dorsal to the orbits, converging gradually posteriorly, meeting at a sagittal crest that forms only on the interperital, just anterior to the nuchal crest. There are two temporal foramina along the squamosal-parietal suture; one just anterior to the nuchal crest, the other more anterior, dorsal to the posterior end of the zygomatic arch. This same feature of two temporal foramina is also present in *Dipoides* (Wagner 1983) and on the referred skull of *Monosaulax pansus* from New Mexico (Korth 2002b). The interparietal is triangular in outline, abutting the nuchal crest. The neurocranium is widest at the posterior base of the zygomatic arches.

Table 1. Cranial measurements (in mm) of *Monosaulax skinneri* and *Temperocastor valentinensis*.

Measurement	*M. skinneri*		*T. valentinensis*
	UNSM 49627	UNSM 49628	UNSM 45392
Total length of cranium	77.69	63.39	51.12
Maximum width of rostrum	15.86	–	9.89
Postorbital constriction	9.68	–	7.83
Posterior width (occiput)	39.0	–	–
Length upper diastema	26.33	25.34	19.53
Length of incisive foramen	6.23	6.13	4.79
Alveolar length P4–M3 (right)	17.16	16.90	11.54
(left)	17.87	16.14	–
Depth of cranium at M2	28.03	–	–
Angle of procumbency A[a]	90°	90°	104°
Angle of procumbency B[a]	97°	92°	116°

[a] As defined by Korth and Rybczynski (2003: fig. 7).

In lateral view (Fig. 2B), the skull is very similar in shape to that of *Dipoides* and *Prodipoides* (Wagner 1983: figs. 2, 3; Korth 2007a: fig. 6). The upper diastema slopes slightly upward towards the incisors. The upper incisors are directed ventrally, showing no signs of procumbency. The skull is sciuromorphous with the infraorbital foramen opening anteriorly, just anterior to the zygomatic plate at mid-depth of the rostrum. The maxillary-premaxillary suture descends the side of the rostrum in a nearly viertical line anterior to the infraorbital foramen.

The orbital wall is well preserved and undistorted on UNSM 49027 (Fig. 2B). The nasolacrimal foramen is large and in the anterodorsal corner of the orbital wall. A sphenopalatine foramen is high on the orbital wall, about at mid-depth of the skull, dorsal to M1. It is entirely within the maxilla, just below the maxillary-frontal suture. Directly posterior to the sphenopalatine foramen, dorsal to the posterior margin of M2, is the optic foramen. It is a small oval within the orbitosphenoid, opening anterodorsally. The ethmoid foramen is entirely within the frontal bone, positioned dorsal to the optic and sphenopalatine foramina, about midway between them. There are three identifiable interorbital foramina. The smallest is just anterior and slightly ventral to the optic foramen, a second is posterior and ventral to the optic, and a third, much larger, oval foramen is posterior and ventral to the second interorbital foramen. All are within the orbitosphenoid bone. The palatine contribution to the floor of the orbital wall, and the dorsal palatine foramen that it contains, is blocked laterally by the alisphenoid and cannot be seen on Fig. 2B. In the posteroventral corner of the alisphenoid are two small foram-

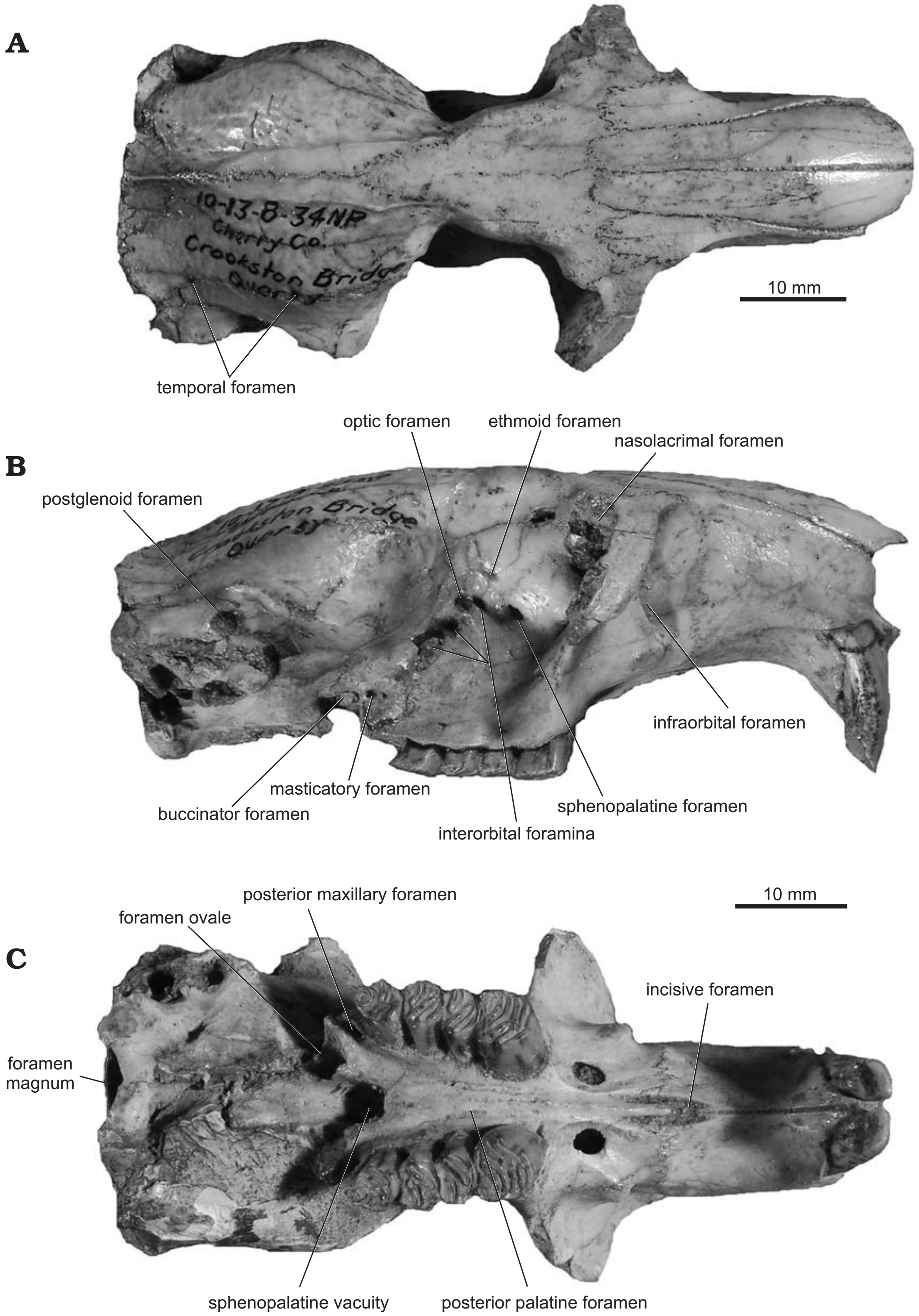

Fig. 2. The beaver *Monosaulax skinneri* Stout, 1999, specimen UNSM 49027 from the middle Miocene Valentine Formation of Nebraska, USA. Cranium in dorsal (**A**), right lateral (**B**), and ventral (**C**) views.

ina. The anterior of the two is interpreted as the masticatory and the posterior as the buccinator foramen. A large postglenoid foramen is present just posterior to the glenoid fossa.

Ventrally, the premaxillary-maxillary suture crosses the center of the rostrum near the center of the incisive foramina, which are almost exactly in the center of the upper diastema

(Fig. 2C). The length of the incisive foramen is 24% that of the total length of the upper diastema (Table 1) which is in the low end of the range for castoroidines (Korth 2007a: table 3). On the uncrushed skull, UNSM 49027, there is a fairly large oval opening just anterior to the tooth row on both sides of the skull. These are not foramina, but mark the base of the upper incisor where the bone is very thin and is often broken away. In life, these openings would not have been present.

The tooth rows diverge strongly posteriorly and P4 is the largest of the cheek teeth. There are two distinct grooves on the palate, one on either side of the midline, running from the posterior margin of the incisive foramen for the entire length of the palate, widening at the posterior margin of the palate where the tooth rows are the farthest apart. The maxillary-palatine suture starts in the center of the palate at a point even with the lingual roots of M2 and runs just medial to the alveolar margin of the tooth rows. A posterior palatine foramen is at the anterior margin of this suture within the grooves of the palate medial to M2. Posterior to M3, there is a small posterior maxillary foramen within the maxillary-palatine suture. The pterygoid flanges are broken away on both available specimens. The large posterior opening for the sphenopalatine vacuity opens posteriorly at the back end of the palate, even with M3. The foramen ovale is just posterior to the tooth row and anterior to the bulla.

The basicranial area is only preserved on the crushed skull, UNSM 49028, and is slightly distorted (Fig. 3A). The bulla is inflated as in *Dipoides* and other early castoroidines. The external acoustic meatus is a short tube that runs posterodorsally. Just posterior to the opening for the external acoustic meatus is a small foramen for the posttemporal canal, along the nuchal crest, within the mastoid-squamosal suture. Two foramina are recognizable along the medial border of the bulla: the jugular foramen at the posteromedial corner of the bulla and the opening for the carotid canal near the anteromedial corner of the bulla. In Fig. 3A, the carotid canal appears more posterior because the right side of the skull was pushed backward when the cranium was crushed. The hypoglossal foramen is on the ventral part of the occipital, just anterior to the occipital condyle.

On the occiput, the identifiable foramina are the foramen magnum, the posttemporal canal and a small mastoid foramen (Fig. 3B). The mastoid foramen is along the occipital-mastoid suture above the level of the top of the foramen magnum and lateral to it. The mastoid contribution to the occiput is minimal, extending less than one-fourth the width of the occiput from the side. The occiput is nearly vertical in orientation and there is no indication of any well-defined ridges.

In Evander's (1999) original description of this species, he described the lower molars but did not describe the upper dentition of *Monosaulax skinneri* because he had no upper teeth in the hypodigm. The two crania of *M. skinneri* have complete dentitions, allowing for a complete description of the upper teeth.

The cheek teeth are mesodont and rooted. The cheek teeth of both specimens are well worn. P4 is the largest of the upper cheek teeth. On the lingual side the hypostriia extends nearly to the base of the crown, so the hypoflexus remains open lingually. It is oriented anterobuccally, and extends about half the width of the occlusal surface (Fig. 4D). On the buccal half of the occlusal surface there are three fossettes formed. The anterior parafossette is transversely oriented. The lingual end of the parafossette abuts the buccal end of the hypoflexus on UNSM 49027. The mesofossette is the longest of the lingual fossettes, extending nearly the entire width of the tooth. It curves posteriorly, ending lingually posterior to the hypoflexus. The metafossette is the shortest of the fossettes, reaching less than half way across the occlusal surface of the tooth.

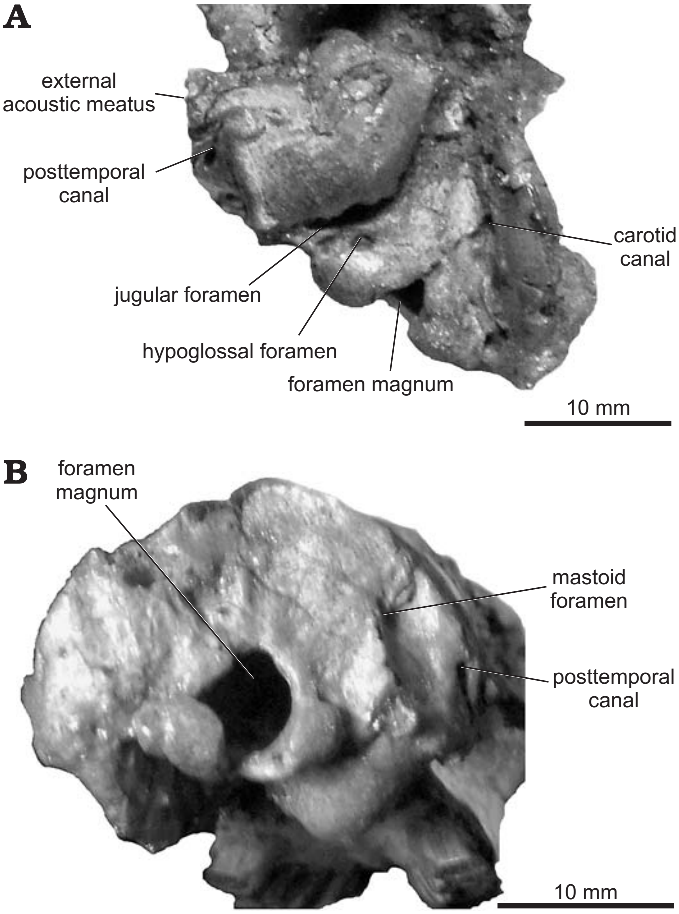

Fig. 3. The beaver *Monosaulax skinneri* Stout, 1999, specimen UNSM 49028 from the middle Miocene Valentine Formation of Nebraska, USA. Posterior fragment of skull. **A**. Cranial basis in ventral view (anterior to the top). **B**. Occipital plate in posterior view.

On both specimens, M1 is the most worn tooth. Due to the tapering of the tooth, it is shortened anteroposteriorly. Only the hypoflexus and mesofossette are preserved. The hypoflexus is oriented as in P4, and reaches about three-fourths the way across the surface of the tooth. The mesofossette is short, not reaching the center of the tooth, and curved slightly posteriorly. The second upper molar is nearly identical to the first but less worn, and the parafossette and metafossette are preserved as minute circles along the buccal edge of the

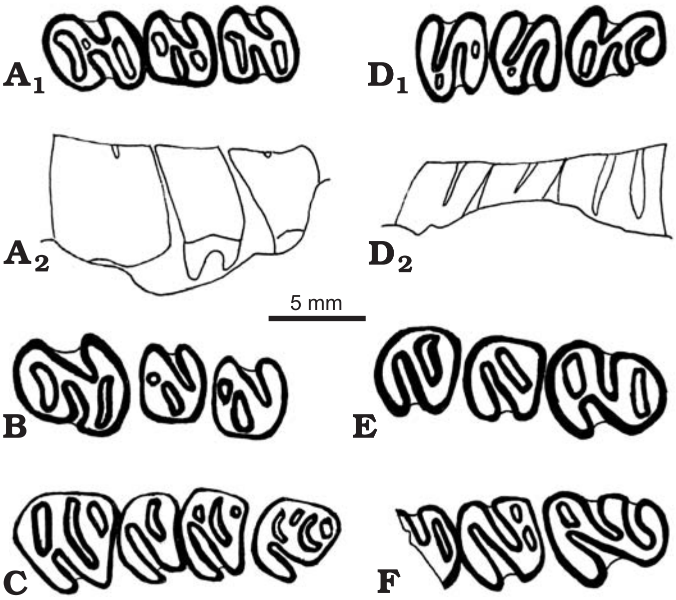

Fig. 4. The beavers from the middle Miocene Valentine Formation of Nebraska, USA. **A**–**C**. *Monosaulax skinneri* Stout, 1999. **D**–**F**. *Prodipoides dividerus* (Stirton, 1935). Cheek teeth: **A**. FAM 64315, right p4–m2 from Devil's Gulch Member in occlusal (A$_1$) and medial (A$_2$) views. **B**. FAM 64317, right p4–m2 from Devil's Gulch Member. **C**. UNSM 49027, left P4–M3 from Crookston Bridge Member. **D**. FAM 64319, left p4–m3 from Devil's Gulch Member; in occlusal (D$_1$) and medial (D$_2$) views. **E**. FAM 64316, right p4–m2 from Devil's Gulch Member. **F**. FAM 64314, right p4–m2 (partial) from Crookston Bridge Member. Anterior to left for specimens of *M. skinneri*, anterior to right for specimens of *P. dividerus*.

occlusal surface, anterior and posterior to the mesofossette, respectively.

M3 is approximately the same width as the first two molars, but is much longer. In UNSM 49027, it is slightly expanded at the posterobuccal corner. The morphology of the hypoflexus and parafossette is similar to that of P4. The mesofossette is short and strongly curved posteriorly, forming a C-shape and isolating the posterobuccal corner of the tooth. The metafossette is in the posterobuccal corner of the occlusal surface. It is a small oval that is obliquely oriented (anterobuccal-posterolingual). On the left M3 of UNSM 49027 there is a minute, circular accessory fossette anterior to the buccal end of the mesofossette.

The lower cheek teeth are similar to those of *Monosaulax* described elsewhere (Stirton 1935; Evander 1999). The occlusal surface of the molars is primitive (Fig. 4), retaining the parafossettid and metafossettid, well after the formation of the mesofossettid. FAM 64322 is an isolated, unworn p4. The crown height index (ratio of total crown-height to anteroposterior length) for the tooth is 1.24, much lower than species of *Prodipoides* or *Eucastor* that range from 1.50 to 1.70 (see Korth 1999: table 2; Korth 2002a: 17). The lower premolars are similarly primitive with a very short or absent parastriid, and a mesostriid that extends approximately half the total height of the crown. The morphology of the cheek teeth of the specimens from the Devil's Gulch Member is identical to that from the earlier horizons.

Discussion.—Previously, the only castoroidine reported from the Crookston Bridge Quarry was *Eucastor tortus* (Voohries 1990a). However, the measurements from the sample of beavers from this quarry exceed those of *E. tortus* reported elsewhere, and are closer in size to *Monosaulax skinneri* (see Korth 2006: table 1, and references therein). The primitive occlusal morphology of the molars (retention of the para- and metafossettes [-ids]), lower crown-height of the cheek teeth, and the shallow to absent lingual striids on p4 distinguish this material from *Eucastor*, and are the condition seen in specimens referred to *M. skinneri*.

The occurrence of *M. skinneri* from the Devil's Gulch Member of the Valentine Formation is the latest occurrence of the species as well as the genus. Specimens of *Prodipoides dividerus* are reported from this horizon as well (see below) and are of similar size. These two species can be easily separated on the basis of the molar morphology: *M. skinneri* has the primitive condition of retaining the para- and metafossettids after the formation of the mesofossettid, and the specimens of *P. dividerus* have attained the S-pattern of the occlusal surface with the elimination of the para- and metafossettids. The crown-height of the premolars is also different, being greater in *P. dividerus* (>1.60). The depth of the lingual striids on p4, especially the parastriid (Fig. 4B, F), is also greater on the specimens of *P. dividerus* than those of *M. skinneri*.

The cranial morphology of *Monosaulax skinneri* is generally primitive for castoroidine beavers (see Korth 2007a). However, there are two features of the skull of *M. skinneri* that are shared with Hemphillian *Dipoides* that are not present in Clarendonian species is *Prodipoides*: the double temporal foramen along the parietal-squamosal suture, and multiple interorbital foramina posterior to the optic foramen, both otherwise unique to *Dipoides* (Wagner 1983; Korth 2007a). In all other cranial features, the skull of *M. skinneri* is similar to that of other species of *Monosaulax* and *Prodipoides* (Korth 2007a). It is not likely that *Monosaulax* is closer to *Dipoides* than *Prodipoides* based on these features alone. The more derived dentition in *Prodipoides*, and the position of some of the cranial foramina of *P. dividerus* strongly suggest that *M. skinneri* is not directly ancestral to *Dipoides*. The precursor of *Dipoides* came from within *Prodipoides* with a more derived dental morphology.

Stratigraphic and geographic range.—Previously reported specimens are from UNSM quarries of the same horizon as the holotype in Nebraska, as well as early–late Barstovian UNSM quarries in Cornell Dam Member, Valentine Formation, Nebraska (Voorhies 1990a). Material discussed above: UNSM 49027, 49028, 49030, and 49031, are from Crookston Bridge Quarry, and FAM 64292 from the Railway Quarry, both late Barstovian Crookston Bridge Member, Valentine Formation, Cherry County, Nebraska. FAM 64956 and FAM 64322 from latest Barstovian Devil's Gulch Horse Quarry and FAM

Table 2. Dental measurements (in mm) of catoroidine beavers from the middle Miocene Valentine Formation of Nebraska. Abbreviations: L, anteroposterior length; W, transverse width. Measurements of tooth rows (p4–m3) taken at alveolar margin. Length and width measurements of lower premolar taken at the base of the tooth (maximum dimensions) where possible, otherwise taken as close to base of the tooth as possible.

Species/specimen	p4L	p4W	p4–m3	i1W	diastema
Monosaulax skinneri					
UNSM 49030	5.96	4.71		3.80	
UNSM 49031	6.42	5.06	18.20	4.33	13.48
FAM 64292	6.28	4.76	18.30	3.82	12.73
FAM 64295	6.62	5.80	21.48	4.85	11.98
FAM 64296	7.08	5.05	19.88	4.66	14.33
FAM 64297	6.91	4.35	19.31	4.86	15.25
FAM 64299	7.09	4.86			
FAM 64315	6.32	5.00	19.70	4.93	
FAM 64317	6.65	5.39	19.62	4.83	
FAM 64322	6.86	4.92			
FAM 64956	6.54	4.66	18.80	3.65	
Average	6.61	4.96	19.41	4.41	13.55
Prodipoides dividerus					
FAM 64319	6.13	4.66	19.58	4.39	12.92
FAM 64318	6.52	4.90	18.26		14.37
FAM 64316	6.62	5.24	20.42	4.46	14.34
FAM 64314	6.48	5.42		4.45	15.14
Average	6.42	4.93	19.42	4.43	13.88
Prodipoides burgensis					
UNSM 49029	5.95	4.91	17.33	4.44	
FAM 64857	5.79	4.93	16.57	4.15	11.52
FAM 64957	5.50	4.26	16.51	4.20	
FAM 64958	6.16	4.66	17.35	4.231	2.50
FAM 64959	6.46	4.92	17.42	4.52	12.45
FAM 64963			15.90	4.39	11.30
CM 18875	5.43	4.90	16.25		11.51
Average	5.88	4.76	16.76	4.36	11.86
Eucastor tortus					
FAM 65262	4.64	3.97			12.24
FAM 64966(r)	4.89	4.47	14.35	4.25	12.75
(l)	5.00	4.47	14.22	4.05	12.02
CM 18876	4.40	3.71	13.52	3.34	
CM 18878	4.62	4.54		3.61	
Average	4.71	4.23	14.03	3.81	12.34
Temeperocastor valentinensis					
FAM 65252	4.45	3.72	12.66	3.98	11.18
FAM 65254	4.21	3.56	12.43	3.50	9.96
UNSM 45392	3.72	3.32	11.61	3.55	10.80
UNSM 45393	3.96	3.56	12.93	3.78	10.71
UNSM 45395	3.75	3.87	12.11		
UNSM 45398	4.40	3.31	12.89	3.28	
UNSM 45399	4.42	3.32		3.70	
Average	4.13	3.52	12.44	3.63	10.66

64315 and FAM 64317 from Fairfield Creek Falls Quarry, both quarries in the Devil's Gulch Member, Valentine Formation, Cherry County, Nebraska.

Genus *Prodipoides* Korth, 2007

Type species: *Eucastor dividerus* Stirton, 1935; Clarnedonian (Miocene), Nevada.

Prodipoides dividerus (Stirton, 1935)

Fig. 4E–H.

1935 *Eucastor dividerus* sp. nov.; Stirton 1935: 431, figs. 101–105.
2007 *Prodipoides dividerus* (Stirton, 1935); Korth 2007a: 125, figs. 4B, C, 5, 6.

Holotype: UCMP 29691, mandible with p4–m3.

Type locality: Fish Lake Valley beds, Esmeralda County, Nevada.

Type horizon: Clarendonian (Miocene) Esmeralda Formation.

Material.—FAM 64314, 64319, 64316, and 64318, mandibles with cheek teeth; and FAM 64324, partial cranium with incisors and right and left P4–M2.

Discussion.—There is no difference between the specimens cited here from the late Barstovian Devil's Gulch Member and those from higher in the Nebraska section. A single specimen from the subjacent Crookston Bridge Member is present in the FAM collections, FAM 64314 from the Nenzel Quarry in Cherry County (Fig. 4G). This specimen is clearly referable to this species and not *Monosaulax skinneri* (the most common beaver from this fossil quarry in the Frick Collections). The lingual striids on p4, especially the parastriid, is much deeper on FAM 64314 than in any specimen of *Monosaulax*. The mesofossettids have not yet formed on the molars but the metafossettid is already eliminated on m1 and there are two minute fossettids anterior to the hypoflexid. These will likely disappear before the closure of the mesoflexid because the mesostriid extends another 1.22 mm below the current occlusal surface. Although *Prodipoides burgensis* is also present at this horizon (see below), FAM 64314 is clearly too large to belong to this species (Table 2). This is the only specimen that can definitely be referred to *P. dividerus* from any horizon below the Devil's Gulch Member.

This is the first recognition of *P. dividerus* from before the early Clarendonian (Korth 2002a). As noted above, specimens of *Monosaulax skinneri* are also present in these lower horizons and are of similar size to specimens of *P. dividerus*. These two species are distinguishable based on the morphology of the lower premolar and molars (see above discussion). However, in very late stages of wear, when the para- and metafossettids are worn away on the molars in specimens of *M. skinneri* they cannot be separated from specimens of *P. dividerus*. For example, FAM 65344, a mandible with only an extremely worn p4 from the Devil's Gulch Member, cannot be assigned here to *P. dividerus* or *M. skinneri* due to the lack of distinguishing characters.

Stratigraphic and geographic range.— Previously cited specimens from quarries in the early Clarendonian Burge Member of the Valentine Formation and late Clarendonian Merritt Dam Members of the Ash Hollow Formation of Nebraska

(Korth 2002a). Material described above: FAM 64318 is from Devil's Gulch Horse Quarry; FAM 64316 is from Fairfield Creek Falls Quarry; FAM 64319 and 65344 are from Meisner Quarry (the latter three quarries are in Cherry County); and FAM 64324 is from Elliot Quarry, Brown County, all from the Devil's Gulch Member, Valentine Formation, Nebraska. FAM 64314 is from late Barstovian Nenzel Quarry, Crookston Bridge Member, Valentine Formation, Cherry County, Nebraska.

Prodipoides burgensis (Korth, 2002)

Figs. 5, 6A.

2002 *Eucastor burgensis* sp. nov.; Korth 2002a: 18, fig. 2.

2007 *Prodipoides burgensis* (Korth, 2002a); Korth 2007a: 124, fig. 3, 4A.

Holotype: FAM 64975, mandible with complete lower dentition.

Type locality: Lucht Quarry, Brown County, Nebraska.

Type horizon: Early Clarendonian (Miocene), Burge Member, Valentine Formation.

Material.—UNSM 49029, FAM 64857, 64956, 64957, 64958, 64959, and CM 18875, mandibles with cheek teeth; and FAM 65343, partial skull with right P4 and left M1.

Description.—Only a small portion of the cranium is preserved on FAM 65343. Dorsally, only the frontals are present. The postorbital constriction is 11.39 mm in width, slightly greater than the previously described skull of *P. burgensis* (Korth 2007a: table 1). Just posterior to the constriction is a low, but sharp sagittal crest. This part of the cranium is preserved on the skull of *P. burgensis* from the early Clarendonian, and there is no sagittal crest. Ventrally, there is little information preserved about the morphology. The palate is deeply grooved, but little else can be determined.

P4 is in a moderate state of wear. The hypoflexus and mesoflexus are still open, and the parafossette and metafossette have formed. In all other features, the tooth is similar to those previously described for *P. burgensis* (Korth 2002a, 2007a). The single upper molar has the occlusal pattern of a long hypoflexus and a mesofossette. No other fossettes are present.

Both the paraflexid and mesoflexid remain open on p4 of all but one specimen, FAM 64958, which has a greater amount of wear than the other specimens. Otherwise the morphology of p4 is like that previously figured for *P. burgensis* (Korth 2002a: fig. 2; Korth 2007a: fig. 4A). On the least worn specimen, FAM 64957, the parastriid is as deep as the mesostriid on the lingual side of the tooth. This is different than on any of the other specimens and the specimens previously described.

The lower molars on all of the specimens are at a state of wear where the mesofossettid has formed and the para- and metafossettids are lost, producing the *Dipoides*-like S-pattern (Fig. 5). However, on two specimens, one from the Devil's Gulch Member (FAM 64958) and one from the Crookston Bridge Member (FAM 64957) there is a minute metafossettid present on the former and a metafossettid and parafossettid on the latter on m2 after the mesofossetid has formed. In both cases, the retained fossettids are minute and will likely disappear after very little additional wear. The m1 on both of these specimens has attained the S-pattern. This indicates that the S-pattern is not yet fully attained on some specimens of m2 of *P. burgensis* from earlier Valentine horizons.

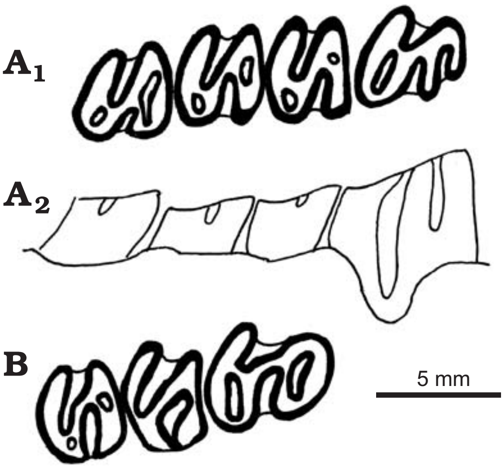

Fig. 5. The beaver *Prodipoides burgensis* (Korth, 2002) from the middle Miocene Valentine Formation of Nebraska, USA. **A**. UNSM 49029, left p4–m3, from the Crookston Bridge Member in occlusal (A_1) and medial (A_2) views. **B**. FAM 64857, left p4–m2, from Devil's Gulch Member. Anterior to right.

Discussion.—In a faunal list of the Ogallala fossil quarries of Nebraska, Voorhies (1990a: table 2) listed *Eucastor tortus* as the only species of castoroidine beaver from the late Barstovian Crookston Bridge Quarry. No tables, figures or descriptions of this material were provided. A reexamination of the material in the University of Nebraska collections from Crookston Bridge and Railway quarries has resulted in the recognition of specimens of *Prodipoides burgensis* in the samples that were originally referred to *E. tortus*. The lower dentitions of *E. tortus* and *P. burgensis* are similar in having the same degree of crown height and development of lingual striids on the lower premolar and they both generally have the S-pattern on the occlusal surface of the molars. However, *P. burgensis* is clearly larger than *E. tortus* (Voorhies 1990b: A97; Korth 2002a: table 2). Features of the cranium are very distinct between these two species as well (Korth, 2007a). The specimens referred here to *P. burgensis* are separable from those of *E. tortus* in size (Table 2) as well as the relative length of the diastema, development of the digastric process, and the position of the ascending ramus. In a sample of mandibles of these two species, the relative length of the lower diastema to the alveolar length of the tooth row in *E. tortus* ranged from 0.77 to 1.00 with a mean of 0.88, whereas in *P. burgensis* the range was from 0.62 to 0.78 with a mean of 0.71. This is not surprising because the same relationship exists between the upper diastema length and the upper tooth row, where the upper diastema is proportionally longer in *Eucastor* than in *Prodipoides* (Korth 2007a: table 3).

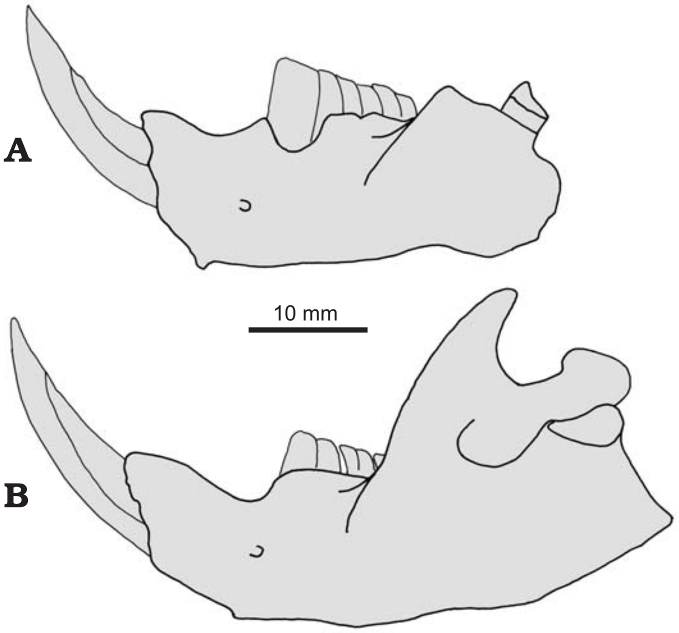

Fig. 6. The beavers from the middle Miocene Valentine Formation of Nebraska, USA. **A**. *Prodipoides burgensis* (Korth, 2002). **B**. *Eucastor tortus* (Leidy, 1858). Left mandibles in lateral view. **A**. FAM 64857, from Crookston Bridge Member. **B**. FAM 64966, from the Devil's Gulch Member.

The anterior margin of the ascending ramus on the mandible in specimens of *E. tortus* begins lateral to m1 and blocks all but the anterodorsal tip of m2 from lateral view (Stirton 1935: fig. 94). In *Prodipoides burgensis*, the ascending ramus originates lateral to m2, blocking only the posterior portion of m3 from lateral view (Fig. 6). It also appears that the digastric process is larger on *Prodipoides* than on *Eucastor.* In the case of the two specimens of *P. burgensis* recognized from quarries in the Crookston Bridge Member, size and these mandibular differences are consistent.

Prodipoides burgensis was originally reported only from the early Clarendonian Burge Member of the Valentine Formation (Korth 2002a). Previously, no castorids had been reported from the subjacent late Barstovian Devil's Gulch Member. The presence of *P. burgensis* from the Crookston Bridge Member along with its occurrence in the Devil's Gulch extends its known occurrence from the early Clarendonian back into the late Barstovian, overlapping the occurrence of *Monosaulax* and *Eucastor*.

Stratigraphic and geographic range.— Previously referred specimens from fossil localities in the early Clarendonian Burge Member of the Valentine Formation, Nebraska (Korth 2002a). Material described above: UNSM 49029 is from Crookston Bridge Quarry and FAM 64857 is from Railway Quarry A, Cherry County, Nebraska, Crookston Bridge Member, Valentine Formation; FAM 64957, 64958, 64959, 64961, and 65343 are from Meisner Quarry, FAM 64956 is from Devil's Gulch Horse Quarry, both of the latter quarries are in Cherry County, Nebraska and CM 18875 is from Verdigre Quarry, Knox County, Nebraska; these three quarries are in the Devil's Gulch Member, Valentine Formation.

Tribe Nothodipoidini Korth, 2007

Genus *Eucastor* Leidy, 1858

Type species: *Castor (Eucastor) tortus* Leidy, 1858; Barstovian (middle Miocene), Nebraska.

Eucastor tortus (Leidy, 1858)

Figs. 6B, 7A–C.

1858 *Castor (Eucastor) tortus* sp. nov.; Leidy 1858: 23.
1877 *Eucastor tortus* (Leidy, 1858); Allen 1877: 449.

Holotype: USNM 11020, partial palate and rostrum with incisors and right and left P4–M3.

Type locality: "Niobrara River, Loup Fork beds. Exact locality unknown." (Stirton 1935), Nebraska.

Type horizon: Barstovian (middle Miocene), Valentine Formation.

Material.—FAM 64966, nearly complete left and right mandibles with all cheek teeth; FAM 65262, right partial mandible with incisor and p4–m2; FAM 65252, fragmentary cranium with both incisors, left P4–M2 and right M1; CM 18876, partial left mandible with p4–m2; CM 18877, fragmentary left mandible with m2–m3; CM 18878, fragmentary right mandible with p4–m1; and CM 19672, partial maxilla with right M1–M2.

Description.—The partial cranium, FAM 65257, is badly broken and partially covered with matrix. The observable features are the same as those of the previously described skulls from lower in the Valentine Formation. The ratio of the length of the rostrum to that of the upper cheek tooth row is 1.70, at the lower end of the range for this species (Korth 2007a: table 3). The upper diastema is strongly dorsally arched, again as in other skulls of this species. The procumbency indices are: A= 100° and B= 110°. The only other diagnostic feature that can be determined is the relative size of M3. Although the tooth is lacking on the specimen, the alveolus is present on the left side and is much smaller than that of M2. All of these features indicate that FAM 65257 is referable to *Eucastor tortus*.

The morphology of the cheek teeth does not differ from that described previously (Stirton 1935; Voorhies 1990b, Evander 1999; Korth 2005 [as "*Monosaulax*" *valentinensis*]). The mesostriid on all observable p4s reaches more than half the height of the tooth. All of the specimens are at a level of wear that the parastriid is eliminated, forming the parafossettid (Fig. 7A–C). This indicates that the parastriid was very short. The only difference in the morphology of the premolar is that the parafossettid is gently concave anteriorly. Usually in *E. tortus* this fossettid is straight.

Voorhies (1990b) noted that the S-pattern of the occlusal surface of the molars was not fully attained in specimens of *E. tortus* from the earlier Cornell Dam Member. Evander (1999) described the molars of *E. tortus* from the Crookston Bridge Member as having eliminated the para- and metafossettids on the lower molars after the formation of the mesofossettid. Similarly, Korth (2005: fig. 2) figured specimens of *E. tortus* (misidentified as *Monosaulax valentinensis* [see Korth 2006]) from the same horizon as Evander's sample where only a minute metafossettid was present shortly after the formation of the mesofossettid. All of the specimens of *E. tortus* from the Devil's Gulch Member have the para- and metafossettids absent by the time of the formation of the mesofossettid. This appears to be a progressive change through the stratigraphic section where the molars become more *Dipoides*-like in the development of the occlusal pattern of the molars.

The nearly complete mandibles of *E. tortus*, FAM 64966, preserve the entire posterior end of the mandible, lacking only the top of the bony knob that covers the base of the incisor. It is evident from the size of the knob and the deep pocket on the ascending ramus lateral to it, that it was very large (Fig. 6B). This is a characteristic of tooth-digging rodents where rapid growth of the incisor is necessary (Korth and Rybczynski 2003) and compliments the tooth-digging adaptations of the cranium (Korth 2007a).

Discussion.—Evander (1999) described the rodent fauna from the Railway Quarries that were from the same age and geographical area as the Crookston Bridge Quarry. Evander identified three species of castoroidine beavers including a sample of *E. tortus* that had a very wide range of size of dental measurements, particularly p4–m3 (Evander 1999: table 4; also repeated in Korth 2006: table 1); these measurements are much wider than the size range of this species that had been reported previously (Voorhies 1990b: A97). One of the sets of measurements presented by Evander date had a coefficient of variation value exceeding 10, usually an indication of the presence of more than one species. It appears that the Railway Quarry sample of *E. tortus* included a specimen of *Monosaulax skinneri*, FAM 64292 (Evander 1999: fig. 8A) and one specimen of *Prodipoides burgensis* (see above discussion) that expanded the range of size of the sample.

FAM 64292, originally assigned to *E. tortus* by Evander (1999), contains a p4 that is not completely erupted so the crown-height index can be determined. The crown-height index for this specimen is 1.20, far below the range for *E. tortus* (average = 1.50), and similar to the lower-crowned *Monosaulax skinneri* (see above and Korth 1999: table 2). The morphology of the parafossettid on FAM 65292 is also that of *M. skinneri*; the parafossettid is curved with an accessory fossettid anterior to it. In *E. tortus* the parafossettid is usually straight and there are no accessory fossettids. Clearly, FAM 64292 is a specimen of *M. skinneri*.

All of the specimens referred here to *Eucastor tortus* resemble those from populations of this species described elsewhere (Stirton 1935; Voorhies 1990b). This is the first recognition of this species in the Devil's Gulch Member of the Valentine Formation. All specimens referred previously to this species were from the subjacent Cornell Dam and Crookston Bridge Members of the Valentine Formation.

Stratigraphic and geographic range.— Previously cited specimens are from localities in the Cornell Dam and Crookston Bridge Members of the Valentine Formation, Nebraska (Voorhies 1990a). All referred specimens listed above are from Devil's Gulch Member, Valentine Formation, Nebraska. FAM 64966 and FAM 65262 from Rattlesnake Gulch Quarry, Brown County; FAM 65257 from Devil's Gulch Horse Quarry, Cherry County; and all CM specimens from Verdigre Quarry, Knox County (see Voorhies 1969, for locality data).

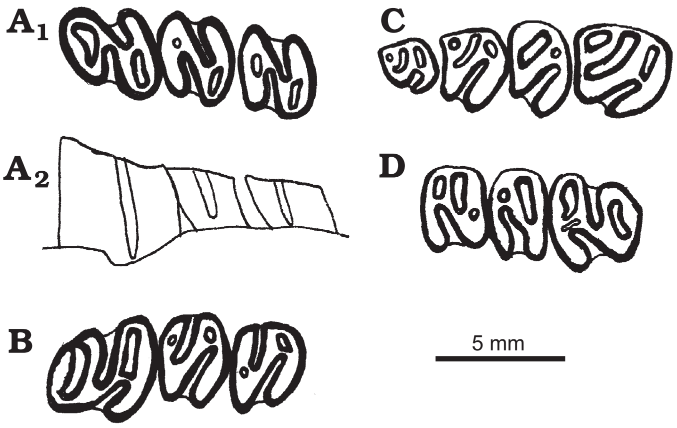

Fig. 7. The beavers. **A**, **B**. *Eucastor tortus* (Leidy, 1858) from th latest Barstovian Devil's Gulch Member of the Valentine Formation. **C**, **D**. *Temperocastor valentinensis* (Stout, 1999) from the late Barstovian Crookston Bridge Member equivalent of the Valentine Formation. Cheek teeth: **A**. FAM 65262, right p4–m2 in occlusal (A_1) and medial (A_2) views. **B**. CM 18876, left p4–m2. **C**. UNSM 46392, right P4–M3. **D**. UNSM 45385, right p4–m3. A, B, anterior to left; C, D, anterior to right.

Genus *Temperocastor* nov.

Type species: *Eucastor valentinensis* Stout, 1999, by monotypy; see below.

Derivation of the name: From Latin, *tempero*, blend or mix in due proportion; and *castor*, beaver.

Diagnosis.—Small castoroidine (smaller than *Eucastor tortus*); cheek teeth mesodont and rooted, similar in crown-height to species of *Eucastor* and *Monosaulax*. Primitive dental characters as in *Monosaulax*: lingual striids on premolars minute to absent on unworn specimens; parafossettid generally curved and accessory fossettids commonly present on p4; molars maintain primitive castoroid occlusal pattern, mesofossette (-id) forms before elimination of the parafossette (-id) and metafossette (-id). Derived characters shared with *Eucastor*: procumbent upper incisors (procumbency >100°); M3 markedly smaller than anterior molars; high, arched upper diastema; ridge on posterior wall of orbit; more anterior position of ascending ramus on mandible (m2 blocked from lateral view).

Stratigraphic and geographic range.—Early–late to late Barstovian (Miocene) of Nebraska.

Temperocastor valentinensis (Stout, 1999)

Figs. 7D–E, 8.

1935 *Monosaulax curtis* [sic] (Matthew and Cook); Stirton 1935 (in part): 420.

1990 "*Monosaulax*" *curtus* (Matthew and Cook); Voorhies 1990a: tables 1, 2.

1990 *Monosaulax”* cf. *curtus* (Matthew and Cook); Voorhies 1990b: A93–A94.

1999 *Eucastor valentinensis* sp. nov.; Stout, 1999 in Evander 1999: 250–251, fig. 10.

1999 *Monosaulax valentinensis* (Stout); Korth 1999: 262.

Holotype: UNSM 67201, right mandible with p4–m3.

Type locality: Railway Quarry A, Cherry County, Nebraska.

Type horizon: Late Barstovian (middle Miocene), Crookston Bridge Member, Valentine Formation.

Material.—UNSM 45392, partial skull with associated mandibles, and right scapula and radius; UNSM 45393, 49395, 49398, 49399, mandibles with cheek teeth. (Also see Evander [1999: 250] for list of topotypic specimens.)

Diagnosis.—Only species of the genus.

Description.—UNSM 45392 consists of nearly the entire right half of the skull and both associated mandibles (Fig. 8). The occiput and basicanial area are almost entirely missing, and the nasal is lacking on the side that is preserved. The cranium is also laterally flattened. In overall outline, the skull strongly resembles that of *Eucastor tortus* (Korth 2007a). The dorsal diastema is long and strongly arched dorsally. The ratio of the length of the upper diastema to the alveolar length of the cheek teeth is 1.70, at the lower end of the range observed for *Eucastor* and *Nothodipoides* (Korth 2007a: table 3). The upper incisors are procumbent with angles of greater than 100°, greater than in *Monosaulax* and typical of nothodipoidines (Korth 2007a: table 2). Dorsally, the premaxillary bone extends posteriorly even with the lacrimal, more posterior than the nasals. The lacrimal is very small and at the anteromedial corner of the orbit. The jugal extends anteriorly along the dorsal side of the zygomatic arch, but ends anteriorly about 2 mm short of contacting the lacrimal. The frontals are flat. The postorbital constriction is not as narrow as in *Eucastor*. The least width of the frontals relative to the width of the rostrum is 0.79, greater than in *E. tortus*, and similar to *Prodipoides* (Korth 2007a: table 3). The temporal crest is extremely low. It arises dorsal to the orbits. On the parietals, the temporal crest runs parallel to the sagittal suture to the interparietal. Due to breakage, the posterior end of the temporal crest is not preserved. However, a triangular interparietal is present with a distinct sagittal crest that fuses posteriorly with a high nuchal crest. The surface of the parietals is rugose. There appears to be a small temporal foramen along the parietal-squamosal suture just anterior to the nuchal crest. A small, circular postglenoid foramen is just posterior to the glenoid fossa within the squamosal.

The skull is sciuromorphous. The infraorbital foramen is C-shaped and opens anteriorly. It is positioned just anterior to the zygomatic plate at about mid-depth of the rostrum. The premaxillary-maxillary suture runs almost directly ventrally just anterior to the zyogmatic plate and crosses the center of the palate at the posterior end of the incisive foramen. The incisive foramen is at the center of the diastema (slightly posterior to the center in *Eucastor*) and its length is 25% that of the length of the upper diastema, typical of all castoroidines (Korth 2007a: table 3). Due to breakage, very little can be determined about the palate. The tooth rows strongly diverge posteriorly, and there are recognizable anteroposterior grooves present, but all sutures and foramina are obscured by damage to the specimen. The only part of the acoustic bulla that remains is the outline of the external meatus which is a tube that extends posterodorsally as in most castoroidines. A small foramen for the posttemporal canal is present along the mastoid squamosal suture posterior to the external acoustic meatus as in *Eucastor* and other castorids. The only other identifiable foramen on the occiput is a mastoid foramen along the mastoid-occipital suture, medial to the posttemporal canal. The mastoid contribution to the occiput is very small.

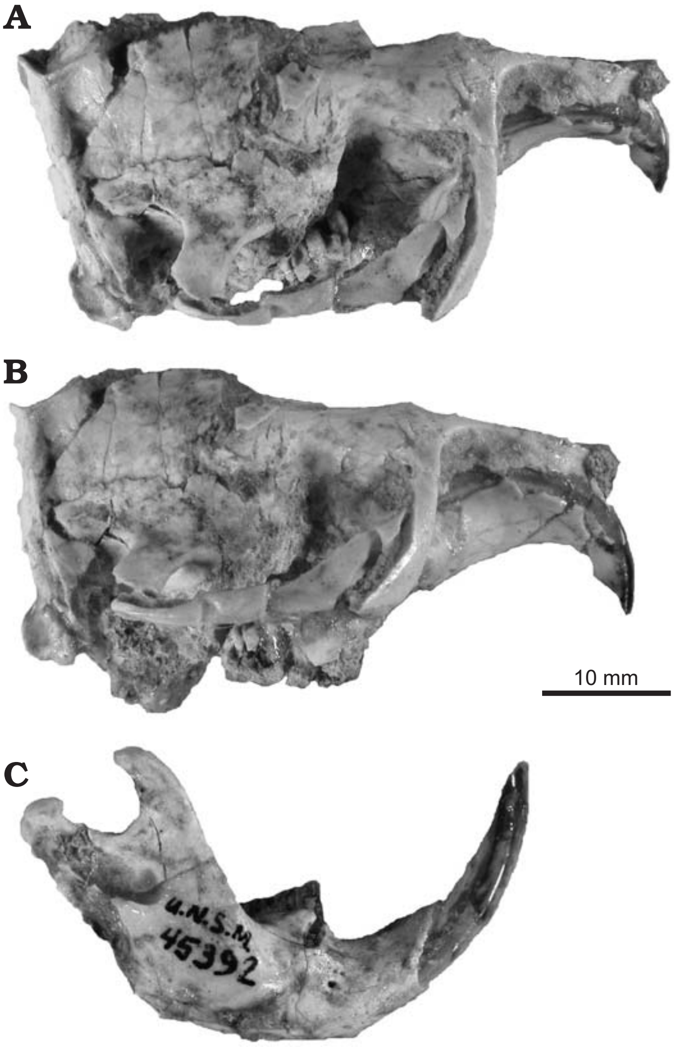

Fig. 8. The beaver *Temperocastor valentinensis* (Stout, 1999), specimen UNSM 45392 from the Crookston Bridge Member equivalent at Myers Farm Quarry. Cranium in dorsal (**A**) and right lateral (**B**) views. **C**. Mandible in lateral view. Anterior to right.

The orbital wall is badly damaged, so the only observable foramen is the nasolacrimal foramen in the anterodorsal corner of the orbit. All other foramina and sutures are unrecognizable. Along the posterodorsal wall of the orbit is the short ridge that is also present in *E. tortus* and *Nothodipoides*

(Korth 2007a, b). The zygomatic arch is complete. It is relatively light in structure compared to *Castor*, being thickest at a point where the maxillary contribution and the jugal overlap, marking the posterior margin of the orbit.

The mandible is similar in shape to that of contemporaneous castoroidines (Fig. 8C). It is deep for the size of the animal. The diastema is shallow and long, being only slightly shorter than the length of the tooth row. A single mental foramen is present below the anterior margin of the premolar near the center of the depth of the mandible. On the right side of UNSM 45392, there are two additional, minute foramina dorsal to the mental foramen. On two other specimens, UNSM 45395 and UNSM 45398, there is a single additional foramen. These accessory mental foramina are not present on any of the other specimens. The diagastric process, along the ventral border of the mandible just below the mental foramen, is very small. The masseteric scar extends anteriorly to below the center of p4 in a V-shape. The ascending ramus arises even with m1, blocking m2 and m3 completely from lateral view. This is identical to the condition in *Eucastor tortus* and more anterior than in *Monosaulax* where m2 is visible. Although the complete angle of the mandible is not present on any specimen, the coronoid process, condyle and angle of the jaw appear to form the zig-zag pattern typical of castoroidines where the condyle is medial to the other processes. The only difference is that the coronoid is not displaced as far laterally as in *Eucastor* and other castoroidines. On the lateral side of the ascending ramus is a very deep pocket just anterior to the lateral bulge of bone that is formed by the base of the incisor. This appears relatively deeper than in specimens of *Monosaulax*, suggesting a larger prominence of bone, indicating a more rapidly growing incisor, typical of tooth-digging rodents (Korth and Rybczynski 2003).

Evander (1999) provided a complete description of the lower cheek teeth but had no maxillary teeth in his collection. The upper dentition has not been previously described, although Voorhies (1990b) listed some maxillary specimens. The partial skull, USNM 45392, retains the upper incisor and all of the cheek teeth on the right side (Fig. 7D). The anterior enamel surface of the upper incisor is nearly completely flattened with only a very slight convexity along the edges. There are no grooves or ridges present on the enamel surface. The enamel extends onto only about 1/3 the medial and lateral sides of the tooth. In cross-section, the tooth is slightly wider than long.

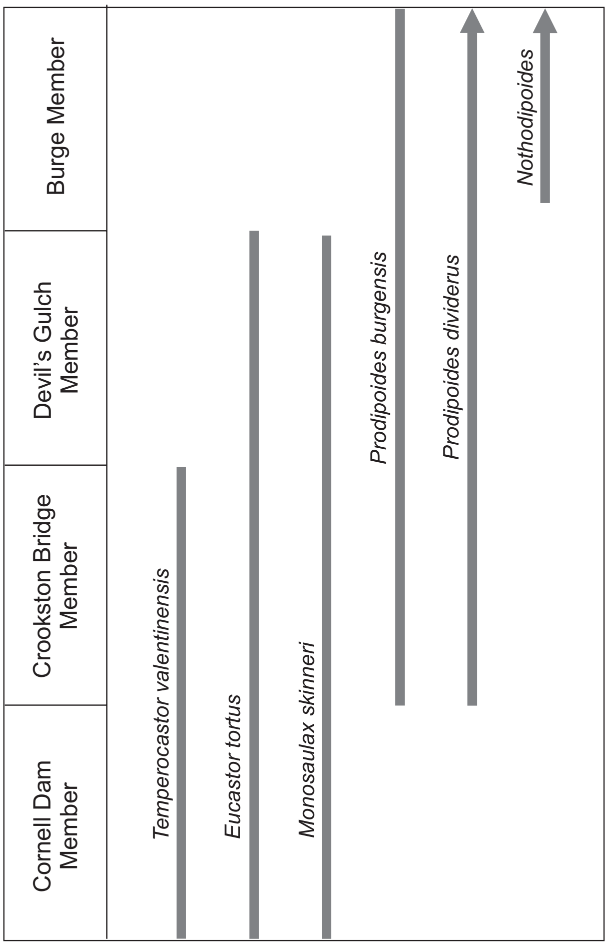

Fig. 9. Occurrence of the castoroidine species through the middle Miocene Valentine Formation of Nebraska. Width of members not intended to represent time or stratigraphic thickness of layers. Arrows indicate continued occurrence in superjacent layers.

Typically, the premolar is the largest of the cheek teeth that decrease in size posteriorly. The teeth are mesodont and rooted. The occlusal surface is at a stage of moderate wear; there are no open buccal flexi, a fossette has formed in all cases. The hypoflexus remains open lingually on all the cheek teeth. The occlusal surface of P4 consists of three fossettes and the hypoflexus. The hypostria extends to the base of the crown, thus the hypoflexus will remain open lingually until very late stages of wear. The hypoflexus is oriented anterobuccally and extends across about half the occlusal surface of the tooth. The parafossette abuts the buccal end of the hypoflexus and is oriented slightly obliquely, ending just short of the buccal border of the tooth. The mesofossette is the longest of the fossettes, extending nearly the entire width of the tooth. It curves posteriorly on its lingual half, posterior to the hypoflexus, but paralleling it. The metafossette is very short and obliquely oriented, anterobuccal-posterolingually. It is in the posterobuccal corner of the tooth.

M1 and M2 are similar in size and morphology. M1 is slightly more worn and also shorter because of its slightly later stage of wear. On both molars the hypoflexus is angled anterobuccally and crosses about three-quarters of the occlusal surface, ending near the anterobuccal corner of the tooth just short of the margin of the tooth. A minute parafossette is at the buccal end of the hypoflexus. On M1 the mesofossette is straight, short, and slanted posteriorly, blocking off the posterobuccal corner of the tooth. There is no evidence of a metafossette. On M2 the mesofossette is slightly longer and gently curved, similar to the morphology of the premolar. There is a minute, circular metafossette in the posterobuccal corner of the occlusal surface. Evander (1999) mentioned in his description of the lower molars that the parafossettid was shallower than the metafossettid and would disappear earlier in wear. It appears that the same is true for the metafossette of the upper molars; it is shallower so it disappears before the parafossette.

M3 is markedly smaller than M1 or M2 and nearly equidimesional. It is roughly triangular shaped in occlusal outline. The hypoflexus is similar to that of the premolar, angled anteriorly and extending only about half the width of the tooth with the parafossette abutting the buccal end. The parafossette is short and is slanted slightly posterobuccally, the opposite of the orientation of the parafossette on the premolar. The mesofossette is small and C-shaped. Because the tooth is much narrower posteriorly, the mesofossette nearly reaches both the lingual and buccal borders of the tooth. The metafossette is a minute, circular fossette in the posterobuccal corner of the occlusal surface as in M2.

Discussion.—*Eucastor valentinensis* was first described by Evander (1999) based on several mandibles with cheek teeth. The generic allocation was based on higher crown-height of the cheek teeth than in *Monosaulax* and the beginning of the development of the *Dipoides*-like S-pattern on the occlusal surface of the molars on some specimens (= shallower parafossettid). Shortly afterwards, Korth (1999) transferred the species to *Monosaulax* because the original diagnosis of the genus and its distinction from *Eucastor* was based on the development of the lingual striids on the lower premolar (Stirton 1935). The specimens referred to *E. valentinensis* had the morphology of *Monosaulax*, and the molars had not fully attained the occlusal S-pattern (Evander 1999: fig. 10).

It is evident from the morphology of the skull that *Temperocastor valentinensis* had the fossorial adaptations of the skull present in *Eucastor* and *Nothodipoides* (Korth 2007a, b), but maintained the primitive morphology of the dentition as in *Monosaulax*. This suggests that *Temperocastor* is a basal nothodipoidine. If this is the case, the Nothodipoidini must be defined by the cranial morphologies for tooth-digging and the development of the more advanced dentition occurred secondarily within the group.

Stratigraphic and geographic range.—Previously referred specimens from several other UNSM localities at the same horizon as the holotype and UNSM quarries from the early late Barstovian of Nebraska (see Voorhies 1990a). Specimens described above from the late Barstovian UNSM locality Wt-15A, base of the Ogallala Group, Webster County, Nebraska.

Discussion

Based on only partial or fragmentary cranial specimens, *Monosaulax* was considered primitive for castoroidine beavers (Korth 2007a: fig. 9). The more complete crania of *Monosaulax skinneri* described above, along with dental evidence, have verified this interpretation. The skull of *Temperocastor valentinesis* has derived cranial features related to tooth-digging that are shared with nothodipoidines, and is thus referred to that tribe. However, based on the primitive morphology of the cheek teeth and some of the cranial features (length of upper diastema, width of postorbital constriction) of *T. valentinensis*, it appears that *T. valentinensis* is the most primitive member of the Nothodipoidini.

The faunal change in the castoroidine beavers through the duration of the Valentine Formation in Nebraska (late Barstovian to early Clarendonian) was previously believed to be dramatic, with species of *Monosaulax* and *Eucastor* restricted to the late Barstovian and species of *Prodipoides* and *Nothodipoides* limited to the Clarendonian. However, it appears that this transition is much more complex and phased than previously thought. The species known from the lowest member (Cornell Dam) are *M. skinneri*, *E. tortus*, and *Temperocastor valentinensis*. Above this, in the Crookston Bridge Member, there is a continuation of these species but the introduction of two species of *Prodipoides*, *P. burgensis*, and *P. dividerus*, both previously only reported from the higher Burge Member or above. Both of these species are rare at this lower horizon, each being known only from one or two specimens. In the Devil's Gulch Member, on top of the Crookston Bridge Member, *T. valentinensis* disappears but the other four species, *M. skinneri*, *E. tortus*, *P. burgensis*, and *P. dividerus* are present. The latter two are more abundant than in the previous horizon, and the former two are less common. Finally, in the uppermost member of the Valentine Formation, the Burge Member, the earlier occurring species, *M. skinneri* and *E. tortus* disappear, and the species of *Prodipoides* continue. At this same horizon *Nothodipoides* first appears.

In Nebraska, instead of a sudden change at the Barstovian–Clarendonian boundary, coincident with the unconformity between the Devil's Gulch and Burge members in the Valentine Formation, there appears to be a gradual replacement of the earlier, morphologically more primitive species (*M. skinneri*, *E. tortus*, *T. valentinensis*) with the later, more advanced species of *Prodipoides* and *Nothodipoides* (Fig. 9).

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