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THE SKULL OF THE BEAVER “*MONOSAULAX*” *VALENTINENSIS* (CASTORIDAE, RODENTIA) FROM THE BARSTOVIAN (MIOCENE) OF NEBRASKA

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ABSTRACT

The skull of *Monosaulax valentinensis* is described. Whereas, the occlusal morphology of the cheek teeth of this species is clearly referable to *Monosaulax* Stirton, the size of the third upper molar relative to the anterior molars is more similar to *Eucastor* Leidy. The skull has features of both genera (strong postorbital constriction of *Eucastor*; shorter rostrum and parallel parasagittal crests of *Monosaulax*). The skull also has several features that suggest that it is fossorially adapted that are not present in either *Eucastor* or *Monosaulax* (tapered, shortened rostrum; procumbent incisors). It is suggested that *“M.” valentinensis* may represent an as yet unnamed genus of fossorial castoroidine, possibly related to the later *Microdipoides*. If this proves to be the case, it demonstrates that fossorial tooth-digging evolved at least three times within the North American castorids; twice in the Arikareean (Palaeocastorinae and *Migmacastor* Korth and Rybczynski) and again in the middle to late Miocene within the Castoroidinae.

INTRODUCTION

Stirton (1935) recognized three species of beavers from the Niobrara Sands of northcentral Nebraska and referred them to *Monosaulax pansus* Stirton (1935)*, M. curtus* (Matthew and Cook, 1909)*, and “Monosaulax* or *Eucastor*.” Voorhies (1990), based on many more specimens, also recognized three different sized castoroid beavers from the middle Barstovian (middle Miocene) Norden Bridge Quarry in the Cornell Dam Member of the Valentine Formation, Brown County, Nebraska, from the same approximate area of Stirton's collections. (For precise locality and stratigraphic information on all cited fossil localities, see Skinner and Johnson [1984] and Voorhies [1990].) Voorhies (1990) referred the three species to ”*Monosaulax*” cf. *curtus* (smallest species), *“Monosaulax”* sp. (lagest species), and *Eucastor tortus* (intermediate sized species), the latter including the specimens previously identified as *Monosaulax* or *Eucastor* by Stirton (1935). Evander (1999) discussed a collection of fossils from Railway Quarry, from the slightly younger Crookston Bridge Member of the Valentine Formation in Cherry County, Nebraska. He followed Voorhies (1990) in assigning the intermediate sized species to *Eucastor tortus* but referred the other two to new species; one was assigned to *Monosaulax* Stirton (1935), *M. skinneri* (=“*Monosaulax”* sp. of Voorhies), and the other to *Eucastor* Leidy (1858), *E. valentinensis* (=”*M.* cf. *curtus* of Voorhies). Both species were based on numerous lower jaws. Later, Korth (1999) referred *E. valentinensis* to *Monosaulax* based on dental characters and provided measurements and indices of crown height based on a large collection of beavers from West Valentine Quarry (data provided by Voorhies) from the same horizon as the material described by Evander (1999).

A previously undescribed partial skull in the Frick Collections of the American Museum of Natural History (FAM) from the same area and horizon as the samples described by Voorhies (1990) is assignable to *Monosaulax valentinensis*. Characters of the skull used to separate *Eucastor* from *Monosaulax* (Korth, 2002a) can be applied to this skull in an effort to determine its generic allocation. Two mandibles referable to *M. valentinensis* from a slightly higher stratigraphic level (equivalent to that of Evander’s sample) from the collections of the University of Nebraska State Museum (UNSM) are also described.

METHODS AND MATERIALS

Specimens—Partial skull, FAM 65293, includes the complete anterior half of the skull originating posteriorly at the anterior edge of the parietals dorsally and at the posterior margin of the palate ventrally. The only teeth lacking are M2-M3 on the right side. The skull is three-dimensional with no indication of crushing or distortion.

UNSM 50990 and UNSM 50991 are two nearly complete mandibles. Both contain the incisor and p4-m2 with the alveolus for m3. The cheek teeth in UNSM 50990 are only slightly worn, those of UNSM 50991 are heavily worn.

Locality and Horizon—The skull specimen is from Egelhoff Quarry (USNM locality Kp 101) in the Cornell Dam Member, Valentine Formation, Keya Paha County, Nebraska. The two mandibular specimens are from Stewart Quarry (UNSM locality Cr-150), Crookston Bridge Member, Valentine Formation, Cherry County, Nebraska.

Age—Late Barstovian (middle Miocene).

Terminology—Dental terminology used follows that of Stirton (1935). Capital letters indicate upper teeth; lower case letters indicate lower teeth. Identification of cranial foramina follows that of Wahlert (1974, 1977). Indices for procumbency of incisors (Table 3) as defined by Korth and Rybczynski (2003:table 4, fig. 7).

DESCRIPTION

Skull—In dorsal view, the rostrum is straight sided with no indication of tapering. The nasals are only slightly narrower anteriorly and posteriorly, the widest point is just posterior to the anterior ends. A small nutritive foramen is present on both nasals just posterior to the middle of its length. The nasals end posteriorly just beyond the anterior margin of the zygoma, anterior to the premaxillary-frontal sutures.

The suture for the jugal is preserved on the right side, and it is evident that it ended anteriorly well short of contact with the lacrimal. The postorbital constriction is more severe than in other *Monosaulax*, but not as much as in *Eucastor tortus* (see Table 1 and 2). The skull is broken so only the anteriormost piece of the parietals are present. The parasagittal crests are low, arising along the dorsal border of the orbits and converging posteriorly. The two crests are closest at the postorbital constriction (1.4 mm apart) The crests do not fuse on any part preserved on the skull; they run parallel to one another for the length of the frontals.

In lateral view the rostrum tapers anteriorly. The upper diastema is arched dorsally. The infraorbital foramen is a laterally compressed slit, just anterior to the zygomatic plate, about mid-depth of the rostrum. The incisors project slightly anterior to the end of the nasals. The incisive foramina are 6.4 mm in length and situated approximately halfway between the incisors and P4. The premaxillary-maxillary suture descends the side of the rostrum vertically. On the palatal surface, it nearly reaches the center of the incisive foramina, but turns sharply posteriorly and crosses the foramen at its posterior end.

Two parallel, deep grooves extend posteriorly from the incisive foramena onto the palate where they broaden between the rows of cheek teeth. The tooth rows diverge posteriorly. The palatine extends anteriorly on the palatal surface to the level of M1. The posterior palatine foramina are along the suture even with the border of M1 and M2. The posterior maxillary foramen is a small slit along the maxillary-palatine suture, posteromedial to M3.

Most of the medial orbital wall is preserved on both sides of the specimen. The lacrimal foramen is large and oval, situated at the anterodorsal corner of the medial orbital wall. Posterior to the lacrimal foramen, within the frontal bone, is a small ethmoid foramen, dorsal to M1. Ventral to the ethmoid are three foramina that form an anteroposterior line. The anterior most (above P4) is the sphenopalatine. It penetrates the bone just ventral to the frontal-maxillary suture. The other two foramina are within the orbitosphenoid bone. The most posterior foramen (above M2) opens anterolaterally, and is the optic foramen. The central foramen is identified as an interorbital foramen. On the left side of the skull, another foramen is visible posterior and ventral to the optic foramen. This is either the dorsal palatine foramen or a second interorbital foramen.

TABLE 1. Cranial and mandibular measurements of *"Monosaulax" valentinensis,* FAM 65293, UNSM 50990 and 50991. Measurements in mm.

Length of upper diastema	22.94
Length of incisive foramen	4.92
Maximum width of rostrum	12.76
Width of postorbital constriction	8.19
Depth of skull (measured at M2)	21.06
Anterior depth of rostrum	12.59
Posterior depth of rostrum	20.01
Alveolar length P4-M3	12.91
Alveolar length p4-m3	14.81-15.34
Length of lower diastema	10.38-10.55
Depth of mandible (below m1)	11.75-12.81

TABLE 2. Cranial indices for species of *Eucastor tortus* and *Monosaulax*. *Monosaulax* spp. includes *M. tedi, M. curtus, M. pansus* and *Monosaulax* sp. Based on measurements presented in Korth (1999, 2002). Abbreviation: poc = width of postorbital constriction.

	E. tortus	*Monosaulax* spp.	*M. valentinensis*
diastema/tooth row	2.19-2.25	1.42-1.54	1.78
poc/rostral width	0.36-0.55	1.09	0.64

Upper Dentition—The upper incisors are broad and only gently convex anteriorly. The enamel is thick, and there is no ornamentation on the anterior surface. The incisors appear procumbent because they extend anteriorly beyond the anterior margin of the nasals. The indices for procumbency for the specimen are greater than any other previously figured castoroidine (Table 3), and as high as the at least one of the fossorial palaeocastorines, *Palaeocastor fossor* (Korth and Rybczynski, 2003:table 4).

P4 is the largest of the cheek teeth. At the current stage of wear, which appears moderate, only the parastria is present on the buccal side of the tooth but is minute. On the lingual side of the tooth the hypostria is continuous to the base of the crown. On the occlusal surface the paraflexus and hypoflexus remain open, all other flexi have been closed off into fossettes (meso- and metafossette). The paraflexus and hypoflexus extend approximately half the width of the tooth. The mesofossette is curved posteriorly and extends nearly the entire width of the tooth. The metafossette is small and oriented obliquely.

M1 and M2 are similar in size and morphology. Only the hypoflexus remains open. It extends nearly three-quarters the width of the tooth buccally, and is oriented anterobuccally across the tooth. The mesofossette is roughly parallel to the hypoflexus but slightly curved. It extends from near the buccal margin of the tooth to a point beyond the middle of the tooth. Both the parafossette and metafossette are present, but are very small. Both are transversely elongated, the parafossette being slightly larger than the metafossette on all the teeth.

M3 is by far the smallest cheek tooth. It is similar in occlusal morphology to the anterior molars, but its posterior half is greatly reduced. The hypoflexus is much shorter than on the anterior molars, but the parafossette is proportionally longer. The mesofossette is shorter but more strongly curved. The metafossette is reduced to a minute circle of enamel along the posterior border of occlusal surface of the tooth.

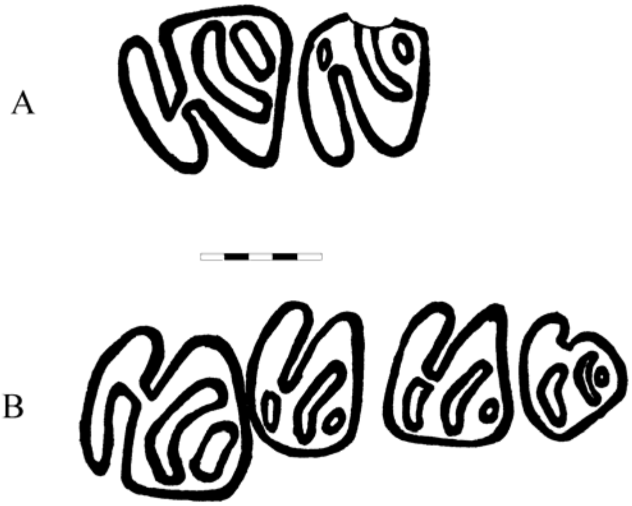

FIGURE 2. Upper dentition of *"Monosaulax" valentinensis,* FAM 65293. A, left P4-M1. B, right P4-M3 (anterior to left). Bar scale = 5 mm.

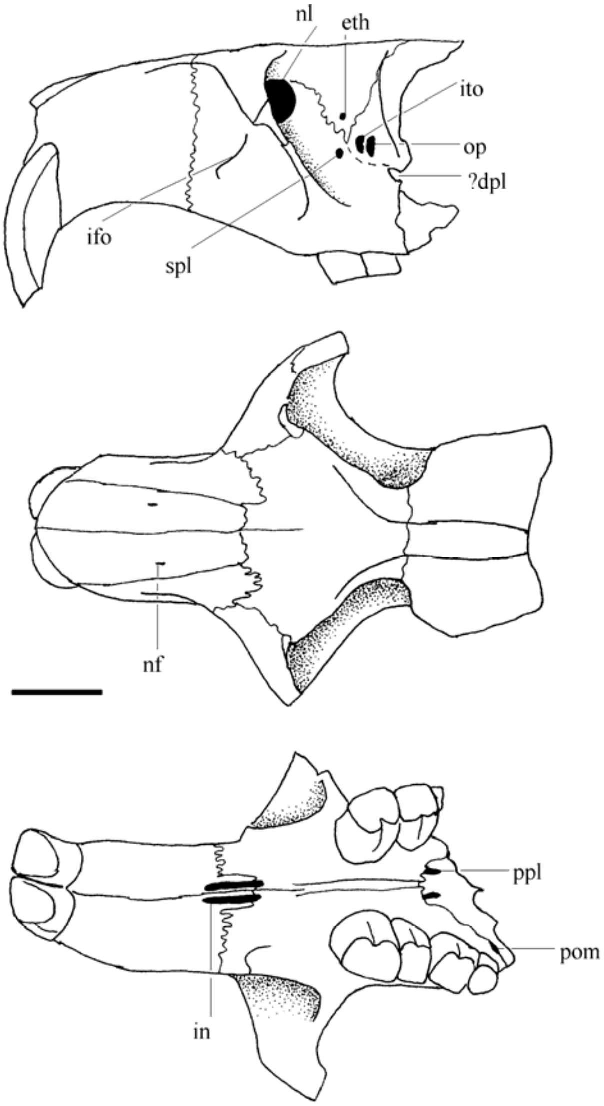

FIGURE 1. Skull of *"Monosaulax" valentinensis,* FAM 65293. Left lateral view (top). B. Dorsal view (center). C. Ventral view (bottom). Abbreviations for foramina: dpl, dorsal palatine; ifo, infraorbital; in, incisive; ito, interorbital; nf, nutritive; nl, nasolacrimal; op, optic; pom, posterior maxillary; ppl, posterior palatine; spl, sphenopalatine. Bar scale = 1 cm.

TABLE 3. Procumbency indices for selected castoroidine beavers. Measurements species other than *M. valentinensis* taken from figures elsewhere: *M. tedi* from Korth (1999), *M. pansus* from Korth (2002a), *D. tanneri* from Korth and Rybczynski (2003:table 4), and *Dipoides* spp. from Rybczynski (2003).

	Index A	Index B	Age
M. valentinensis	95°	105°	late Barstovian
M. tedi	80°	85°	early Barstovian
M. pansus	80°	85°	late Barstovian
Dipoides tanneri	90°	95°	late Clarendonian
Dipoides spp. (composite)	90°	95°	Hempillian-Blancan

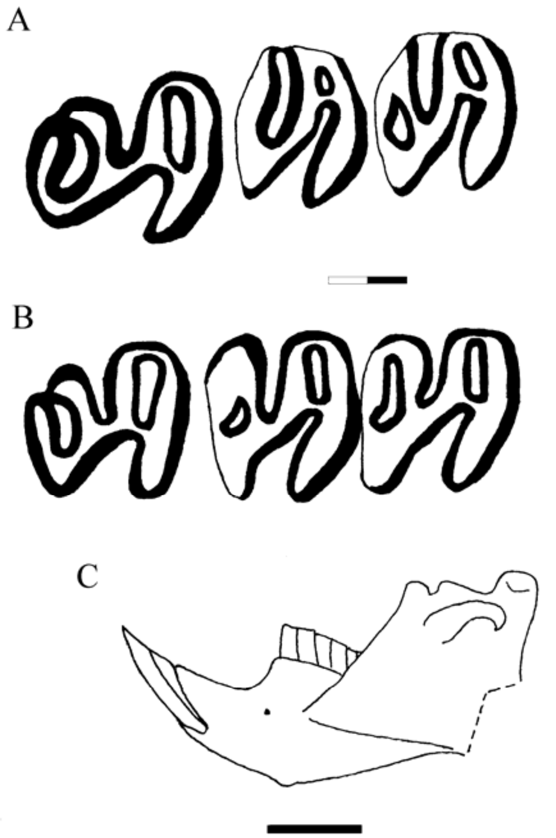

FIGURE 3. Mandible and lower dentition of "*Monosaulax*" *valentinensis*. A, left p4-m2, UNSM 50991. B, left p4-m2, UNSM 50990. C, lateral view of mandible, UNSM 50991. Bar scale for teeth = 2 mm. Bar scale for mandible = 1 cm.

Mandible—The mandible is deep and robust, as in nearly all catorids (Figure 3C). The disatema is short (approx-imately 30% shorter than length of tooth row). The dorsal surface of the diastema drops nearly vertically anterior to p4 and slopes gently upward towards the incisor.

The digastric eminence along the ventral margin of the mandible is very small, but present. The mental foramen is single and small, situated just anterior to the tooth row near the centerline of the mandible. The masseteric scar extends anteriorly to below the posterior root of the premolar. The scar is marked by a low, rounded ridge that runs dorsally along the anterior edge of the ascending ramus. The ventral margin of the scar is similarly marked and runs posteroventrally toward the angle of the jaw.

The anterior edge of the ascending ramus is steeply sloped (nearly vertical) and blocks nearly all of m2 from lateral view. The condyle is well above the occlusal level of the cheek teeth. The coronoid process is mostly preserved on UNSM 50991, and is short and rounded, not extending more dorsally than the condyle. The angle on both mandibles is broken away, but it is evident that the medial bend of the angle, typical of castoroidines, was present.

The base of the incisor is marked by a small, round knob, just anterior and ventral to the condyle. Medial to the base of the incisor is a deep excavated area.

Lower Dentition—The incisor has a smooth enamel surface and is gently convex anteriorly. The mesoflexid on the premolar remains open, even on the heavily worn specimen (UNSM 50091) indicating a deeper mesostriid than typical of *Monosaulax* (see Korth, 1999:table 2). Both the metafossettid and parafossettid have formed on both specimens. It is evendent by the width of the connection of the wear facet on the anterolingual corner of the tooth that the parafossettid has just closed, even on the worn specimen.

The first two molars are nearly identical in size. On the little worn specimen (UNSM 50990) the mesoflexid remains open. and the para- and metafossettids are formed (Figure 3B). On m1 the parafossettid is s small circle, but more elongated (transversely) on m2.

On the more worn specimen (Figure 3A), the mesofossettid has formed on both molars. The parafossettid is lacking on m1 and the metafossettid is a minute circle. The second molar has both of these fossettids, but they are small ovals. The mesofossettid (or flexid) and hypoflexid are much longer than the other two fossettids on both specimens.

DISCUSSION

The specimens described above are referred to *Monosaulax valentinensis* based on similar size, especially of lower dentitions (="*Monosaulax*" cf. *curtus* Voorhies, 1990:A93; *Eucastor valentinensis* Evander, 1999:table 4) and occlusal morphology of the cheek teeth (meosfossettes [-ids] form before para- and metafossettes [-ids] are eliminated). Voorhies (1990) has also reported this species (="*Monosaulax*" cf. *curtus*) from the same quarry that FAM 65293 was recovered (Eglehoff Quarry).

The arching of the upper diastema (tapering rostrum), procumbent incisor, and shortening of the rostrum in FAM 65293 is also present in the Arikareean beaver *Migmacastor* (Korth and Rybczynski, 2003). In *Migmacastor* the procumbent incisor was interpreted as an indicator of tooth-digging. *M. valentinensis* differs from *Migmacastor* in having derived castoroidine characters: 1) posterior palatine foramina within the maxillary-palatine suture on the palate; 2) jugal not in contact with the lacrimal bone; 3) cheek teeth higher-crowned with thin, elongated fossettes (-ids) approaching the condition in *Eucastor*; and 4) referred mandibles have the alternating condyle and processes (zig-zag pattern). However, the fossorial adaptations of *Migmacastor* are also present in *M. valentinensis* suggesting that the latter was also adapted for digging and that these features were attained through convergence.

The degree of procumbency in *M. valentinensis* is less than angnotocastorines, anchitheriomyines, *Migmacastor* and some palaeocastorines, but greater than *Castor* and any other castoroidines (Korth and Rybczynski, 2003:table 3; Table 3 this paper).

CONCLUSIONS

Stirton (1935) distinguished contemporaneous species of *Monosaulax* from *Eucastor* based on the morphology of the striids of the lower premolar. He noted that *Eucastor* had deeper lingual striids (thus more persistent flexids) that approached what he called "rabbit-like" morphology. In *Monosaulax* the lingual striids of p4 were very short, and the flexids became fossettids after only minimal wear. Stirton (1935) also noted that, more derived species of *Eucastor* developed the "S-pattern" on the occlusal surface of the cheek teeth as in *Dipoides* where the mesoflexus (-id) and hypoflexus (-id) remain open when the parafossette (-id) and metafossette (-id) are eliminated. The character is not present in any species of *Monosaulax*, but variably present in middle Barstovian *Eucastor tortus* (Voorhies, 1990).

Eucastor and *Monosaulax* species within the Barstovian are most difficult to distinguish because the earliest species of *Eucastor* has not yet fully developed the S-pattern of the cheek teeth. Some authors have suggested that *Eucastor* and *Monosaulax* were synonyms because their respective type species, *E. tortus* and *M. pansus*, were synonyms, which they are not (see Korth [2002a] for historical review). Examination of large samples of Barstovian beavers led to further distinctions in the dentitions of these two genera (Voorhies, 1990; Korth, 1999). In *Monosaulax*, not only are the lingual striids on the lower premolar shorter, but also the parafossettid is curved, whereas in *Eucastor* it is generally straight. It also appears that in *Monosaulax* there is more likely accessory fossettids on the lower premolar (usually anterior to the parafossettid) than in *Eucastor*). A final difference between *E. tortus* and *M. pansus* is the relative size of M3. In *Monosaulax* it is nearly equal in size to the anterior molars, but in *Eucastor* it is greatly reduced in size (Voorhies, 1990).

Korth (2002a) compared cranial material of the two type species along with an additional species of *Monosaulax* from the Barstovian of New Mexico and found several differences in the skulls of the two genera. The skull of *Eucastor* has a longer, narrower rostrum with a more pronounced postorbital constriction that do the species of *Monosaulax*. The sagittal crest in *Eucastor* originates at the postorbital constriction and is continuous to the posterior end of the skull. In *Monosaulax*, two parasagittal crests run parallel to one another and either never fuse, or fuse on the posterior part of the parietals.

The skull and dentition of *Monosaulax valentinensis* are a mosaic of the *Eucastor* and *Monosaulax* distinguishing characters. The dentition has the primitive occlusal morphology of *Monosaulax* (no S-pattern; curved parafossettid and accessory fossettids on p4), but the M3 is reduced in size, typical of *E. tortus*. The morphology of the sagittal crest and relative length of the rostrum are similar to *Monosaulax* (Table 2). However, the narrow postorbital constriction on the skull of *M. valentinensis* more closely approaches the condition in *E. tortus*.

Two autapomorphic characters distinguish the skull of *"M." valentinensis* from the skulls of both *Eucastor* and *Monosaulax*: 1) strongly arched ventral surface of the diastema; and 2) procumbent incisors (extend anterior to nasals). These latter features are also found in the fossorial (tooth-digging) beavers such as palaeocastorines (Stirton, 1935; Martin, 1987; Xu, 1996) and *Migmacastor* (Korth and Rybczynski, 2003). The only castoroidine beaver that has been suggested as being fossorially adapted are the Clarendonian *Microdipoides* (Korth and Stout, 2002). Unfortunately, *Microdipoides* and the supposedly closely related *Nothodipoides* (Korth, 2002b) are not known from complete cranial material, so comparisons cannot be made with the skull of *M. valentinensis*.

If the cranial adaptations of *M. valentinensis* reflect adaptations for tooth-digging, then this type of adaptation was attained several times within the beavers; during the Arikareean, the diverse Palaeocastorinae and the problematical *Migmacastor*, and again in the Barstovian with *M. valentinensis* and possibly again with the late Clarendonian with *Microdipoides*. The differences between the skull of *M. valentinensis* and topotypic skulls of the type species of *Monosaulax* suggest that the former may belong in a different genus that has adapted for burrowing. However, at the present time, it is more convenient to retain *valentinensis* in *Monosaulax* with quotations, as *"Monosaulax" valentinensis* until associated lower jaws can be compared and cranial material of other possible fossorial castoroidines *Microdipoides* and/or *Nothodipoides* are recovered.

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