

OCCASIONAL PAPERS OF THE MUSEUM OF
ZOOLOGY
UNIVERSITY OF MICHIGAN
ANN ARBOR, MICHIGAN

DIPODROID RODENTS FROM THE VALENTINE
FORMATION OF NEBRASKA

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IN 1962 and 1963 Dr. Joseph A. Tihen and field parties from the University of Notre Dame collected fossil vertebrates at a locality in Brown County, Nebraska. The site lies east of the Norden-Johnstown road about 300 yards south of the bridge by which the road crosses the Niobrara River. Tihen and Chantell (1963) named the site the "Norden Bridge Quarry" and called the faunal assemblage the Norden Bridge local fauna. The site is in the lower part of the Valentine formation and can be regarded as late Miocene, early Pliocene, or transitional between the two epochs. Estes and Tihen (1964) summarized the fish, amphibian, and reptile faunas. Mammalian fossils were also recovered from the quarry. The thirty-five fragments pertaining to dipodoid rodents are described in this report. The remainder of the rodent fauna will be treated in a later paper.

The Norden Bridge rodents were deposited in the Museum of Paleontology, University of Michigan (hereafter designated UMMP). Specimens from another Valentine quarry, the University of California locality V-3218 in Cherry County, Nebraska, were also studied. These are housed in the Museum of Paleontology, University of California at Berkeley (designated UC).

Procedures for measuring and illustrating the specimens are those of Klingener (1963). Nomenclature of dental pattern elements follows Wood and Wilson (1936).

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FAMILY DIPODIDAE (*sensu* VINOGRADOV, 1937)

SUBFAMILY SICISTINAE

? *Plesiosminthus* sp.

MATERIAL.—UMMP No. 52872, a right mandible with incisor and M_1 – M_3 ; UMMP No. 52873, 2 isolated M_1 's; all from the Norden Bridge Quarry, SE $\frac{1}{4}$ SW $\frac{1}{4}$ of Sec. 33, T. 33 N, R. 23 W, Brown County, Nebraska; also UC No. 36106, a left mandible with M_1 – M_3 ; UC No. 36107, a right mandible with M_1 – M_2 ; and UC No. 36137, a left mandible with M_1 – M_3 ; all from University of California locality V-3218, between NW and SW quarters, Sec. 24, T. 34 N, R. 26 W, Cherry County, Nebraska.

DESCRIPTION.—The mandible is slender, and the molars agree in pattern and degree of hypsodonty with those of described species of *Plesiosminthus*, *sensu* Wilson, 1960. The masseteric crest extends forward to the level of the anterior edge of M_1 . The anteroconid of M_1 varies considerably. In the Norden Bridge sample the anteroconid may be represented by a labial cusp and a ridge running anteromedial from the protoconid (Fig. 2B), a single cusp, or a pair of cusps. In the series from UC locality V-3218 the anteroconid may be a single cusp, a pair of cusps, or a small labial cuspule with a low cingular crest. The mesolophid is present but low in both series, and the mesoconid is recognizable. The metaconid is connected with the central ridge of the tooth by a single crest. A distinct hypoconulid is present.

The anteroconid of M_2 has labial and lingual cingular arms and is connected centrally to the anterior ridge of the metalophid. The mesolophid in this tooth is a low crest, and the mesoconid is not distinguishable.

The single M_3 from the Norden Bridge Quarry (Fig. 2B) lacks one lingual crest, probably the mesolophid, and differs in this respect from other described M_3 's of *Plesiosminthus*. The crest is present in the material from UC V-3218, however, and its absence in the Norden Bridge specimen can probably be attributed to individual variation.

Dimensions of 3 M_1 's in the Norden Bridge sample are: 1.4×1.1 , 1.5×1.2 , and 1.4×1.1 mm. Dimensions of one M_2 are 1.4×1.1 , and of one M_3 1.0×1.0 . The single tooththrow is 3.9 mm. long.

The Valentine specimens were compared with the type of *Macrognothomys nanus*, described by Hall (1930) from the Lower Pliocene Fish Lake Valley beds of Nevada. *Macrognothomys* differs in that the mandible is proportionately much more slender, the masseteric crest

reaches only the level of the protoconid of M_2 , and, as Wilson (1960) notes, the dental pattern approaches that of *Sicista*, particularly in the tendency toward formation of strong central ridges in the molars. The type of *Macrognothomys nanus* (UC No. 29634) differs from Hall's illustration (Hall, 1930, fig. 13) in that the low mesolophid on M_1 reaches the lingual margin of the tooth, and there is a low mesolophid on M_2 , not shown in the drawing.

Wood (1935), Galbreath (1953), Black (1958), and Wilson (1960) described species of *Plesiosminthus* from early Miocene North American deposits. The Valentinian form seems to be referable to the same genus, but in view of the extensive variability of fossil populations of *Plesiosminthus*, definite assignment to genus and species should await discovery of more Tertiary sicistine material. It is unlikely, however, that the Valentinian form is congeneric with *Macrognothomys nanus*.

SUBFAMILY ZAPODINAE

Megasminthus tiheni, genus and species new

TYPE.—UMMP No. 52874, a fragmentary palate with partial left and right toothrows.

REFERRED MATERIAL.—(all UMMP) Nos. 52875 and 52876, broken left mandibles with M_1 – M_3 ; No. 52883, 4 isolated M_1 's; No. 52877, 7 isolated M_2 's; No. 52878, 5 isolated M_3 's; No. 52879, 5 isolated M^1 's; No. 52880, a fragmentary right maxilla with P^4 – M^2 ; No. 52881, a fragmentary right maxilla with M^1 – M^3 ; and No. 52882, 5 isolated M^2 's and 1 isolated M^3 .

TYPE HORIZON.—Valentine formation, Norden Bridge Quarry.

TYPE LOCALITY.—SE $\frac{1}{4}$ SW $\frac{1}{4}$ of Sec. 33, T. 33 N, R. 23 W, Brown County, Nebraska.

DIAGNOSIS.—A large jumping mouse, intermediate in most palatal and dental characters between sicistine and advanced zapodine rodents.

DESCRIPTION.—Available palatal material (Fig. 1) shows that the skull is heavily constructed. The large anterior palatine (incisive) foramina terminate posteriorly at the level of the anterior edge of P^4 , as in the North American Miocene *Plesiosminthus* (*Schaubeumys*) *sabrae* (Black, 1958, fig. 1A) and in the Asian Oligocene *Plesiosminthus* (*Parasminthus*) *tangingoli* (Bohlin, 1946, fig. 2:8). In Recent *Eozapus* these foramina reach slightly farther back, and in Recent *Zapus*, *Napaeozapus*, and

Sicista they extend back to or beyond the level of the anterior border of M^1 .

The posterior palatine arterial foramina are at the maxillopalatine suture opposite M^2 , and they are closer together than in *Zapus*. Anterior to them the maxilla is deeply grooved by the posterior palatine arteries. In the palatine bones behind the posterior palatine arterial foramina is a pair of foramina set in pits. In many Recent rodents, comparable foramina transmit the posterior palatine veins. Presumably these foramina did so in *Megasminthus* also. These posterior, presumably venous, foramina are found in Recent *Sicista* (Vinogradov, 1937) and in *Plesiosminthus tangingoli* (Bohlin, 1946). They are not found in fossil or Recent *Eozapus*, *Zapus*, or *Napaeozapus*.

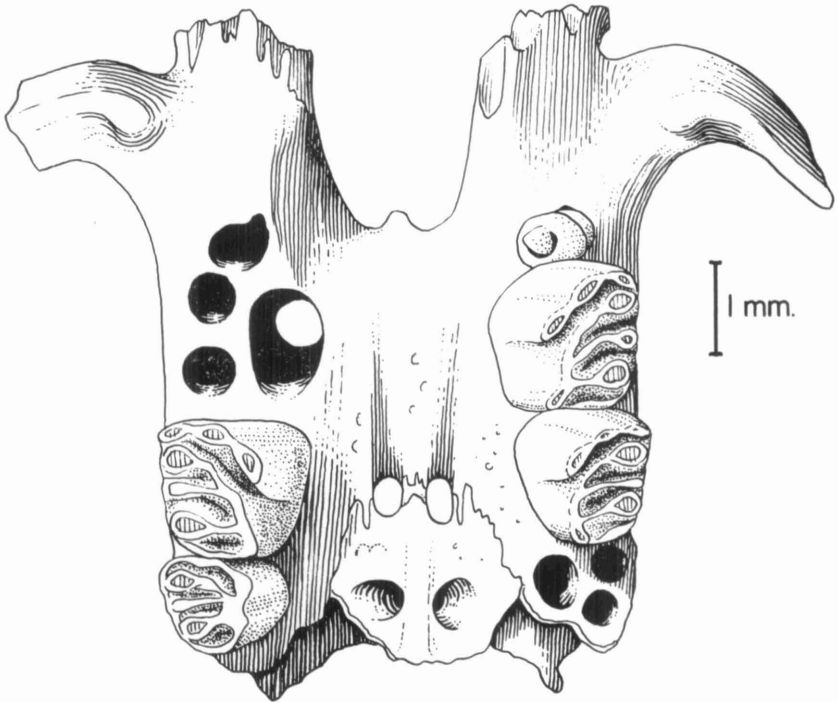


FIG. 1. Palate of *Megasminthus tiheni* (type specimen), UMMP No. 52874.

The ventral surface of the inferior zygomatic root in *Megasminthus*, as in other dipodoids, bears a distinct tubercle for the origin of *M. masseter superficialis*. Laterad from this tubercle curves the line of origin of *M. masseter lateralis profundus*. Dorsally, the inferior zygomatic root is deeply grooved by the channel for the passage of the

infraorbital branch of the maxillary nerve and the infraorbital blood vessels. The lateral lamella which separates the nervous and circulatory channel from the muscular foramen is very low in *Megasminthus*, as in some specimens of *Sicista* (Bohlin, 1946). The channel is usually open dorsally in sicistines, but it is closed in other dipodoids by fusion of the dorsal rim of the lamella with the lateral wall of the rostrum.

In both upper and lower molars the degree of hypsodonty in *Megasminthus* is intermediate between the brachydont condition seen in *Plesiosminthus* and the subhypsodont condition seen in *Eozapus*, *Zapus*, and *Napaeozapus*. The cusps in *Megasminthus* are bulbous, rather than pointed, so that occlusal surface increases rapidly with wear, and the valleys intervening between cusps become narrow. The molars of *Megasminthus* are somewhat larger than those of the largest living sicistine and zapodine rodents.

The upper toothrow tapers strongly, being broader anteriorly. P⁴ is strongly inclined posteromedial against M¹ and bears a single central cusp. M¹, in contrast to the other molars, has a rounded anteromedial corner. In M¹ the protocone, anterocone, and anterior cingulum are united to form a ridge separated from the hypocone, mesocone, and paracone by a deep valley. This valley is the lateral continuation of the internal re-entrant fold. In figured specimens of *Plesiosminthus* this valley is interrupted by a connection between protocone and mesocone. *Zapus* and *Napaeozapus* resemble *Megasminthus* in this character, since in young individuals the valley is usually open. The posterior cingulum in M¹ of *Megasminthus* is almost independent of the hypocone.

M² differs from M¹ in size and shape, but the pattern differs only in that the mesoloph tends to be better developed, and the posterior cingulum tends to be more closely connected with the hypocone. In the M² of *Eozapus*, *Zapus*, and *Napaeozapus*, the internal re-entrant is cut off by a connection between hypocone and protocone even in little-worn teeth. *Megasminthus* differs from other zapodines and resembles *Plesiosminthus* in that this re-entrant remains open into late wear stages.

The mandible of *Megasminthus* is massive by comparison with other zapodines and sicistines. The masseteric crest terminates anteriorly at the level of M₁.

The lower dentition (Fig. 2A) is morphologically intermediate between *Plesiosminthus* and *Zapus*. M₁ is slightly broader posteriorly than anteriorly. The anteroconid is a single small cusp in the midline

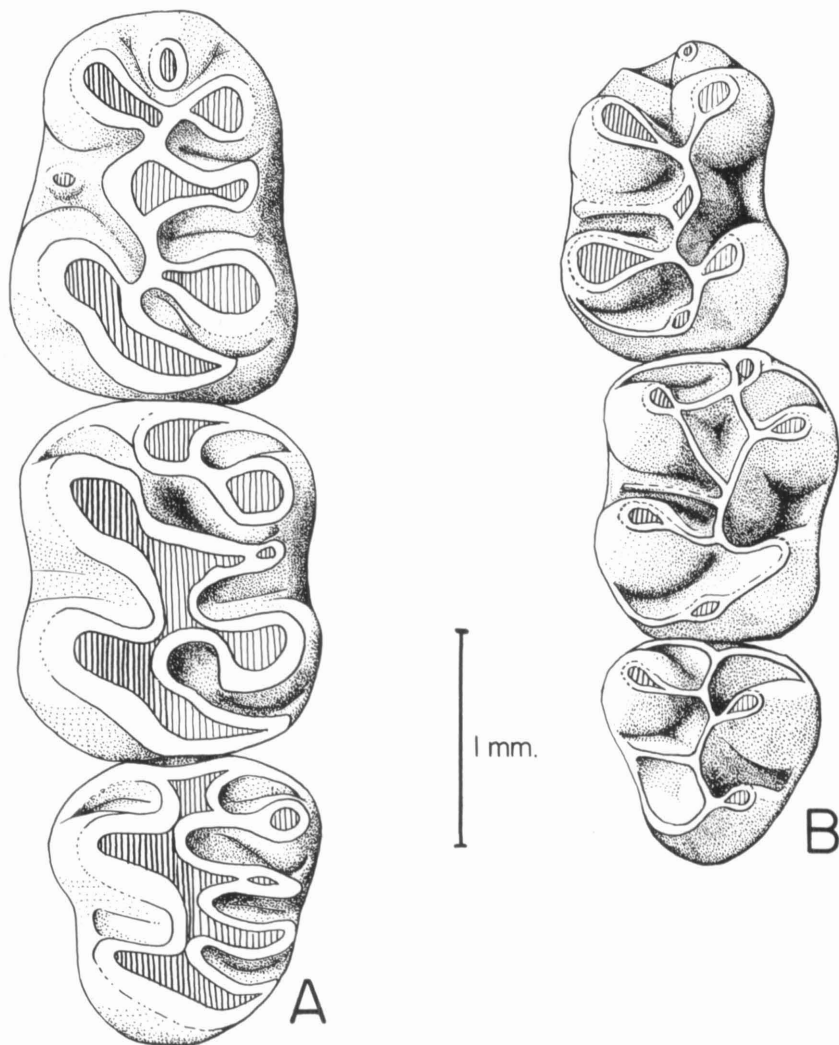


FIG. 2. A: Left lower toothrow of *Megasminthus tiheni*, UMMP No. 52876. B: Right lower toothrow of *Plesiosminthus* sp., UMMP No. 52872.

of the tooth and is constant in 5 available M_1 's. In *Plesiosminthus* the anteroconid is often highly variable (Bohlin, 1946; Black, 1958; Wilson, 1960). It is also variable in *Eozapus* and seems to be absent in *Pliozapus*, but in *Zapus* and *Napaeozapus* it is a major structural element of the tooth (Klingener, 1963). The mesolophid in *Megasminthus* is relatively higher than in *Plesiosminthus*. Lateral to the mesoconid and lying in the external re-entrant is a small hillock that may represent Schaub's

"Gegensporn," but only in worn teeth does the surface of this element join that of the mesoconid. The "Gegensporn" is a much higher and important part of the pattern in advanced zapodines and jerboas (Stehlin and Schaub, 1951). The hypoconulid in the posterior cingulum is well developed in *Megasminthus*. The postentoconid fold seems to close off earlier than the postmetaconid or postmesoconid folds do. In little-worn teeth a trench separates the mesoconid from the metalophid. This trench is present in *Plesiosminthus* and *Eozapus*, and rarely in *Zapus* (Klingener, 1963).

In M_2 the anteroconid has a high lingual arm and a lower labial arm, and is joined to the metaconid. In 2 of 6 specimens there is no ridge between anteroconid and protoconid, so that the pattern of the tooth resembles that illustrated for *Plesiosminthus* (*Schaubeumys*) *grangeri* by Wood (1935). The hypoconulid is present.

M_3 is a large, complicated tooth, not reduced and simplified as in *Zapus* and *Napaeozapus*.

Measurements of the teeth are given in Table I.

TABLE I
MEASUREMENTS OF TEETH OF *Megasminthus tiheni*, IN MM.

Tooth	Number		Observed range	Mean
M_1	(5)	Length	(1.8-2.0)	1.88
		Width	(1.4-1.5)	1.42
M_2	(8)	Length	(1.8-2.0)	1.85
		Width	(1.4-1.6)	1.50
M_3	(7)	Length	(1.5-1.6)	1.56
		Width	(1.4)	1.4
M^1	(8)	Length	(1.8-2.1)	1.91
		Width	(1.7-2.1)	1.92
M^2	(9)	Length	(1.5-1.7)	1.58
		Width	(1.6-2.0)	1.76
M^3	(3)	Length	(1.1-1.2)	1.17
		Width	(1.4-1.6)	1.53

DISCUSSION

The ?*Plesiosminthus* remains in the Valentine faunas indicate that primitive, brachydont sicistines persisted in North America into the early Pliocene. *Macrognothomys* might have evolved from this American stock, or it might have evolved in Asia. The ?*Plesiosminthus* series from the Norden Bridge Quarry and from UC locality V-3218 seem to be referable to the same species; larger series from both localities would

be desirable. Estes and Tihen (1964) regarded the faunas from these quarries as approximately contemporaneous but ecologically different.

Megasminthus is structurally transitional between sicistine and advanced zapodine rodents; it could as well be assigned to the sicistine subfamily as to the zapodine. Sicistine characters of the genus include structure of the palatine foramina, structure of the inferior zygomatic root, and many details of molar pattern. The dentition of *Zapus* is presaged, however, in the increased hypsodonty of the molars, the constant, single, central anteroconid in M_1 , the incipient "Gegensporn" in the same tooth, the increased importance of the mesolophid in the lower molars, and the deep penetration of the internal re-entrant fold in M^1 . The palate, mandible, and molars of *Megasminthus* are indeed more massive than those of any living *Zapus*, and this might indicate that *Megasminthus tiheni* is not genetically ancestral to *Zapus*. It is probable, however, that massiveness of the mandible and lower dentition decreased in at least one species lineage of *Zapus* between the uppermost Pliocene and the Recent (Klingener, 1963), and if a comparable trend existed between early and late Pliocene, *Megasminthus* might well be the direct ancestor of *Zapus*. In any event, the structural intermediacy of *Megasminthus* between *Plesiosminthus* and *Zapus* strengthens the hypothesis that *Plesiosminthus* was ancestral to zapodines.

The existence of *Megasminthus* also has implications regarding the position of *Pliozapus* in dipodoid phylogeny. Previously (Klingener, 1963) I noted that *Pliozapus* lacks some dental features which would be expected in a mid-Pliocene ancestor of *Zapus*. The existence of *Megasminthus*, a better structural ancestor of *Zapus*, in the earliest Pliocene implies that *Pliozapus* is not on the line leading to *Zapus*. Furthermore, Sulimski (1962, 1964), in describing *Sminthozapus janossyi* from the lower Pliocene of Poland, recognized strong similarities between *Sminthozapus*, *Pliozapus*, and *Eozapus*. Sulimski regarded *Sminthozapus* as a steppe form with Central Asian, rather than European, affinities. Perhaps *Sminthozapus*, *Pliozapus*, and *Eozapus* belong to a rather isolated subgroup of zapodines centered in Asia, with a history extending at least as far back as the early Pliocene.

ACKNOWLEDGMENTS

For permission to describe these specimens, and for their assistance during the work, I am deeply indebted to J. A. Tihen and C. W. Hibbard. I am also grateful to R. A. Stirton and associates at the

University of California at Berkeley for putting the rodent collection and the facilities of the Museum of Paleontology at my disposal.

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Accepted for publication November 22, 1965

