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COMMENTS ON NORTH AMERICAN FOSSIL ZAPODIDAE (RODENTIA: MAMMALIA) WITH REFERENCE TO *MEGASMINTHUS*, *PLESIOSMINTHUS*, AND *SCHAUBEUMYS*

MORTON GREEN¹

ABSTRACT *Megasminthus tiheni* Klingener from the Bijou Hills, South Dakota, is redescribed. Evidence is presented that the alleged character differences between *Plesiosminthus* and *Schaubeumys* are not valid and that the latter name should not be used. *Parasminthus* may be present in the North American Miocene.

Key Words: Zapodidae, Miocene, *Megasminthus*, *Plesiosminthus*, *Schaubeumys*.

The purposes of this paper are to amplify knowledge of *Megasminthus tiheni* Klingener based on material from the Bijou Hills local fauna (Green, 1985), South Dakota, and to discuss the validity of the genera *Plesiosminthus* and *Schaubeumys* and their occurrence in North America and Europe. The possibility of a migration of *Parasminthus* between Eurasia and North America in the Miocene also is considered.

Green (1977:1008) referred specimens from SDSM Loc. V731, Bijou Hills local fauna, to *Megasminthus tiheni*; this site later was designated as the F.O. Quarry (Green, 1985:141). Herein, I deal with a few additional specimens from the F.O. Quarry, a larger number of specimens from the nearby F.U. Quarry, and specimens of *M. tiheni* from the Egelhoff Locality, Nebraska. The availability of these specimens allows a more accurate assessment of variations in dental pattern than was possible in 1977.

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Wilson (1960) reviewed the question of the generic validity of *Schaubeumys* and opted to assign it subgeneric status within the genus *Plesiosminthus*. Green (1972) placed *Schaubeumys* in the synonymy of *Plesiosminthus* and Engesser (1979) subsequently reestablished *Schaubeumys* as a valid genus. Although a number of authors have accepted Engesser's taxonomic arrangement, I remain unconvinced of the validity of their rationale and address this issue herein.

MATERIALS AND METHODS

In an earlier zapodid paper, Green (1977) used the dental terminology recommended by Wood and Wilson (1936). Their paper not only established names for the major cusps in rodents, but also for the various enamel ridges that connect the cusps; this terminology generally has been accepted, especially by North American workers. The terminological changes suggested by Lindsay (1988) are not followed here because I think that substitution of the term "mure" for ectoloph and ectolophid adds confusion.

Measurements in millimeters were made using an Olympus binocular microscope with a Daedal two-axis linear motion stage having rotary motion positioning. Accurate measurements to 0.01 mm were possible. Each tooth was oriented as closely as possible in the same plane. Chi-square tests of independence were obtained using MINITAB.

Specimens of *Plesiosminthus grangeri* referred to in this paper are those from Green (1977).

Abbreviations: SDSM, Museum of Geology, South Dakota School of Mines and Technology; BBQII, Black Bear Quarry II V-673; F:AM, Frick Collection, American Museum of Natural History; Fm., formation; Loc., locality; SD, standard deviation; CV, coefficient of variation; AP, anteroposterior length; mx, maxilla; Tr, transverse width.

SYSTEMATIC PALEONTOLOGY

Order Rodentia Bowdich, 1821

Family Zapodidae Coues, 1875

Subfamily Zapodinae Trouessart, 1880

Genus *Megasminthus* Klingener, 1966

Emended diagnosis.—Cusps and cuspids bulbous; valley between protoloph and mesoloph completely open or nearly so; ectolophid weak or incomplete between protoconid and mesoconid.

Megasmithus tiheni Klingener, 1966

Referred specimens.—Loc. V731, F.O. Quarry: SDSM 10475: 11 M¹, 15 M², 12 M³. SDSM 10476: 2 maxillary fragments, one with P⁴, one with M¹. SDSM 10464: 7 P⁴, 10 M¹, 9 M², 5 M³. Loc. V731, F.U. Quarry: SDSM 10461: 65 M₁; SDSM 10462: 117 M₂; SDSM 10463: 112 M₃; SDSM 10465: 10 P⁴; SDSM 10458: 101 M¹; SDSM 10459: 170 M²; SDSM 10460: 141 M³. Loc. V733, Valentine Fm., SDSM 8010: left and right P⁴–M³. Egelhoff local fauna, Keya Paha Co., Nebraska (see Holman, 1973): F:AM 101677: jaw w/M₁–M₃; 101675: jaw w/M₁–M₃; 101678: jaw w/M₁–M₃; 101681: jaw w/M₁–M₃; 101684: jaw w/M₁–M₃; 101673: jaw w/M₁–M₃; 101687: jaw w/I, M₁–M₃; 101685: jaw w/I, M₁–M₃; 101679: jaw/M₁–M₃; 101682: jaw w/M₁–M₃; 101672: jaw w/I, M₁–M₃; 101680: jaw w/I, M₁–M₃; 101686: jaw w/I, M₁–M₃; 101688: jaw w/M₁–M₃; 101691: mx w/L P⁴–M³, R P⁴–M²; 101694: mx w/L P⁴–M², R P⁴–M²; 101695: mx w/L P⁴–M³, R P⁴–M³; 101693: mx w/L M¹–M³, R M¹–M³; 101699: mx w/L P⁴–M³, R M¹–M³; 101698: mx w/L P⁴–M², R M¹; 101692: mx w/L P⁴–M²; 101697: mx w/L M², R M²; 101696: mx w/L P⁴–M³, R P⁴–M³; 101689: mx w/L P⁴–M², R M¹–M²; 101690: mx w/L P⁴–M³, R P⁴–M³.

Description.—The following characters of the first lower molar (M₁) of *Megasmithus tiheni* have been tabulated: (1) anteroconid joined to ectolophid or not, (2) anteroconid median or lingual, (3) mesostylid crest present or absent, (4) ectostylid present or absent, (5) ectostylid crest present or absent, (6) ectolophid connected to Metalophulid II or not, and (7) hypolophulid weak or absent.

Observed variation in these characters of the first lower molar of *Megasmithus tiheni* from the Bijou Hills, South Dakota, and the Egelhoff Quarry, Nebraska, are tabulated in Table 1. The different values for the total number of specimens observed for various characters result from some specimens lacking a character because of breakage or wear. The same is true if these numbers are matched against the total number of teeth studied (see Fig. 1). There are noticeable differences in percentages for Characters 2 and 4–6. Chi-square results for probability of differences as large as those observed indicate that there are no differences in proportion of the characters in the two populations for Characters 2, 4, and 5, but the results for Character 6, are ambivalent. I attribute this to the small sample of selected specimens from Egelhoff. The same is true for Character 3 of M¹ shown in Table 2. Character 2, anteroconid median or lingual, is included because it has been used by other authors. I find this trait highly subjective and believe that it should not be used at all.

Characters for the first upper molar seem more reliable than those for the lower teeth. These are: (1) anterior valley, open or closed, (2) endoloph between mesocone-hypocone, present or absent, (3) endoloph between mesocone-protococone, present or absent, (4) mesoloph, present or absent,

Table 1. Tabulation of observations of M_1 characters of *Megasminthus tilheii*. Character 1: anteroconid connected to ectolophid, present or absent; Character 2: anteroconid median or lingual (median = +); Character 3: mesostylid crest present or absent; Character 4: ectostylid present or absent; Character 5: ectostylid crest present or absent; Character 6: ectolophid to Metalophulid II, present or absent; Character 7: Hypolophulid I weak or absent. Presence indicated by +; absence by -.

	Characters												
	1	2	3	4	5	6	7						
	+	-	+	-	+	-	+						
Bijou Hills	<i>n</i>	8	107	35	86	118	8	32	88	72	49	72	45
	%	7.0	93.0	28.9	71.1	96.7	3.3	93.4	6.6	26.7	73.3	59.5	40.5
Egelhoff	<i>n</i>	1	12	2	11	12	1	10	3	6	7	11	2
	%	7.7	92.3	15.4	84.6	92.3	7.7	76.9	23.1	46.2	53.8	84.6	15.4
Chi Square	Value	0.01	1.08			0.64		4.28		2.18		3.14	0.17
	<i>P</i>	>0.2	>0.5			>0.5		<0.05		>0.1		0.05 < <i>P</i> > 0.1	>0.5

Table 2. Tabulation of observations of M_1 characters of *Megasminthus tilheii*. Character 1: anterior valley, open or closed; Character 2: endoloph between mesocone-hypocone, present or absent; Character 3: endoloph between mesocone-protococone, present or absent; Character 4: mesoloph present or absent; Character 5: mesostyle present or absent; Character 6: Protolophule II present or absent. + indicates presence; - indicates absence.

	Characters												
	1	2	3	4	5	6							
	+	-	+	-	+	-							
Bijou Hills	<i>n</i>	65	23	85	3	5	83	73	15	88	0	66	22
	%	73.9	26.1	96.6	3.4	5.7	94.3	83.0	17.0	100.0	0.0	75.0	25.0
Egelhoff	<i>n</i>	5	3	9	0	5	4	8	1	9	0	8	1
	%	62.5	37.5	100.0	0.0	55.6	44.5	88.9	11.1	100.0	0.0	88.9	11.1
Chi Square	Value	0.48	0.32			22.0		0.21		0.87			
	<i>P</i>	>0.5	>0.5			<0.005		>0.5		>0.5			

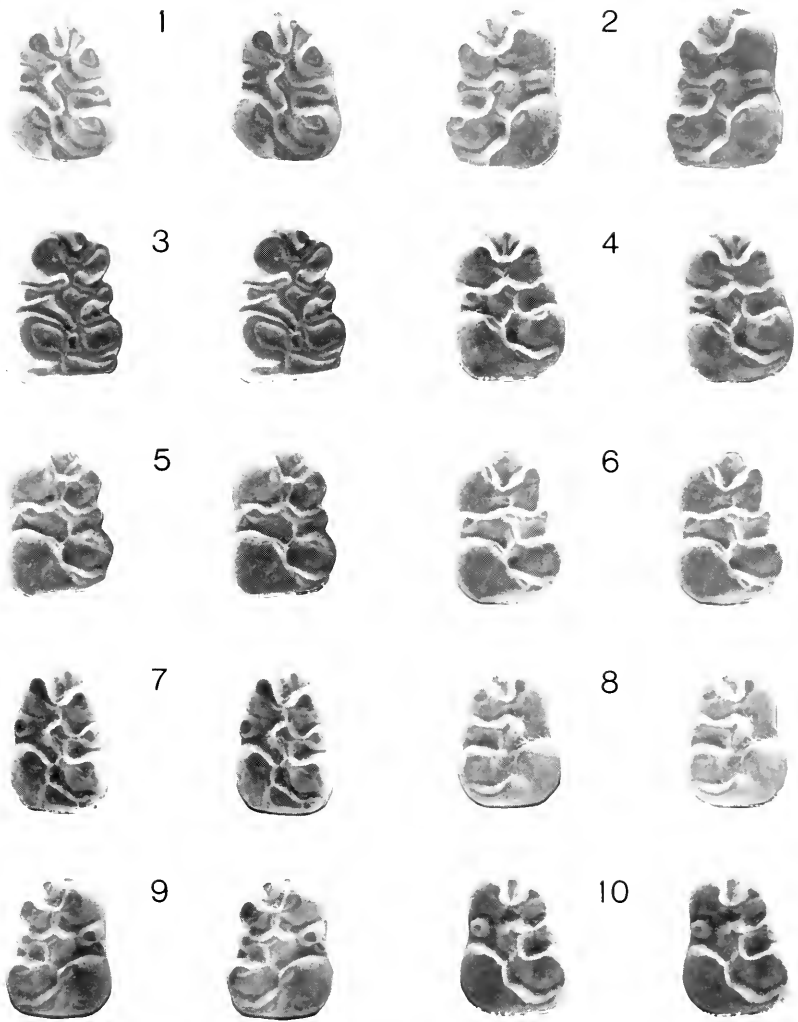


Fig. 1. *Megasmimthus tihenii*, SDSM 10461. SEM stereopairs. 1. Anteroconid connected to ectolophid; left M_1 . 2. Anteroconid not connected to ectolophid; right M_1 . 3. Anteroconid median; left M_1 . 4. Anteroconid lingual; left M_1 . 5. Ectolophid connected to Metalophulid II; left M_1 . 6. Ectolophid connection to Metalophulid II absent; left M_1 . 7. Ectostylid present; left M_1 . 8. Ectostylid absent; right M_1 . 9. Ectostylid crest present; right M_1 . 10. Ectostylid crest absent; left M_1 .

(5) mesostyle, present or absent, and (6) Protolophule II, present or absent.

The Chi-square value for Character 3 indicates that there might be a real difference in the two populations, but as with the lower teeth, this may reflect the small sample size of selected specimens.

Remarks.—The presence or absence of enamel-ridge connections in lower and upper teeth historically has been used as a criterion to distinguish species and genera. This has been possible because usually there have been few specimens from a given locality for a particular genus. In the case of SDSM Loc. V731, F.U. Quarry, South Bijou Hill, the number of specimens (i.e., individual teeth) is enormous in comparison to previous discoveries. Thus, I have been able to observe many characters and to tabulate percentages of presence or absence. It becomes increasingly clear that differences observed in only a few specimens from different localities are not necessarily taxonomic criteria for establishing new species because they may reflect individual or populational differences rather than interspecific variation. When this has been done, are we really dealing in "quarry or locality species"? I urge extreme caution in naming new species when only a few specimens are available, especially in the Muroidea.

The statistical analysis confirms the observational evidence of the variability of enamel crests in the molars of *Megasmithus tiheni*. In addition, I refute Korth's (1980) allegation that SDSM 8010 from the Valentine Formation (*M. tiheni* fide Green, 1977:1012) should be referred to *Megasmithus* sp. *Megasmithus tiheni* lacks a complete endoloph. Korth (1980) also stated that the right M¹ of SDSM 8010 has an endoloph that extends from the mesocone to the anterocone; this is true only in the left and right M². He considered SDSM 8010 too large to be referred to *M. tiheni*; however, the results presented herein indicate that SDSM 8010 fits neatly into the size range of specimens of *M. tiheni* from the Egelhoff Quarry. Here again, it is a matter of having a sufficient number of specimens from a given locality in order to determine the range of variability of the species or population (Tables 3–4).

Table 3. Measurements in millimeters of M₁ of *Megasmithus tiheni*. Stat = statistic; M = mean; SD = standard deviation; R = range; CV = coefficient of variation.

Stat	Egelhoff (n = 17)			Bijou Hills (n = 79)		
	AP	Tr(a)	Tr(p)	AP	Tr(a)	Tr(p)
M	1.90	1.12	1.41	1.87	1.10	1.40
SD	0.10	0.07	0.07	0.10	0.08	0.08
R	1.74–2.06	0.89–1.22	1.26–1.51	1.07–2.11	0.91–1.29	1.25–1.64
CV	5.25	6.40	4.99	5.4	7.27	5.71

Subfamily Sicistinae Allen, 1901

Plesiosminthus Viret, 1926

Schaubemmys Wood, 1935

Plesiosminthus grangeri (Wood)

Schaubemmys grangeri Wood, 1935

Referred specimens.—Loc.: V673 BBQII: SDSM 7951: 119 M₁; SDSM 7954: 97 M¹. Early Hemingfordian.

Discussion.—Green (1977) referred *Schaubemmys* Wood, 1935 to *Plesiosminthus* Viret, 1926. Later, Engesser (1979:35) separated *Schaubemmys* from *Plesiosminthus* despite acknowledging that he “found no morphological differences, but only quantitative ones” between European and North American species of zapodids. It should be borne in mind that a primary objective in Engesser’s paper was to show that there was no migration from the Old World to the New World in the early Miocene.

These differences are not many and seem to me to be of specific characters rather than generic. For example, the primary difference concerns the ectolophid of M₁, which according to Engesser, “almost always joins the protoconid” in European forms, whereas in American species, it “extends straight anteriorly towards the anteroconid and contacts the ridge connecting protoconid and metaconid.” (This ridge is called Metalophulid II by Green, 1977:Fig. 1B). Engesser also pointed out that the type of *S. grangeri* resembles the European species, rather than the North American and noted that in 80% of isolated M₁’s from Black Bear Quarry II, the ectolophid does not reach the Metalophulid II (see Green, 1977:Fig. 2E). In individuals in which the ectolophid continues anteriorly, it connects to the protoconid 60% of the time and connects with the center of the Metalophulid II 40% of the time (see Green, 1977:Fig. 2F); these variations are clearly marked in Green’s (1977) figure and labeled in the legend. Korth (1980; 1987) followed Engesser in the use of *Schaubemmys* for North American species and, in particular (1980), emphasized the following

Table 4. Measurements in millimeters of M¹ of *Megasminthus tihenii*.

Statistic	Egelhoff (n = 20)		Bijou Hills (n = 101)	
	AP	Tr	AP	Tr
Mean	1.91	1.86	1.88	1.85
SD	0.07	0.11	0.09	0.11
Range	1.81–2.04	1.70–2.09	1.61–2.08	1.58–2.08
CV	3.44	5.69	4.63	5.83

as important differences between the two genera. *Plesiosminthus*, M_1 ectolophid always to protoconid; *Schaubeumys*, M_1 ectolophid joined to metalophid or protoconid (Metalophulid II fide Green, 1977) via anteroposterior lophid (ectolophid fide Green, 1977). *Plesiosminthus*, M_1 mesoconid weak; *Schaubeumys*, M_1 strong. *Plesiosminthus*, M^1 protoloph connects to endoloph nearer the protocone; *Schaubeumys*, M^1 protoloph connects to endoloph nearer the mesoloph. *Plesiosminthus*, M^1 protocone and hypocone compressed transversely (=AP greater); *Schaubeumys*, M^1 protocone and hypocone compressed anteroposteriorly (Tr greater); *Plesiosminthus*, M^1 metacone anteroposteriorly compressed with a straight metaloph; *Schaubeumys*, M^1 metacone rounded with a curved metaloph.

In order to test Korth's (1980; 1987) assertions regarding the anteroposterior and transverse compressions of *Schaubeumys* versus *Plesiosminthus* in M^1 , measurements of specimens from Black Bear Quarry II (from Green's 1977 study) were made of the protocone, hypocone, and metacone of 82 individual M^1 . Because of the curvature of the cusps, they were measured at their bases and not at the crowns which enlarge with wear (Fig. 2). The results are shown in Table 5.

It can be seen that transverse or anteroposterior compression of the protocone and hypocone is not a reliable character to use for generic separation. Moreover, if these specimens are supposed to belong to *Schaubeumys*, 28% of them should be separated as *Plesiosminthus* on the basis of protocone measurements and 23% on the basis of hypocone measurements. In addition, some of the differences are only 0.01 mm—19 for the protocone and six for the hypocone. Differences of 0.02 mm are four for the protocone and 14 for the hypocone. As for the metacone, all 82 specimens

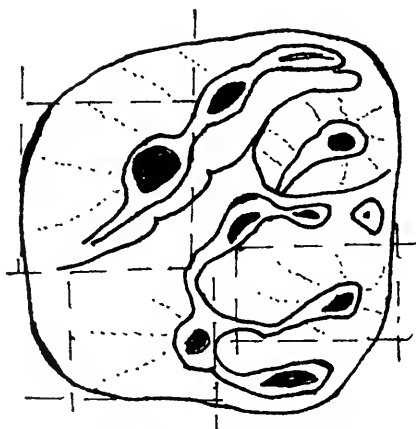


Fig. 2. Diagram of zapidid left M^1 showing limits of individual cusps for AP and Tr measurements. Lingual side to the left.

from BBQH are compressed anteroposteriorly (Green, 1977:Fig. 3). This is precisely the opposite of Korth's statement (1980:314) (see Table 6).

Curiously, Korth (1980) referred one North American species, *Plesiosminthus clivosus* Galbreath to what he claims is an Old World genus (*Schaubeumys*). In doing so, he placed *P. geringensis* L. D. Martin (1974) in the synonymy of *P. clivosus*. Whether or not this is correct is moot. However, according to Korth's analysis, the type of *P. geringensis*, a lower jaw, should be referred to *Schaubeumys* whereas the upper teeth have the characters of *Plesiosminthus*. If this were true, we would have to refer the lower teeth to *Schaubeumys* and the upper teeth to *Plesiosminthus*. This seems unlikely. Clearly, Korth (1980) and Engesser (1979) disagree. Korth believed both genera to be present in North America, whereas Engesser reserved *Plesiosminthus* for Old World species only. Barnosky (1986) followed Korth using *Schaubeumys* rather than *Plesiosminthus* on the basis of size. Skwara (1988) referred small zapodid teeth from the Topham local fauna (Saskatchewan) to *Schaubeumys clivosus* (contra Korth, 1979; 1980). This is a result of her belief that the European and North American forms are not congeneric. Skwara (1988) stated that circularity of arguments regarding intercontinental migration is eliminated by allocating the species to different genera. In essence, she derives North American forms of Zapodidae from a North American ancestor and the European Zapodidae from an Old World ancestor ascribing the similarities to parallelism; Skwara, as Engesser, does not subscribe to Miocene migration. *Plesiosminthus* well may have migrated from Asia to North America in the late Oligocene or early Miocene.

There is no real justification for retaining *Schaubeumys* as a valid genus. In my opinion, based on the variety of patterns evident in the more than 200 lower molars and 200 upper molars examined, the differences allegedly separating the two genera are at best no more than characters of specific value.

One other factor may alter current thinking regarding the geographic distribution of sicistine zapodids. Rasmussen (1977) pointed out that a characteristic of *Plesiosminthus* and *Schaubeumys* is grooved upper incisors.

Table 5. Measurements of protocone versus hypocone of specimens of *Plesiosminthus grangeri* (SDSM 7954).

Statistic	Protocone (<i>n</i> = 82)		Hypocone (<i>n</i> = 82)	
	AP	Tr	AP	Tr
Mean	0.45	0.47	0.47	0.50
SD	0.04	0.05	0.04	0.05
Range	0.38–0.53	0.39–0.55	0.35–0.57	0.36–0.61
CV	7.77	10.85	8.72	10.20

Table 6. *Plesiosminthus grangeri*, SDSM 7954. Percentages of cusp measurements in millimeters of 82 M¹.

Protocone	Hypocone	Metacone
AP > Tr = 23 = 28%	AP > Tr = 19 = 23%	AP > Tr = 0 = 0%
Tr > AP = 52 = 63%	Tr > AP = 58 = 70.7%	Tr > AP = 82 = 100%
AP = Tr = 7 = 8.5%	AP = Tr = 5 = 6%	—

In the collection from the Cabbage Patch Locality, there are two sicistine anterior moieties with smooth upper incisors, a characteristic of the Asian genus *Parasminthus*. There are two implications here. First, identification of sicistine genera based on molars alone can be risky. Second, if these Cabbage Patch (=Gering/Monroe Creek) specimens are *Parasminthus*, migration from Asia to North America did take place in the late Oligocene or early Miocene (contra Engesser, 1979). Grooved upper incisors are known from the Cabbage Patch Locality thereby indicating the presence of two genera—*Parasminthus* and *Plesiosminthus*.

A comment should be made regarding the temporal distribution of specimens that have been referred to *Plesiosminthus grangeri*. This species ranges from the Arikareean to the Barstovian (see Korth, 1980:Table 4). This is an exceptionally long time for the existence of one species; it may be the longest specific range given for any mammal. Given the variation seen in teeth both as to enamel patterns and size and lacking skulls, our ability to discriminate species of sicistines on teeth alone may not be great.

The range of individual variation seen in BBQII specimens confirms my interpretation that *Schaubenmys* Wood should remain in the synonymy of *Plesiosminthus* Viret and that the alleged differences separating them into Old World and New World genera are either individual variations or, at best, specific differences.

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Apologia: Figure 1A in Green (1977) is of a right M¹⁻², not a left.

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