Insectivore faunas from the Lower Miocene of Anatolia — Part 5: Talpidae

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Hoek Ostende, L. W. van den. Insectivore faunas from the Lower Miocene of Anatolia — Part 5: Talpidae. — Scripta Geol., 122: 1-45, 5 figs., 5 pls, Leiden, June 2001.
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Keywords: Anatolia, Talpidae, Uropsilinae, classification, new taxa, Early Miocene.
Two new genera of Talpidae, *Theratiskos* gen. nov. and *Suleimania* gen. nov., and five new species, *T. mechteldae* sp. nov., *T. rutgeri* sp. nov., *S. ruemkae* sp. nov., *Geotrypus haramiensis* sp. nov. and *G. kesekoeyensis* sp. nov., are described from the Lower Miocene of Anatolia. The literature on the very diverse genus *Geotrypus* is reviewed. The aberrant genus *Suleimania* is placed in a separate subfamily, Suleimaninae subfam. nov. *Theratiskos* is considered an uropsiline talpid. The taxonomy and classification of the Uropsilinae is discussed. On the basis of the morphology of the humerus the genera *Asthenoscaptor* and *Mygatalpa* are included in the Uropsilinae, showing that the diversity of this subfamily during the Early Miocene was much larger than previously assumed.

Contents

Introduction

The Talpidae formed the most diverse insectivore family during the Early Miocene. Ziegler (1985, 1990a, 1994) described a total of twenty species of moles from the Lower Miocene of southern Germany, and the locality Ulm-Westtangente alone has eight different species.

In this paper the Early Miocene Talpidae from Anatolia are discussed. It is the fifth paper in a series on the Anatolian insectivores from this time interval. The Erinaceidae were discussed in the first paper (van den Hoek Ostende, 1992), the second and third dealt with the Heterosoricidae and the Dimylidae, respectively (van den Hoek Ostende, 1995a,b). The talpid genus *Desmanodon* was already discussed in the fourth paper (van den Hoek Ostende, 1997) and the sixth paper will deal with the Soricidae (van den Hoek Ostende, 2001b). These papers concentrate on the taxonomy and the stratigraphic distribution of the various species. Our aim is to come to environmental reconstructions of the various localities and to make an attempt at monitoring climatic changes during the Early Miocene. In order to do so, the taxonomy of the insectivores must first be elaborated.

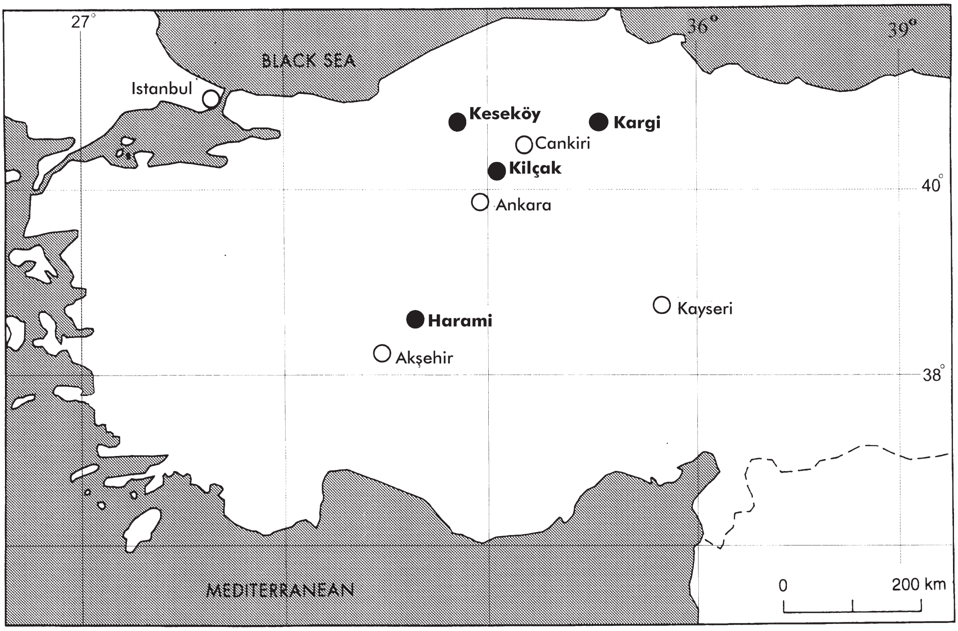

Fig. 1. Lower Miocene mammal localities in Anatolia.

The geographical position of the localities is shown in Fig. 1. A total of eight assemblages has been studied: four from the Kilçak section (Ki 0, Ki 0", Ki 3A and Ki 3B), three assemblages from the Harami section (Ha 1, Ha 2 and Ha 3) and one assemblage from Keseköy (Ke). The study of these assemblages is part of the project 'Reconstruction of the changes in the continental Neogene of Anatolia', a joint venture of the Mineral Research and Exploration General Directorate of Turkey (M.T.A.) in Ankara with Utrecht University, supported by NATO grant CRG 910750. The rodents of the various localities are discussed in a separate series. So far articles have appeared on various muroid genera (de Bruijn & Saraç, 1991, 1992, de Bruijn et al., 1993, de Bruijn & von Koenigswald, 1994) and on the Gliridae (Ünay, 1994).

Methods and collections

We follow van den Hoek Ostende (1989) for the nomenclature of parts of molars and the method of measuring. The nomenclature for the parts of the humerus follows Hutchison (1974). Measurements are given in millimetres. With the exception of the M_3 of *Suleimania*, which lacks the talonid, the width given for lower molars is always the width of the talonid. The number in brackets in a description refers to the number of specimens used in that description.

The material described in this paper was collected during joint fieldwork in the period 1987-1993 by Engin Ünay, Gerçek Saraç (both from the M.T.A.), and Hans de Bruijn from Utrecht University. Teeth were obtained by wet-screening. All specimens will be stored in the collections of the M.T.A. (Ankara). This is publication 990601 of the Netherlands Research School of Sedimentary Geology (NSG).

Systematic part

Talpidae Fisher von Waldheim, 1817
Uropsilinae Dobson, 1883
Theratiskos gen. nov.

Derivatio nominis — Theratiskos (Greek) = small hunter; the slender humeri of this small shrew-mole indicate that it probably was an active hunter.

Diagnosis — The lower dentition is complete; the P_2 is larger than the P_3. The M_1 and M_2 are of the same length. The oblique cristid of the M_1 and M_2 ends against the middle of the protoconid-metaconid crest or lingually of that point, rarely reaching the metaconid. The entocristid is well developed; a metacristid may be present. The protocone of the P^4 is cone-shaped. The upper molars have undivided mesostyles, weakly developed protoconules and well-developed hypocones. The posterior side of the M^1 and M^2 may be slightly concave. The humerus is slender, with an open bicipital groove.

Differential diagnosis — The slender humerus with an open bicipital groove is here considered typical for the subfamily Uropsilinae. The discussion is therefore restricted to the genera of this subfamily. The contents of the Uropsilinae will be discussed below.

Theratiskos differs from *Desmanella* in having a two-rooted P_3 and in the direction of the oblique cristid of the lower molars, which ends more labially in *Theratiskos*. The protocone of the P^4 is weaker in *Theratiskos*. Its M^1 and M^2 do not show the strongly concave posterior outline found in *Desmanella* and the protoconule is less developed. The humerus of *Theratiskos* is much more slender than that of *Desmanella*.

Theratiskos differs from *Asthenoscaptor* in the direction of the oblique cristid of the lower molars, which ends more labially in *Theratiskos*. The P^4 of *Theratiskos* is relatively longer. The hypocone of the M^1 and M^2 of our new genus is better developed than that of *Asthenoscaptor*, and the posterior outline of these molars is less concave. The humerus of *Theratiskos* has a larger entepicondyle and olecranon fossa and shows a more pronounced pectoral process.

Theratiskos differs from *Mygatalpa* in having an undivided mesostyle. The hypocone of the M^1 and M^2 of *Theratiskos* is better developed. The humerus of *Theratiskos* has a larger entepicondyle and olecranon fossa. The pectoral process is more pronounced.

Theratiskos differs from *Mystipterus* in having a complete dentition. The P^4 of *Theratiskos* is longer and has a less developed protocone. The hypocone of the M^1 is weaker than that of *Mystipterus* and the posterior outline of the M^1 and M^2 is less concave. The humerus of *Theratiskos* differs from that of *Mystipterus* in having a longer teres tubercle.

Theratiskos differs from *Uropsilus* in having a complete dentition. The hypocone of the M^1 and M^2 is weaker and the posterior outline of these molars is less concave than in *Uropsilus*. The humerus of *Theratiskos* differs from that of *Uropsilus* in having a larger entepicondyle and a longer teres tubercle.

Type species — *Theratiskos mechteldae* sp. nov.

Other species included — *T. rutgeri* sp. nov.; *Desmanodon* sp. from Sariçay (Engesser, 1980).

Stratigraphical and geographical range — Lower-Middle Miocene of Anatolia.

Theratiskos mechteldae sp. nov.
Pl. 1, figs. 1-7; Figs. 2-3.

Derivatio nominis — This species is named after Mechteld van den Hoek Ostende, the author's daughter.

Diagnosis — All lower premolars are two-rooted. The P_2 is larger than the P_3. The M_1 and M_2 are subequal in length. Both molars have an entocristid, but no metacristid; the oblique cristid ends against the middle of the protoconid-metaconid crest. The M^1 and M^2 have large hypocones and poorly developed protoconules. The posterior outline of the M^1 and of the M^2 is straight or slightly concave.

Type locality — Keseköy (MN 3).

Holotype — Mandibula sin. with P_4-M_3 (Ke 6975) Pl. 1, fig. 3a-b; $P_4 = 1.09 \times 0.65$, $M_1 = 1.69 \times 0.99$, $M_2 = 1.73 \times 1.10$, $M_3 = 1.25 \times 0.61$.

Description of the holotype — The holotype is a damaged ramus horizontalis bearing the P_4, M_1, M_2 and M_3, and showing the two alveoles of the P_3. It is broken at the posterior alveole of the P_2. The processus coronoides is broken off at het level of the dentition; the processus angularis is damaged. A small foramen mentale lies in the middle of the ramus horizontalis below the trigonid of the M_1.

The P_4 consists mainly of the large protoconid, which has a rounded anterior side and a rather straight posterior flank. Along the postero-lingual side of the protoconid runs a faint posterocristid. A short cingulum is present at the antero-lingual side of the protoconid. The talonid is short. The lingual side of this talonid is clearly higher than the labial side. A low ridge runs along the posterior side of the premolar. A faint ridge connects the middle of the posterior ridge to the posterocristid.

The M_1 and M_2 have about the same size. The trigonid of the M_1 is clearly narrower than the talonid, giving the molar a subtriangular outline. Trigonid and talonid of the M_2 are of similar width; the outline in occlusal view is subrectangular. The entocristid is present in the M_1 and M_2; there are no metacristids. The oblique cristid ends against the middle of the protoconid-metaconid crest in both molars. The anterior and posterior cingulums are well developed. The development of the anterior cingulum of the M_2 is somewhat stronger than in the M_1. The re-entrant valley is bordered by a well-developed labial cingulum. The entostylid of the M_1 is somewhat larger than that of the M_2, which nevertheless is well developed.

The trigonid of the M_3 resembles the trigonid of the M_2. The talonid, however, is reduced. Hypoconid and entoconid are two low cusplets. The oblique cristid ends somewhat lingually of the middle of the protoconid-metaconid crest. The talonid basin is bordered by an entocristid; there is no metacristid. The anterior cingulum is very well developed. It continues along the base of the paraconid and ends near the metaconid. The re-entrant valley is bordered by a short labial cingulum.

Measurements — The measurements are listed in Table 1.

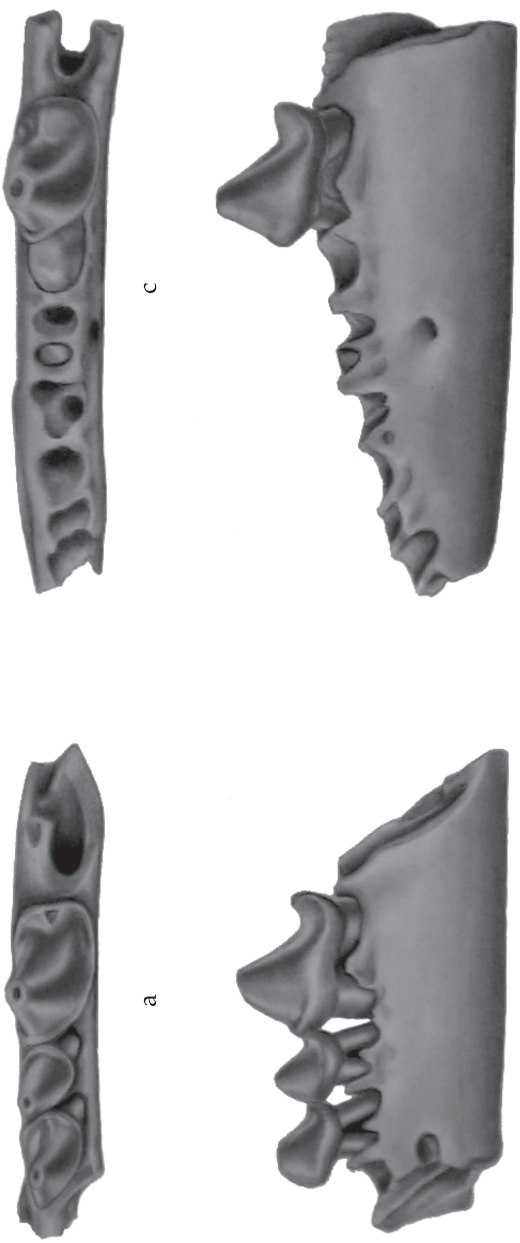

Fig. 2. Mandible fragment of *Theratiskos mechteldae* sp. nov. with the P_2-P_4 (Ke 6823); a: occlusal view; b: labial view. Mandible fragment of *Theratiskos mechteldae* sp. nov. with the P_4 and the alveoles of the anterior dentition (Ke 6824); c: occlusal view; d: labial view (× 12.5).

Description

Mandible — The external temporal fossa is shallow. The ramus horizontalis is deepest under the M_2/M_3. There are two foramina mentale. The posterior one lies usually between the roots of the M_1 (18), but may also be positioned under the trigonid of that molar (8) or under the P_4. The anterior foramen lies under the P_1/P_2. A well-preserved anterior part of the mandible (Fig. 2c and d) shows ten alveoles in front of the P_4. Four of these certainly belong to the P_2 and P_3, leaving six alveoles for the remaining elements. The three anterior ones are small and presumably belong to the incisors. The fourth, probably belonging to the canine, is the largest. This leaves the small fifth and sixth alveole for the P_1, which, like the other premolars, is therefore two-rooted.

P_2 (3), P_3 (5) — A large number of ramus horizontalis fragments of *Theratiskos mechteldae* has been found. Some of these contain the P_2 (1), the P_3 (3) or both these elements (2). Due to their small size, these premolars have not been found isolated. The P_2 and P_3 have a very similar morphology, the P_2 being a somewhat larger version of the P_3 (Fig. 2a and b). Both are two-rooted unicuspids. The outline in occlusal view is elliptical. The tip lies just in front of the middle of the premolar. Behind the tip lies a well-developed cingulum, which continues along the lingual and labial sides and ends next to the tip.

D_4 (30) — The outline of the occlusal surface is elliptical. The pyramid-shaped protoconid is the only cusp. It occupies the front part of the milk molar. The edges between the antero-lingual, antero-labial and posterior flank of the protoconid are rounded. The posterior part of the D_4 consists of a large talonid, which is surrounded by a ridge. In some specimens this ridge is interrupted in the postero-labial corner. The lingual side of the talonid is clearly higher than the labial side. There is a small cusplet close to the postero-lingual corner, which is incorporated in the posterior ridge. In 9 of the 30 specimens a central ridge is present, which connects the posterior ridge to the middle of the posterior flank of the protoconid.

P_4 (48); M_1 (71); M_2 (79); M_3 (77) — These elements have been described in the description of the holotype. The morphological variation in the lower dentition is small.

D^4 (25) — The outline of the occlusal surface is triangular. The paracone is the largest cusp. Its tip lies in the front part of the milk molar, at about one third of its length. A long posterocrista runs from the tip backwards. The anterior face of the paracone is rounded. The parastyle lies in front of the paracone on a rather large shelf. Postero-lingually of the tip of the paracone lies the protocone. This is a low, blade-like cusp, which lies close to the flank of the paracone at its anterior end, but is well separated from the paracone at its posterior end. The D^4 is surrounded by wide cingulums. The widest is the postero-lingual cingulum. The labial cingulum, which runs from the parastyle to the back of the milk molar, is only somewhat narrower. The cingulum connecting the parastyle to the protocone becomes very narrow near the base of the paracone and is in some cases interrupted at this point.

P^4 (53) — The outline of the occlusal surface is subtriangular. The labial side is convex. The antero-lingual side is concave; the postero-lingual side is slightly concave or straight. The paracone forms the largest part of the premolar. It has a strongly convex anterior side. The tip of the paracone lies in the middle of the P^4. The straight

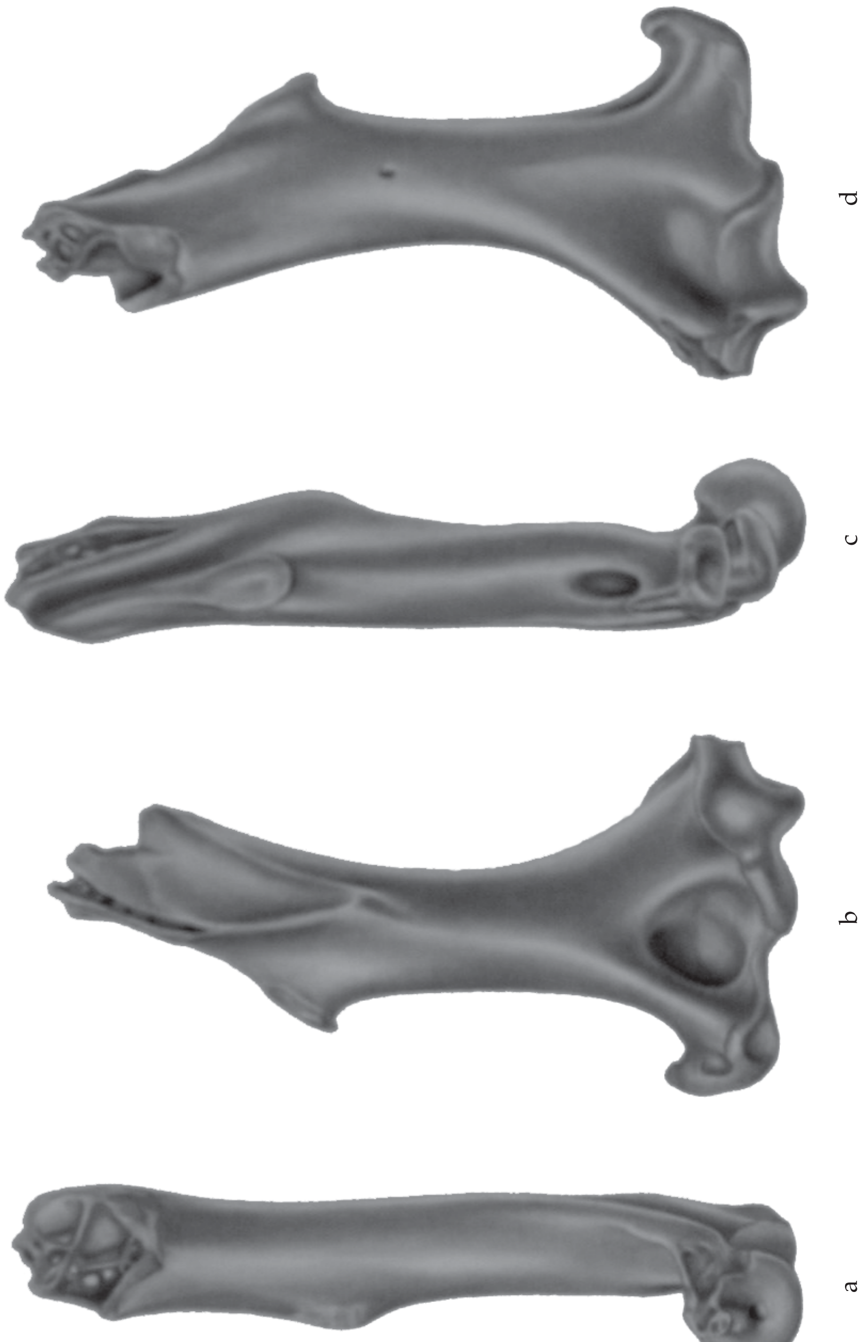

Fig. 3. Humerus of *Theratiskos mechteldae* sp. nov. (Ke unnumbered); a: medial view; b: posterior view; c: anterior view; d: lateral view (× 9).

posterocrista runs from the tip backwards. The cone-shaped protocone lies lingually of the tip of the paracone. It is a small cusplet that lies on a lingual extension. The protocone is connected to the parastyle by the antero-lingual cingulum. The parastyle is a very small cusplet that lies in front of the paracone. It is even lower than the protocone. The postero-lingual cingulum connects the protocone to the posterior end of the posterocrista. This cingulum is strong and broad. The well-developed labial cingulum runs along the base of the posterocrista.

M^1 (56) — The outline of the occlusal surface is irregularly quadrangular. The protocone is large. Its anterior arm runs along the anterior side of the molar and is connected to the parastyle. The protoconule lies directly in front of the protocone. It is little more than a thickening in the anterior arm of the protocone, and disappears quickly with wear. It can only be observed in 19 out of the 56 specimens. The posterior arm of the protocone continues as a ridge that runs over the hypocone. The hypocone is lower but only slightly smaller than the protocone. The parastyle lies directly in front of the paracone. It protrudes slightly. The posterior arm of the paracone is S-curved. It is connected to the mesostyle. The mesostyle is undivided, although the two separate cusps can be discerned in unworn specimens. The metacone is the highest cusp of the M^1. The arms of the metacone are straight. The anterior arm is clearly shorter than the posterior arm. The latter extends to the postero-labial corner of the M^1. The posterior cingulum is well developed. It runs from the hypocone along the base of the posterior arm of the metacone. Specimens with a somewhat less developed cingulum usually have a concave posterior outline, in the others the posterior side is straight. A weak labial cingulum may be present along the metacone. There is a small patch of lingual cingulum between the bases of the protocone and the hypocone.

M^2 (73) — The outline of the occlusal surface is subrectangular. The large protocone lies in the antero-lingual corner of the molar. The tiny protoconule is usually incorporated in the anterior arm of the protocone and only recognizable in slightly worn specimens. The anterior arm of the protoconule ends against the anterior flank of the paracone, but reaches the parastyle in 11 out of the 73 specimens. The posterior arm of the protocone connects to the well-developed hypocone, which lies postero-labially of the protocone, making the lingual side of the molar slightly concave. The hypocone is smaller and clearly lower than the protocone. The posterior arm of the hypocone continues as the posterior cingulum. This cingulum ends against the posterior flank of the metacone, either near the base or further lingually. In 17 out of 73 specimens this cingulum reaches the postero-labial corner of the M^2. The labial cusps are of about the same size and height. The anterior arm of the paracone bends to form the parastyle, which does not protrude. The anterior cingulum is wide near the parastyle. Mostly this cingulum is short and ends against the flank of the paracone. The posterior arm of the paracone is connected to the mesostyle, which is undivided. The posterior arm of the metacone bends to form the metastyle. The metastyle may be slightly protruding. In contrast to the parastyle, there is no cingulum near the metastyle. In 39 out of the 73 specimens there is a short lingual cingulum between the protocone and the hypocone.

M^3 (60) — The posterior outline of the occlusal surface is nearly half a circle. The large protocone occupies the lingual part of the molar. The anterior arm of the proto-

Table 1. Measurements of *Theratiskos* (Keseköy = *T. mechteldae* sp. nov.; Harami and Kilçak = *T. rutgeri* sp. nov.).

tooth	loc.	N	Length range	mean	Width range	mean	tooth	loc.	N	Length range	mean	Width range	mean
D_4	Ke	30	0.99-1.25	1.14	0.57-0.75	0.65	D^4	Ke	18	1.23-1.60	1.35	0.79-1.00	0.90
								Ha3	3	1.31-1.39	1.35	0.82-0.89	0.85
								Ha2	—				
								Ha1	1		1.38		0.94
								Ki3A	1		1.34		0.83
								Ki0″	—				
								Ki0	—				
P_4	Ke	49	0.94-1.19	1.09	0.51-0.72	0.61	P^4	Ke	53	1.40-1.69	1.51	0.95-1.17	1.08
	Ha3	4	1.06-1.23	1.17	0.62-0. 71	0.67		Ha3	5	1.37-1.61	1.51	1.06-1.18	1.11
	Ha2	—						Ha2	1		1.36		0.99
	Ha1	30	1.01-1.24	1.12	0.51-0.70	0.62		Ha1	13	1.47-1.65	1.53	1.01-1.17	1.08
	Ki3A	—						Ki3A	—				
	Ki0″	2	1.01-1.04	1.03	0.56-0.63	0.60		Ki0″	1		1.43		1.08
	Ki0	—						Ki0	—				
M_1	Ke	71	1.58-1.86	1.73	0.93-1.19	1.05	M^1	Ke	44	2.05-2.47	2.25	1.29-1.49	1.40
	Ha3	12	1.61-1.79	1.71	0.91-1.14	1.03		Ha3	5	2.09-2.30	2.18	1.28-1.38	1.35
	Ha2	—						Ha2	—				
	Ha1	36	1.51-1.81	1.70	0.89-1.10	1.00		Ha1	17	2.14-2.36	2.24	1.24-1.43	1.35
	Ki3A	1		1.73		1.01		Ki3A	—				
	Ki0″	4	1.58-1.68	1.62	1.01-1.10	1.05		Ki0″	—				
	Ki0	—						Ki0	—				
M_2	Ke	80	1.54-1.99	1.71	0.95-1.17	1.05	M^2	Ke	71	1.39-1.64	1.50	1.67-2.04	1.83
	Ha3	10	1.61-1.75	1.69	0.92-1.11	1.01		Ha3	6	1.43-1.59	1.50	1.72-1.89	1.79
	Ha2	—						Ha2	1		1.49		1.76
	Ha1	41	1.52-1.83	1.66	0.88-1.17	1.02		Ha1	19	1.35-1.58	1.46	1.63-1.92	1.77
	Ki3A	—						Ki3A	—				
	Ki0″	5	1.64-1.77	1.71	0.99-1.03	1.00		Ki0″	10	1.40-1.60	1.50	1.67-1.98	1.84
	Ki0	1		1.77		1.04		Ki0	—				
M_3	Ke	78	1.16-1.55	1.31	0.58-0.99	0.69	M^3	Ke	55	0.90-1.09	0.97	1.27-1.58	1.45
	Ha3	15	1.21-1.39	1.28	0.61-0.80	0.68		Ha3	9	0.90-1.01	0.97	1.28-1.47	1.39
	Ha2	1		1.21		0.67		Ha2	3	0.93-0.94	0.94	1.28-1.47	1.36
	Ha1	33	1.22-1.41	1.30	0.61-0.94	0.70		Ha1	38	0.83-1.06	0.96	1.15-1.58	1.40
	Ki3A	1		1.37		0.66		Ki3A	1		1.05		1.45
	Ki0″	5	1.23-1.31	1.27	0.62-0.69	0.67		Ki0″	5	0.88-0.97	0.93	1.30-1.45	1.37
	Ki0	1		1.31		0.71		Ki0	—				

cone continues as the anterior cingulum and is connected to the parastyle in 28 of the 60 specimens. In the other specimens the anterior cingulum is interrupted near the base of the paracone. The posterior arm of the protocone is connected to the hypocone. The latter is a small cusp, which lies lingually of the tip of the metacone. More often than not there is a small bulge in the outline at the position of the hypocone. The anterior arm of the paracone is somewhat longer than the posterior arm. It bends slightly at the end to form a small parastyle. The posterior arm of the paracone is connected to the mesostyle, which is undivided. The metacone is small. There are no cingulums other than the anterior cingulum.

Humerus (4) (Fig. 3) — The humerus is very slender. The proximal part of the bone is damaged in all four specimens. The bicipital groove is open throughout. The teres tubercle is small. It lies about halfway the shaft and has a medially directed, elliptical facet. The pectoral process is a protruding, wedge-shaped area. It lies in the centre of the shaft. In three specimens it extends somewhat more distally than the teres tubercle, in the fourth the pectoral process lies directly laterally of the teres tubercle. In one of the specimens the pectoral process is strongly developed, in the others less so. The entepicondyle is small. The elliptical entepicondylar foramen is large. The supratrochlear fossa is large and deep; the olecranon fossa is shallow.

Theratiskos rutgeri sp. nov.
Pl. 1, figs. 8-16; Figs. 4-5.

Derivatio nominis — The species is named after Rutger van den Hoek Ostende, the author's son.

Diagnosis — Dental formula unknown but probably complete. The M_1 and M_2 are subequal in length. The entocristids of the M_1 and M_2 are well developed; metacristids are usually present on the M_2, rarely on the M_1. The oblique cristid ends lingually of the middle of the protoconid-metaconid crest, and may even reach the metaconid. The hypocones of the M^1 and M^2 are well developed; the protoconule is small. The posterior outline of the M^1 is slightly concave.

Differential diagnosis — *Theratiskos rutgeri* differs from *T. mechteldae* in having a metacristid on the M_2, and in rare cases also on the M_1. The oblique cristid of the M_1 and M_2 ends more lingually. The protoconule of the M^1 and M^2 is somewhat larger and the hypocone is smaller than in *T. mechteldae*.

Type locality — Harami 1 (MN 1).

Other localities with T. rutgeri — Kilçak 0, Kilçak 0", Kilçak 3A, Harami 2, Harami 3.

Holotype — M^2 sin. (Ha1 4057; Pl. 1, fig. 15); (1.58 × 1.78).

Description of the holotype — The outline of the occlusal surface of the M^2 is subrectangular. The lingual part of the molar consists mainly of the protocone. The tip of the protocone lies near the front of the tooth, making the outline slightly askew. The protoconule lies directly in front of the protocone. The anterior arm of the protocone becomes very narrow between protocone and protoconule. The anterior arm of the protoconule continues as the anterior cingulum, which is connected to the parastyle. The posterior arm of the protocone is connected to the small hypocone, which lies lingually of the tip of the metacone. The hypocone is lower than the protocone and the

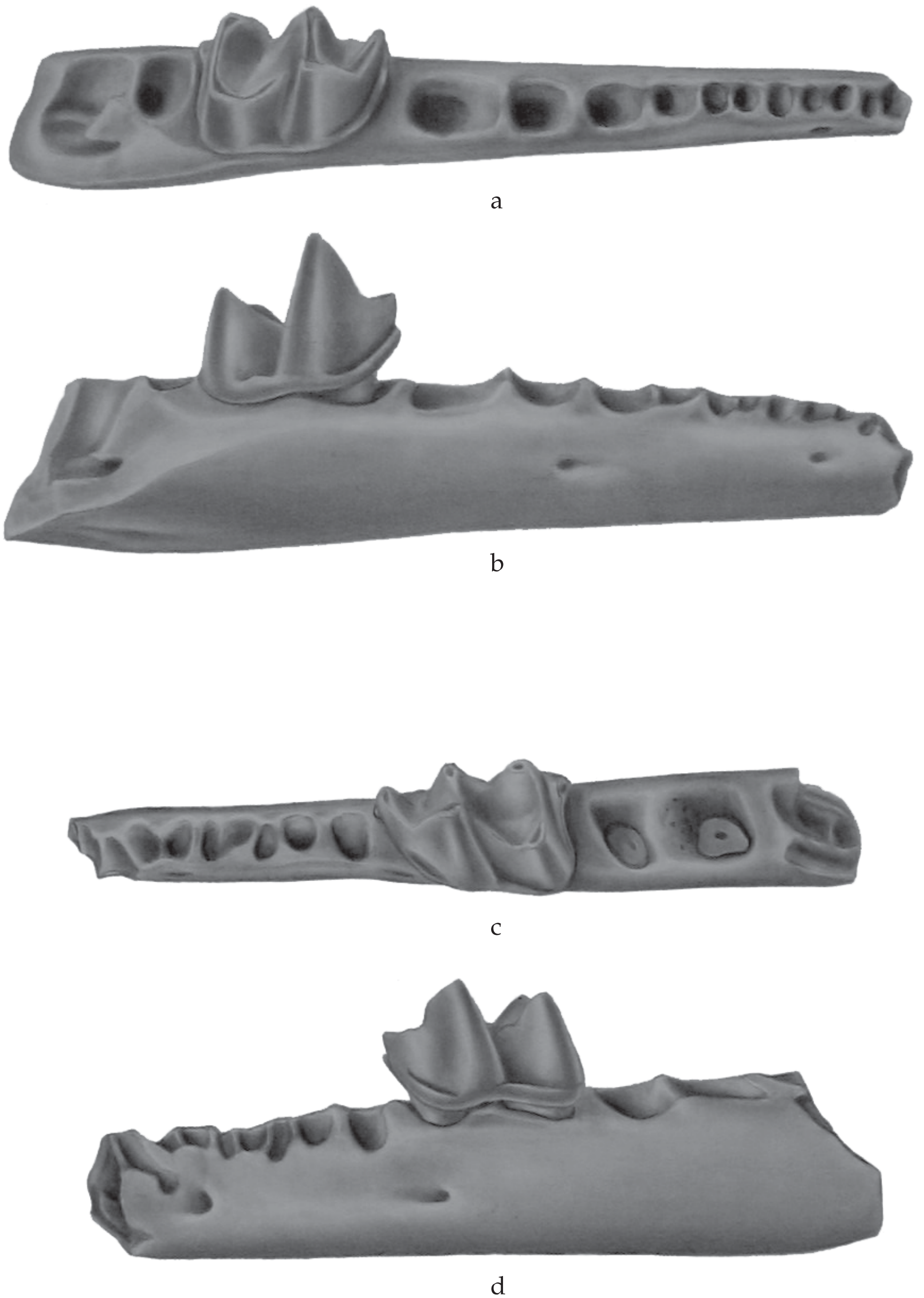

Fig. 4. Mandible dext. of *Theratiskos rutgeri* sp. nov. with M_2 and the alveoles of the anterior dentition (Ha 1 3918); a: occlusal view; b: labial view. Mandible sin. *Theratiskos rutgeri* sp. nov. with M_1 and the alveoles of the anterior dentition (Ki 0″ 2814); c: occlusal view; d: labial view (× 12.5).

protoconule. The posterior arm of the hypocone continues as the posterior cingulum and ends against the flank of the metacone. The labial cusps are equal in size and height. The anterior arm of the paracone bends to form the parastyle, which does not protrude. The posterior arm of the paracone is connected to the undivided mesostyle. The posterior arm of the metacone bends to form the slightly protruding metastyle. There is a short lingual cingulum between the protocone and the hypocone.

Measurements — The measurements are listed in Table 1.

Description

Mandible — Only a few mandibular fragments of *T. rutgeri* have been found. The best-preserved specimen is a mandible with the M_2 from Harami 1, showing 13 alveoles in front of that molar (Fig. 4a-b). This number is corroborated by two mandibular fragments from Kilçak 0″ (Ki 0″ 2813, 2814; Fig 4c-d), which show 11 alveoles in front of the M_1. Determining the exact number of alveoles is difficult, since one cannot be sure that all alveoles are preserved. If they are all preserved, the anterior dentition of *T. rutgeri* would be slightly more reduced than that of *T. mechteldae*, which has 14 alveoles in front of the M_2. The fourth alveole of *T. mechteldae* is large and is interpreted as the alveole of the canine. In *T. rutgeri* all alveoles are of similar size. The interpretation is therefore difficult. The observed reduction in the number of alveoles may either mean that one single-rooted element is missing, or that one of the double-rooted premolars of *T. mechteldae* has only one root in *T. rutgeri*. The external temporal fossa is shallow. The ramus horizontalis has its greatest depth below the M_2/M_3. There are two small foraminae mentale. The posterior one lies between the P_4 and M_1 (6), the anterior one lies below the sixth alveole in front of the M_1 (1).

P_4 (32) — The outline of the occlusal surface is subrectangular. The labial side is slightly convex; the lingual side is straight. The P_4 consists mainly of the large protoconid. It has a rounded anterior side and a straight posterior flank. An indistinct posterocristid runs along the postero-lingual edge of the protoconid. There is a small cingulum along the antero-lingual side of the protoconid. A short talonid lies behind the protoconid. The lingual side of this talonid is clearly higher than the labial side. A low ridge runs along the posterior side of the premolar. A second ridge connects the middle of the posterior ridge to the posterocristid.

M_1 (36) — The outline of the occlusal surface is subrectangular to subtriangular. The trigonid is clearly narrower than the talonid. A deep notch separates protoconid and metaconid. The paraconid is clearly lower than the protoconid and metaconid. It lies at the end of a long paralophid. The trigonid basin is open. The entoconid and hypoconid are about the same height as the metaconid. The oblique cristid ends against the middle of the protoconid-metaconid crest or somewhat lingually of that point. The entocristid is well developed. A very weak metacristid is present in 4 of the 36 specimens. The entostylid and posterior cingulum are well developed. The reentrant valley is bordered by a short labial cingulum. The anterior cingulum, which runs from the base of the paraconid to the base of the protoconid, is well developed. A parastylid may be present, but it is little more than a bulge on the anterior face of the paraconid. Some specimens show a short lingual cingulum along the base of the paraconid.

M_2 (42) — The outline of the occlusal surface is subrectangular. The trigonid and

Fig. 5. Humerus of *Theratiskos rutgeri* sp. nov. (Ha 3 873); a: medial view; b: posterior view; c: anterior view; d: lateral view (× 9).

talonid have about the same length and width. Protoconid and metaconid are separated by a deep notch. The metaconid is somewhat lower than the protoconid; the paraconid is clearly lower than the metaconid. The paralophid is straight or slightly bent. The trigonid basin is narrower than in the M_1. The hypoconid and entoconid are of the same height. These cusps are somewhat lower than the metaconid, but higher than the paraconid. The oblique cristid ends lingually of the middle of the protoconid-metaconid crest, reaching the metaconid in 4 of the 42 specimens. The entocristid is well developed; a clear metacristid is usually present. The anterior cingulum is well developed. The parastylid lies on this cingulum. As a rule, the anterior cingulum bends along the base of the paraconid and continues as a narrow lingual cingulum that may reach the metaconid. The entostylid is well developed. The posterior cingulum is slightly narrower than the anterior cingulum. The re-entrant valley is bordered by a short labial cingulum.

M_3 (32) — The outline of the occlusal surface is subrectangular. The talonid is somewhat shorter and somewhat narrower than the trigonid. The trigonid resembles that of the M_2. Entoconid and hypoconid are low. They are incorporated in a long ridge consisting of the oblique cristid, the posterior arm of the hypoconid and the entocristid. In some M_3 a small metacristid is present. The oblique cristid ends close to the metaconid. The anterior cingulum is well developed. It continues along the base of the paraconid and ends halfway the trigonid basin. The re-entrant valley is bordered by a short labial cingulum.

D^4 (2) — The outline of the occlusal surface is triangular. The paracone is the largest cusp. Its tip lies in the front part of the milk molar, at about one third its length. The posterocrista is straight. The anterior face of the paracone is rounded. The parastyle lies in front of the paracone on a well-developed anterior cingulum. The two arms of the parastyle end against the front of the paracone. The protocone lies lingually of the tip of the paracone. It is a low, blade-like cusp. The short anterior arm of the protocone ends against the flank of the paracone. The posterior arm continues as a ridge on the postero-lingual cingulum. It is connected at its end to the posterocrista. The labial cingulum runs from the flank of the paracone, just labially of its tip, to the back of the milkmolar. Thus the cingulums nearly surround the D^4, with the exception of a part of the labial and lingual flanks of the paracone.

P^4 (20) — The outline of the occlusal surface is subtriangular. The labial side is convex. The paracone forms the largest part of the premolar. The tip of the paracone lies in the middle of the P^4. It has a strongly convex anterior side. The posterocrista is straight. The cone-shaped protocone lies directly lingual of the tip of the paracone. It is a very small cusplet that lies on a lingual extension. The parastyle is even lower than the protocone. The protocone is connected to the parastyle by the antero-lingual cingulum. The postero-lingual cingulum is well developed and runs from the protocone to the posterior end of the posterocrista. There is a short labial cingulum that runs along the base of the posterocrista.

M^1 (22) — The outline of the occlusal surface is irregularly quadrangular. The protocone is large. Its anterior arm runs along the anterior side of the molar and is connected to the parastyle. The posterior arm runs along the lingual side of the M^1. The protoconule appears as a widening of the anterior arm and may disappear with wear. The hypocone lies behind the protocone. It is lower and smaller than the protocone. Due to the position of the hypocone the posterior side of the M^1 is slightly concave. The slightly protruding parastyle lies directly in front of the paracone. The two cusplets of the mesostyle stand directly adjacent to each other. The anterior arm of the metacone is clearly shorter than the posterior arm. The posterior cingulum is well developed. It runs from the hypocone along the base of the posterior arm of the metacone. There is a weak labial cingulum, which runs along the metacone. There is a short lingual cingulum between the base of the protocone and the hypocone.

M^2 (27) — The other M^2 differ from the holotype mainly in the development of the cingulums. The anterior cingulum reaches the parastyle in 16 out of the 27 specimens; in the other 11 specimens it ends against the anterior flank of the paracone. A continuous posterior cingulum is found in 7 specimens. In the other 20 specimens it ends against the posterior flank of the metacone. The short lingual cingulum between the protocone and the hypocone is present in 14 specimens.

M^3 (34) — The posterior outline of the occlusal surface is nearly half a circle. The large protocone occupies the lingual part of the molar. The anterior arm of the protocone continues as the anterior cingulum and is connected to the parastyle. In 12 out of the 34 specimens the anterior cingulum is interrupted near the base of the paracone. The posterior arm of the protocone is connected to the hypocone. The latter is a small to very small cusplet, which lies lingually of the tip of the metacone. The anterior arm of the paracone is only slightly longer than the posterior arm. It bends slightly at the end to form a small parastyle. The posterior arm is connected to the mesostyle, which is undivided. The posterior part of the mesostyle is connected to the small metacone. The anterior cingulum is the only cingulum present.

Material from other localities — The material of *Theratiskos rutgeri* found in the various other localites is given in Table 2. The morphological differences of these specimens with the material from the type locality are discussed below. In this section the P^3 and the humerus, which have not been found in Harami 1, will be described.

Lower dentition — The metacristid of the M_1 seems more frequently present in the Kilçak localities and Harami 3 than in the type locality, where about 11 % show this feature. This percentage is 33 % for Ki 0″ and Ha 3 (2 out of 6 and 4 out of 12 respectively) and 50% for Kilçak 3 A (1 out of 2).

The oblique cristid reaches the metaconid in 2 of the 6 M_2 from Kilçak 0″ and 2 of the 10 from Harami 3. In the only M_2 from Kilçak 0 the oblique cristid ends just short of the metaconid. Thus the oblique cristid of the M_2 appears to end more lingually

Table 2. Elements and their numbers of *Theratiskos rutgeri* sp. nov. from localities other than the type locality.

loc.	P_4	M_1	M_2	M_3	D^4	P^3	P^4	M^1	M^2	M^3
Harami 3	4	12	10	15	3	—	5	9	14	9
Harami 2	—	—	—	1	—	—	1	—	2	3
Kilçak 3A	—	2	—	1	1	—	—	—	—	1
Kilçak 0″	2	6	6	6	-	1	2	8	10	5
Kilçak 0	—	—	1	1	—	—	—	—	—	—

than in Harami 1, in which the metaconid is reached in less than 10%.

With the exception of the specimen from Kilçak 3A, all of the M_3 from the Kilçak localities have a metacristid. In Harami 3 a metacristid is present in 3 of the 10 specimens only. The M_3 from Harami 2 lacks this feature.

Upper dentition — The P^3 is so small, that it has never been found isolated. Only one P^3 is preserved in a fragment of a maxillary, which also bears the P^4 (Ki 0″ 2839). The P^3 is a two-rooted unicuspid, elliptical in occlusal view, with the tip of the cusp in front of the middle of the premolar. There is a faint posterocrista. The P^3 is surrounded by a narrow cingulum, which is somewhat broader at the back of the premolar.

As in Harami 1, the protoconule of the M^1 is usually present. It is absent in 2 of the 8 specimens from Ki 0″ only. The lingual cingulum is absent in 2 of the 9 M^1 from Harami 3.

The percentage of M^2 with a continuous anterior cingulum in Harami 3 is similar to that of Harami 1 (8 out of 14 versus 16 out of 27, respectively). A continuous anterior cingulum is more common in Kilçak 0″ (9 out of 10) and also found in both M^2 from Harami 2. A continuous posterior cingulum is present in 7 out of 27 M^2 in Harami 1 (25 %). For Kilçak 0″ this percentage is 40 % (4 out of 10), for Harami 3 only 17 % (2 out of 12). The posterior cingulum is continuous in one M^2 from Harami 2. The other M^2 from this locality is damaged, so that this feature cannot be observed. The lingual cingulum is also most common in Kilçak 0″ (8 out of 10). It is present in half the number of M^2 from Harami 1 (14 out of 27) and relatively rare in Harami 3 (3 out of 14). The lingual cingulum is present in both M^2 from Harami 2.

With the exception of one of the five M^3 from Kilçak 0″, the anterior cingulum of the M^3 is continuous in Kilçak 3A, Kilçak 0″ and Harami 2. Of the nine M^3 from Harami 3, three have an interrupted anterior cingulum, which is a percentage comparable to that found in Harami 1, where 12 of the 34 specimens have an interrupted anterior cingulum.

Humerus (Fig. 5) — Three humeri of *Theratiskos* have been found in Harami 3. The humerus is very slender for a talpid. The area around the caput is damaged in all three specimens. The bicipital canal is open throughout. The small teres tubercle lies about halfway the shaft. Its elliptical facet is directed medially. The pectoral proces is a strongly protruding, wedge-shaped area. The pectoral tubercle lies in the centre of the shaft, laterally from the teres tubercle. The entepicondyle is well developed. The elliptical entepicondylar foramen is large. The supratrochlear fossa is very large and deep; the olecranon fossa is shallow.

Discussion — The dental morphology of the two *Theratiskos* species is very close to that of *Myxomygale*. However, the humerus differs considerably from the one associated by Ziegler (1985) with *Palurotrichus* [= *Myxomygale*]. The bicipital canal is open throughout, a feature which is considered characteristic for the Uropsilinae. The association of the humeri with the dentition seems to be certain. Four talpid genera and three types of talpid humeri are present in the various Anatolian assemblages. Two of these, the humeri of *Desmanodon* and *Geotrypus* (van den Hoek Ostende, 1994; this paper) are easily recognized, which leaves *Theratiskos* and *Suleimania* as possible candidates for the third type. Since the humerus is very small and slender, and *Suleima-*

nia is a very large talpid, the humerus is associated with the smaller dental elements of *Theratiskos*. Furthermore, three humeri have been found in the Kesekö̈y assemblage in which *Suleimania* is rare and *Theratiskos* is abundant. The association of dentitions and humeri seems therefore established.

The dentitions of *Myxomygale* and *Theratiskos* are also different. In *Myxomygale* all premolars in front of the P_4 are single-rooted. The P_3 of *Theratiskos* has two roots. Furthermore, the deciduous molars attributed to *Theratiskos* show that the members of the genus had a functional milk dentition, whereas milk molars of *Myxomygale* have not been found. The molar morphology of *Theratiskos* and *Myxomygale* is, however, very similar and isolated elements may easily be confused.

Engesser (1980) described two small M_1 from Sariçay (MN 7/8) as *Desmanodon* sp., which were later transferred to *Myxomygale* sp. (van den Hoek Ostende, 1989). However, the two molars agree morphologically and metrically well with those of *Theratiskos mechteldae*. Therefore the two molars may readily belong to *Theratiskos*. More material is needed to confirm this identification.

What are Uropsilinae?

Campbell (1939) noted in his discussion on the shoulder anatomy of extant Talpidae, that the humerus of *Uropsilus* is very primitive and resembles that of the shrew *Blarina*. *Uropsilus* is the only extant talpid with a humerus in which the walls of the bicipital groove have not fused to form a tunnel. An open bicipital groove is also found in the extinct American subfamily Gaillardinae and in the Proscalopidae. The latter used to be considered as a subfamily of the talpids, but was raised by Barnosky (1981) to family level. The humeri of these two groups are massive and also in other respects totally different from those of the Uropsilinae. The combination of an open bicipital groove and an overall slender humerus is considered typical for the Uropsilinae.

The Uropsilinae is the most primitive subfamily of the Talpidae. Nevertheless few fossil representatives have been recognized. The first extinct genus that has been included in this subfamily is *Mystipterus*. This talpid from the Miocene of North America was originally described as a bat (Hall, 1930) and later transferred to the Soricidae (Patterson & McGrew, 1939). Van Valen (1967) recognized its talpid affinities. Hutchison (1968) placed the genus in the Uropsilinae. In his description of the subfamily Hutchison used the open bicipital groove, but he did not consider it typical for the subfamily. The feature is also found in *Asthenoscaptor* Hutchison, 1974. Hutchison placed *Asthenoscaptor* in his "Group I" of the Desmaninae, together with *Desmanella*. Although the humerus of true desmans is in many respects primitive, the bicipital canal in this subfamily is closed (Campbell, 1939).

On the basis of dental morphology and dental formula Rümke (1974) demonstrated that *Desmanella* is not a desman. Contrary to Desmaninae, *Desmanella* presumably has lost its I_3, while the I_1 is much larger than the I_2. Rümke's arguments for placing the genus in the Uropsilinae were the presence of the anterior and posterior cingulums in the lower molars, the length and position of the oblique cristid (extending to halfway the protoconid-metaconid crest), the concave posterior outline of M^1-M^2 and the presence of a labial cingulum in M^1. Engesser (1980) agreed with Rümke and demonstrated that *Desmanella* had a functional milk dentition, which was used as an extra argument for placing the genus in the Uropsilinae (within the Talpidae functional milk dentitions are known in the Uropsilinae and the Urotrichini only). Engesser had a somewhat different interpretation of the tooth reduction in *Desmanella* than Rümke. He assumed that the missing incisor is the I_1 instead of the I_3. Engesser and Rümke did not know the humerus of *Desmanella*. The first complete humeri described by Ziegler (1985) show that the bicipital groove is open.

Whereas *Desmanella* is now generally recognized as an uropsiline, *Asthenoscaptor* is still considered a desmanine (Ziegler, 1990a). This is quite surprising, since *Asthenoscaptor* and *Desmanella* are very much alike in molar morphology (Rümke, 1976; Engesser, 1980). The most conspicuous similarity is the strongly concave posterior outline of the M^1 and M^2, a condition they share with *Uropsilus*. *Asthenoscaptor* is placed here in the Uropsilinae on the basis of this character and the morphology of the humerus.

An open bicipital groove is also found in *Mygatalpa*. This Late Oligocene/Early Miocene genus is generally considered a desmanine (Hugueney, 1972; Hutchison, 1974; Ziegler, 1990a), but was excluded from this subfamily by Rümke (1985). The genus is here included in the Uropsilinae on the basis of its slender humerus with an open bicipital groove and on the basis of the dental morphology. Comparison of the dentition of *Mygatalpa* with that of *Mystipterus*, *Desmanella*, and *Asthenoscaptor* shows that a number of characters are shared. All are small talpids with brachyodont dentitions and well-developed protoconules. All these genera have a P^4 with a conical protocone and a concave posterior outline of the M^1 and M^2. This latter feature is certainly not as conspicuous in *Mygatalpa* as in the others.

In some aspects *Theratiskos* is not characteristic for the Uropsilinae. The posterior outline of the M^2 of *T. rutgeri* and some of the M^1 of *T. mechteldae* is not concave and the protoconule of the M^1 and M^2 is, particularly in *T. mechteldae*, poorly developed and may disappear with wear. However, a place within the Uropsilinae is suggested by the open bicipital groove of its humerus, and supported by the presence of functional decidious molars.

The classification suggested changes the stratigraphical and geographical distribution of the Uropsilinae considerably. Until now, only one genus had been recognized from the Miocene of Europe (*Desmanella*), one from the Miocene of America (*Mystipterus*) and an extant form from Asia (*Uropsilus*). The description of *Theratiskos* and the allocation of *Asthenoscaptor* and *Mygatalpa* to the Uropsilinae, show that this primitive subfamily was quite diverse in Late Oligocene to Early Miocene times.

Subfamily Talpinae Fisher von Waldheim, 1817
Tribus Talpini Fisher von Waldheim, 1817
Geotrypus Pomel, 1848

Review of the literature on Geotrypus. — *Geotrypus* is one of the most diverse fossil talpid genera. Including the Anatolian species described below we recognize eight named species and four hitherto unnamed forms. In most localities where the genus has been found, it is represented by a few specimens only. This accounts for the large number of unnamed species. In the recent literature (e. g. Hugueney, 1972; van den

Hoek Ostende, 1989; Ziegler, 1990a, 1994, 1998) material was often considered too limited to describe a new species, even though the material could not be attributed to any of the known species. Since this cautious attitude is not found in the older literature, some of the unnamed forms are better defined than some of the named species.

Geotrypus was already noted 150 years ago, presumably as a result of its large size and its robust humerus. It was defined by Pomel (1848), who combined a mandible from Cournon and a humerus from Chaffours (both Upper Oligocene, France), which had been illustrated by de Blainville (1840) under the names *Talpa acutidentata* and *T. antiqua*, respectively. Pomel named this species *Geotrypus antiquus*. Ziegler (1990a) referred to this species as *G. antiquus* (Pomel, 1848). However, since Pomel based is description on the illustrations of de Blainville, the species name should be attributed to the latter author. Although *G. antiquus* sensu Pomel is based on the association of a humerus and a mandible that originate from different localities, the association of the two remained unchallenged for a long time. Crochet (1995) suggested that the mandible and the humerus represent two diffent species, which should be named *G. acutidentatus* and *G. antiquus* respectively. Here we follow Crochet's classification. However, for the review of literature it is important to realise that up to 1995 *G. acutidentatus* was considered a synonym of *G. antiquus*.

During the second half of the 19th century more *Geotrypus* material was found, but placed in other genera. In 1877 Filhol described *Protalpa cadurcensis* from the Quercy. This species was synonymized with *G. antiquus* by Lavocat (1951). Crochet (1974) and Brunet et al. (1981) listed *Geotrypus cadurcensis* as a separate species, without however describing this form or indicating any differences with *G. antiquus*. Crochet (1995) synonimized *P. cadurcensis* pro partim with *G. antiquus* and pro partim with *G. acutidentatus*.

Another species of *Geotrypus* initially assigned to *Talpa* is *G. tomerdingensis* (Tobien, 1939). The species is known from postcranial material only. Its type is a very large humerus from the German locality Tomerdingen (MN 1). Hugueney (1972) first recognized its true generic affinity. Ziegler (1990a) described various *Geotrypus* species from southern Germany, but did not find any dental elements referable to *G. tomerdingensis*. He included a fragment of a large ulna and a radius from the type locality in the species. There can be little doubt that *G. tomerdingensis* is a good species, since the bones found are huge in comparison to other species of the genus. However, the absence of molars makes it very difficult to compare *G. tomerdingensis* with other species.

In his thesis on the mammals from the French Upper Oligocene locality Cournon Lavocat (1951) recognized three different species of *Geotrypus*, *G. antiquus*, *G. jungi* and *G. arambourgi*, all of which were based on scarce material. *G. antiquus* de Blainville, 1840 was only represented by the type. *G. jungi* Lavocat, 1951 was described on the basis of a mandible and part of a maxillary in matrix. *G. arambourgi* Lavocat, 1951 was based on a crushed skull, in which the two M^1 and one of the P^4 were preserved. Although two different species of *Geotrypus* may occur in the same locality (e. g. *G.* cf. *jungi* and *Geotrypus* sp. in Codoret; *G. tomerdingensis* and *G.* aff. *montiasini* in Tomerdingen), the presence of three large talpids belonging to one genus in a single locality seems unlikely. Hugueney and Guerin (1981) suggested that only two species of *Geotrypus* are present in Cournon. This was confirmed by Crochet

(1995), who, on the basis of a comparison with *G. antiquus* assemblages from localities in the Quercy concluded that *G. arambourgi* should be considered a junior synonym of *G. antiquus*.

In 1972 Hugueney described the talpids from Coderet (France, MP 30). She found two species of *Geotrypus*. She classified the smaller one as *G.* cf. *jungi*, indicating that the type of the species was 'de taille un peu plus faible'. However, comparison of the measurements given by Hugueney and Lavocat shows that the type falls completely in the variation of the Coderet material. This material could therefore just as well be classified as *G. jungi*. Crochet (1995) considered *G. jungi* a junior synonym of *G. acutidentatus*. The larger species from Coderet, classified as *Geotrypus* sp. by Hugueney, was represented by two M^2, a P^4 and a mandible bearing P_2-P_4 only. Crochet (1995) included this form in *G. antiquus*.

Rümke (1974) described *Geotrypus oschiriensis* from the fauna of Oschiri on Sardinia, which was interpreted as an Early Miocene island fauna (de Bruijn & Rümke, 1974). This species is peculiar in having a very short and wide M^2. According to Crochet (1995) the assemblage from Oschiri is not referable to *Geotrypus*. For the moment we include *oschiriensis* in this genus, although it is indeed an aberrant form.

Geotrypus sp. from Eggingen-Mittelhart (van den Hoek Ostende, 1989) is a very large species. At the time of its description, only four molars were known. These were considered insufficient to describe a new species. Ziegler (1990a) described an additional M^2, but he too considered the material available insufficient to define a species. He noted that the species from Eggingen-Mittelhart is certainly not conspecific with the, also very large, *Geotrypus* sp. from Coderet. The German species has an M^2 which is longer than wide, whereas the M^2 of *Geotrypus* sp. from Coderet is clearly wider than long.

Two of the best-known *Geotrypus* species to date were described by Ziegler (1990a). *G. ehrensteinensis* from the Upper Oligocene fissure filling Ehrenstein 4 is represented by 2 mandibles, 2 maxillaries and 10 isolated elements. The holotype of *G. montiasini* from the Lower Miocene locality Ulm-Westtangente is a partial skeleton in matrix. Apart from the type several humeri and a mandible have been found.

Ziegler (1994) noted in his paper on the insectivore fauna of Wintershof-West, that this locality also contains a species of *Geotrypus*. Although this small form differs from all other species in the genus, Ziegler considered the material insufficient to describe it as a new species. In his paper he noted that the material from Petersbuch 2 and Erkertshofen 1 and 2, which he had earlier described as "*Talpa*" sp. 1 (Ziegler, 1985), is also referable to *Geotrypus*. *Geotrypus* sp. from Stubersheim 3 (Ziegler, 1990a) was considered to belong to the same species. This form is probably closely related to the *Geotrypus* from Wintershof-West.

Crochet (1995) discussed the Oligocene *Geotrypus* finds from France. He concluded that *G. antiquus* and *G. acutidentatus* are two valid species. This conclusion is based on a partial skeleton from Le Garouillas (France, MP 25) which shows that the humerus from Chauffours (type of *Talpa antiqua*) is too large to be associated with the mandible from Cournon (type of *T. acutidentata*). Apart from their sizes, the two species differ according to Crochet in the absence of a lower incisor in *G. acutidentatus*. This reduction in the dental formula is based on the type mandible of *G. jungi*. However, from the description of Lavocat (1951) it is not clear whether the incisor was absent or only missing in the fossil. Crochet gave extensive diagnoses for the genus and for the species *G. antiquus* and *G. acutidentatus*. Unfortunately, he did not give any descriptions, on which his conclusions and diagnoses are based, announcing that he intends to do so in a separate review.

Ziegler (1998) described *Geotrypus* sp. from the fissure fillings from Herrlingen 8 (MP 28) and Herrlingen 9 (MP 29). He considered the material too scarce to classify it with certainty as any known or new species. Below the species assigned to *Geotrypus* in this paper are listed.

Geotrypus acutidentatus (de Blainville, 1840)
Geotrypus antiquus (de Blainville, 1840)
Geotrypus ehrensteinensis Ziegler, 1990
Geotrypus haramiensis sp. nov.
Geotrypus montinasini Ziegler, 1990
Geotrypus oschiriensis Rümke, 1974
Geotrypus kesekoeyensis sp. nov.
Geotrypus tomerdingensis (Tobien, 1939)
Geotrypus sp. from Eggingen-Mittelhart (van den Hoek Ostende, 1989)
Geotrypus sp. from Stubersheim 3 (Ziegler, 1990)
Geotrypus sp. from Wintershof-West (Ziegler, 1994)
Geotrypus sp. from Herrlingen 8 and 9 (Ziegler, 1998)

Van Valen (1967) included *Geotrypus* in the Scaptonychini. This tribe, intended to hold the primitive Talpinae and their relatively unmodified descendants, forms an unnatural group, containing genera that have since been included in the Urotrichini (*Myxomygale*) and the Uropsilinae (*Mygatalpa*). Ziegler (1990a) already indicated that *Geotrypus* also should not be included in the Scaptonychini. Because of its strongly developed humeri, *Geotrypus* is by no means a primitive talpid. On the basis of the humeri, which indicate a fossorial mode of live, Ziegler included the genus in the Talpini. This is corroborated by the caniniform P_1, a feature only found in the Talpini and in the enigmatic genus *Scaptonyx*.

The youngest record of *Geotrypus* is from Petersbuch 2 and Erkertshofen 1 and 2 (MN 4). The only fossil Talpini known from younger localities is *Talpa*, a genus which appears for the first time in MN 2 (Ulm-Westtangente). In the timespan that *Geotrypus* and *Talpa* coexisted, the two can be found in the same localities (Ulm-Westtangente, Wintershof-West). In localities older than MN 2, a larger and a smaller species of *Geotrypus* often co-occur (Cournon, Coderet, Tomerdingen). Apparently *Talpa* slowly replaced *Geotrypus*, first taking over the niche of the smaller Talpini. In younger localities, *Talpa* also fills the niche of the large Talpini. In Pliocene and Pleistocene localities it is quite common to find two species of *Talpa*.

The Anatolian species of Geotrypus

Geotrypus haramiensis sp. nov.
Pl. 2, figs. 1-7.

Derivatio nominis — This species is named after its type locality.

Diagnosis — *Geotrypus haramiensis* is a large species of *Geotrypus* (M^2 = 2.36). The lower dental formula is ?.?.3.3. The P_2 is missing. The mesostyle of the upper molars is slightly divided. The M^2 has no hypocone. Its labial side is straight. The L/W ratio of the M^2 is c. 0.85.

Differential diagnosis — *Geotrypus haramiensis* is smaller than *G. tomerdingensis* and *Geotrypus* sp. from Eggingen-Mittelhart. It is larger than *G. acutidentatus*, *G. oschiriensis*, *Geotrypus* sp. from Wintershof-West, and *Geotrypus* sp. from Erkertshofen. It is comparable in size to *G. antiquus*, *G. montiasini* and *G. ehrensteinensis*.

The absence of the P_2 distinguishes *Geotrypus haramiensis* from *G. ehrensteinensis*, *G. oschiriensis*, *G. acutidentatus* and *G. antiquus*. *G. montiasini* also lacks the P_2; the dental formula of the other *Geotrypus* species is not known.

The slight division of the mesostyle of the M^2 and M^3 distinguishes *G. haramiensis* from *G. ehrensteinensis*, *G. acutidentatus*, *Geotrypus* sp. from Eggingen-Mittelhart, and *Geotrypus* sp. from Wintershof-West. The labial side of the latter is concave, a feature it shares with *Geotrypus* sp. from Stubersheim 3. The labial side of the M^2 of *G. haramiensis* is straight. The M^2 of *G. haramiensis* is relatively wider than that of *Geotrypus* sp. from Eggingen-Mittelhart, *G. montiasini* and *G. ehrensteinensis*, and relatively narrower than the M^2 of *G. oschiriensis*.

G. haramiensis differs from *G. montiasini* in the better developed anterior cingulum of the M_2. The M_2 of *G. oschiriensis* has no anterior cingulum and, in contrast to *G. haramiensis*, the talonid is wider than the trigonid.

Type locality — Harami 3 (MN 1).

Other localities with G. haramiensis *sp. nov.* — Kilçak 3A, Harami 1.

Holotype — Part of a mandible with P_1, P_3-M_3 (Ha 3 781; Pl. 2, fig. 1).

Description of the holotype — The ramus horizontalis and the lower part of the processus coronoides are preserved only. The processus coronoides appears to have been narrow. The ramus horizontalis is slender and has three foramina on the labial side, one below the P_3, one below the M_1 and one just in front of and below the external temporal fossa of the processus coronoides.

The mandible bears six teeth. The M_1 and M_3 are damaged. The trigonid of the M_1 and the talonid of the M_3 are broken. The M_2 is well preserved. The P_3 and P_4 are set obliquely in the jaw. The large, caniniform element in front of the P_3 is considered to be the P_1. This premolar has two roots and a high, peak-like cusp that curves backwards. The P_3 is clearly smaller than the P_4, but these two premolars have a very similar morphology. The main cusp is high. Its tip lies in front of the middle of the occlusal surface. Both P_3 and P_4 have a posterior flattening, which bears a cusplet. The P_4 also has a small anterior flattening.

The cusps of the lower molars are high and pointed. The M_1 has a well-developed entostylid. The talonid of the M_2 is somewhat shorter and narrower than the trigonid. The oblique cristid runs in the direction of the metaconid and ends at about two-thirds of the protoconid-metaconid crest. There is neither a metacristid, nor an entocristid. The M_2 has a well-developed entostylid and a strong parastylid, which continues labially as the anterior cingulum. The M_3 has a similarly strong parastylid.

Measurements — The measurements are listed in Table 3.

Table 3. Measurements of *Geotrypus* (Keseköy = *G. kesekoeyensis* sp. nov.; Harami 1 and 3 = *G. haramiensis* sp. nov.).

tooth	loc.	N	Length range	mean	Width range	mean	tooth	loc.	N	Length range	mean	Width range	mean
P_1	Ha3	1		1.44		0.98							
P_4	Ke	—					P^4	Ke	1		1.49		1.36
	Ha3	2	1.57-1.59	1.58	0.82-0.83	0.83		Ha3	—				
	Ha1	—						Ha1	—				
M_1	Ke	—					M^1	Ke	1		3.55		2.38
	Ha3	—						Ha3	—				
	Ha1	—						Ha1	—				
M_2	Ke	1		2.66		1.59	M^2	Ke	2	2.62-2.64	2.63	3.00-3.09	3.05
	Ha3	1		2.47		1.48		Ha3	1		2.36		2.74
	Ha1	—						Ha1	1		2.42		2.81
M_3	Ke	—					M^3	Ke	1		1.67		2.65
	Ha3	—						Ha3	1		1.43		2.20
	Ha1	—						Ha1	1		1.38		2.08

Description

M^2 (1) — The outline of the occlusal surface is triangular. The cusps are high and pointed. The protocone is large. Its anterior arm ends against the base of the paracone, the posterior arm ends against the base of the metacone. There is neither a protoconule nor a hypocone. The labial cusps are higher than the protocone. The anterior arm of the paracone bends and forms a protruding parastyle. The posterior arm is connected to the mesostyle, which is undivided. The posterior arm of the metacone is slightly longer than the anterior arm. There is no metastyle and there are no cingulums.

M^3 (1) — The outline of the occlusal surface is subtriangular. The paracone is the highest cusp. Its anterior arm is slightly longer than its posterior arm. The anterior arm bends at its end to form a very weak parastyle. The posterior arm is connected to the mesostyle, which is indistinctly divided. The metacone and protocone are of the same height. The metacone has an S-shaped anterior arm, which is connected to the mesostyle. The anterior arm of the protocone ends against the base of the paracone. The protocone does not have a posterior arm. There are no cingulums.

Humerus (3) — The humerus is very robust, indicating a fossorial mode of life. In all three specimens the proximal side is damaged. The greater tuberosity, lesser tuberosity and pectoral crest have not been preserved. The pectoral process is pronounced. The pectoral ridge is well defined. It reaches to about one third of the width of the bone and it is only slightly inclined towards the side of the tuberculum teres. The pectoral tubercle is large and protruding. The supratrochlear fossa and olecranon fossa are large and deep.

Geotrypus haramiensis *from other localities*

In Harami 1 *Geotrypus haramiensis* is represented by one M^2, one M^3, and a fragment of a humerus only. The molars show only minor differences with the corresponding elements from the type locality. The two arms of the paracone of the M^3 are, in contrast to the situation in the specimen from Harami 3, of about the same length. In Kilçak 3A only two damaged humeri of this species have been found. One of these is somewhat more complete than the best preserved specimen from Harami 3, the other is only a small fragment. The tuberculum teres is long. The bicipital groove is rather wide. The pectoral ridge reaches to halfway the width of the humerus. The pectoral process is less pronounced and the supratrochlear fossa and olecranon fossa are smaller than in the specimens from the type locality.

Geotrypus kesekoeyensis sp. nov.
Pl. 3, figs. 1-6.

Derivatio nominis — The species is named after its type locality Keseköy.

Diagnosis — Very large species of *Geotrypus* (M^2 = 2. 63). The P^4 is relatively short and has a large protoconal flange. The mesostyle of the upper molars is undivided. A very small hypocone may be present on the M^1 and M^2.

Differential diagnosis — *Geotrypus kesekoeyensis* is larger than all other species of *Geotrypus*, with the possible exception of *G. tomerdingensis*. Since the latter is known by its humerus only, and since the humerus of *G. kesekoeyensis* is not known, the two species cannot be compared.

Apart from its size *G. kesekoeyensis* differs from other species of *Geotrypus* in having a relatively short P^4 (the P^4 of *G. tomerdingensis*, *G. antiquus*, *G. haramiensis*, *Geotrypus* sp. from Wintershof-West, and *Geotrypus* sp. from Eggingen-Mitelhart are not known). The undivided mesostyle of the upper molars distinguishes *G. kesekoeyensis* from *G. ehrensteinensis*, *G. acutidentatus*, *Geotrypus* sp. from Eggingen-Mittelhart, and *Geotrypus* sp. from Wintershof-West.

Type locality — Keseköy (MN 3).

Holotype — M^2 sin. (Ke 6712) (2.64 × 3.09; Pl. 3, fig. 5).

Description of the holotype — The outline of the occlusal surface is subtriangular. The postero-lingual side is concave. The protocone is small. Its very short anterior arm ends against the base of the paracone. The posterior side of the protocone bears a very faint ridge. This ridge ends against the tiny hypocone, which lies lingually of the base of the metacone and is separated from that cusp by a clear trench. The paracone is broken. Its base extends far towards the lingual side. The anterior arm of the paracone bends at its end and forms a small, protruding parastyle. The posterior arm is connected to the undivided mesostyle. The two arms of the metacone are of the same length. The posterior arm bends at its end and forms a slightly protruding metastyle. There are no cingulums.

Measurements — The measurements are listed in Table 3.

Description

M_1 (1) — The only available specimen is damaged. The area of the paraconid is broken. The outline of the occlusal surface is subrectangular. The cusps are high and pointed. The posterior arm of the protoconid slopes downward and is connected to the metaconid. The talonid is long and wider than the trigonid. The hypoconid is somewhat higher than the entoconid. The long oblique cristid ends against the middle of the protoconid-metaconid crest. There is neither a metacristid nor an entocristid. The entostylid is well developed. There are no cingulums.

M_2 (1) — The outline of the occlusal surface is subrectangular. Even though the specimen is worn, the cusps are very high. The anterior and posterior arms of the protoconid are connected to the paraconid and metaconid, respectively. The two arms are straight and run parallel to each other. There is a notch in the protoconid-metaconid crest at about two-thirds of its length. The talonid is somewhat narrower than the trigonid. The talonid and the trigonid are of about the same length. The cusps of the talonid are clearly lower than those of the trigonid. The oblique cristid is connected to the protoconid-metaconid crest below the notch. There is neither a metacristid nor an entocristid. The parastylid and the entostylid are well developed. There is a short anterior cingulum that runs from the parastylid to halfway the anterior side of the molar.

P^4 (1) — This specimen is preserved in a piece of the maxillary, which also contains the anterior alveoles of the M^1. The outline of the occlusal surface is triangular. The P^4 consists mainly of the very high and very large paracone. The tip of the cusp lies in the middle of the premolar. The anterior face of the paracone is rounded. The sharp posterocrista is slightly curved and runs to the postero-labial corner of the P^4. There is a large lingual shelf that bears a tiny protocone. A small parastyle lies in front of the paracone. The postero-lingual cingulum is the only cingulum. It is wide at its posterior end and becomes narrow near the lingual shelf.

M^1 (1) — The outline of the occlusal surface is triangular. The cusps are high and pointed. The only preserved specimen is unworn. The anterior and posterior arms of the protocone form a straight line. The anterior arm is short and ends close to the base of the paracone. The posterior arm is longer and ends lingually of the base of the metacone leaving a large trench between the protocone and the metacone. There is a very small elevation (hypocone?) near the end of the posterior arm of the protocone. This elevation may be expected to disappear with wear. The paracone is somewhat lower than the metacone. Directly in front of the paracone lies a very well-developed parastyle. The mesostyle is undivided. The posterior arm of the metacone is only somewhat longer than the anterior arm. The posterior arm of the metacone bends at its end and forms a small metastyle. The only cingulum is the very narrow posterior cingulum that runs from the metastyle to halfway the posterior flank of the metacone.

M^2 (2) — In addition to the holotype there is a second M^2. The ridge on the posterior side of the protocone is even more faint and does not connect to the hypocone. The latter cusp is somewhat better developed than in the holotype.

M^3 (2) — The outline of the occlusal surface is triangular. The protocone is small. Its short anterior arm ends against the base of the paracone. The posterior arm is long. It runs along the postero-lingual side of the M^3 and ends against the base of the metacone. The paracone is the largest cusp. Its anterior arm is clearly longer than its posterior arm. The latter connects to the mesostyle, which is undivided. The molar has no cingulums.

Remarks — The two Anatolian species of *Geotrypus* seem to represent one evolutionary lineage; the main difference between *G. haramiensis* and *G. kesekoeyensis* is the larger size of the latter. Unfortunately, the comparison between the two is limited to three elements (M_2, M^2 and M^3). We do not know whether *G. haramiensis* possesed a short P^4, which is typical for *G. kesekoeyensis*, neither do we know whether *G. kesekoeyensis* had three lower premolars like *G. haramiensis*. Little can be said about the relationships between the Anatolian and European representatives of the genus, since the material available of most species is very limited.

Suleimaninae subfam. nov.

The Lower Miocene localities of Anatolia have yielded a dimylid-like talpid, which is so unlike any other fossil or Recent form, that a new subfamily has been established. Since this subfamily contains as yet one genus only, the diagnosis and differential diagnosis for the subfamily are the same as for the type genus.

Suleimania gen. nov.

Derivatio nominis — The genus is named after Suleiman the Magnificent, Sultan of the Ottoman Empire between 1520 and 1566.

Type species — *Suleimania ruemkae* gen. nov. et sp. nov.

Diagnosis — *Suleimania* is a large-sized talpid. The M^3 is missing and the M_3 is small, lacking the talonid. The premolars have sharp cutting edges. The mesostyle of the M^1 and M^2 is strongly divided. The hypocone of the M^1 is very well developed. The cusps of the M^1 and M_1 are slightly inflated.

Differential diagnosis — *Suleimania* differs from all other Talpidae in the loss of the M^3 and in the degree of reduction of the M_3. It differs from all Dimylidae in having sharp premolars and lower molars. In contrast to the Dimylidae, the oblique cristid of the lower molars ends halfway the protoconid-metaconid crest. The development of the hypocone is strong for a talpid, but considerably less than found in the Dimylidae.

Stratigraphic and geographic distribution — Lower Miocene (MN 1- MN 3) of Anatolia.

Suleimania ruemkae gen. nov. et sp. nov.
Pl. 3, figs. 7-10; Pl. 4, figs. 1-8; Pl. 5, figs. 1-10.

Derivatio nominis — The species is named after Dr C. G. Rümke, who introduced the author to the study of fossil insectivores.

Diagnosis — See diagnosis of the genus.

Type locality — Harami 3 (MN 1).

Other localities with Suleimania ruemkae — Kilçak 0, Kilçak 0", Kilçak 3A, Kilçak 3B, Harami 1, Harami 2, Keseköy.

Holotype — M^1 dext. (Ha 3 769) (3.83 × 2.25; Pl. 5. fig. 10).

Description of the holotype — The outline of the occlusal surface is irregularly quadrangular, the labial side being much longer than the lingual side. The protocone is very large. Its anterior arm connects to the parastyle. The posterior arm of the protocone runs along the lingual side of the molar and connects to the hypocone. The protoconule is a mere thickening in the anterior arm of the protocone. The hypocone is a well-developed, crescent-shaped cusp. The anterior arm of the hypocone ends against the base of the metacone; the posterior arm ends against the posterior flank of the metacone. The paracone is of the same height as the protocone. Its posterior arm curves to the mesostyle. The parastyle is a small but distinct cusp directly in front of the paracone. The metacone is the largest and highest cusp of the M^1. Its anterior and posterior arms are straight. The posterior arm is somewhat longer than the anterior arm. The anterior arm connects to the mesostyle, the posterior arm extends to the postero-labial corner of the tooth. The two cusps of the mesostyle are clearly separated. The trigon basin is very deep. There are no cingulums. The tooth has three stout, flat roots, one under each of the main cusps.

Measurements — The measurements are listed in Table 4.

Description

Premolars — The premolars of *Suleimania* are easily recognizable due to their large size. Unfortunately, practically no jaw fragments have been found with the anterior dentition in place, so that we do not know the position of the various premolars in the dentition. Therefore, the various types of premolars are indicated by a roman number except for the P_4 and P^4, which can readily be recognized on basis of their size. The only mandible fragment with a premolar in place is a piece of mandible carrying a Type I premolar. The fragment is broken directly in front of the premolar. There are three alveoli in this vertical section. These alveoli run lengthwise into the mandible and presumably belong to the foremost elements. Directly behind the premolar there is a large alveolus. Between the two roots of the premolar there is a very large foramen mentale which lies in a gutter-like depression in the mandible.

Two groups of premolars can be distinguished. The first group has the tip of the main cusp in front of the middle of the tooth. These premolars have a straight lingual side and a convex labial side. The second group has the tip of the main cusp in or just in front of the centre and the premolars are more or less elliptical in occlusal view. Premolars of the first group (Type I, II, IV, VI) are considered to represent the lower dentition and the largest of these is considered to be the P_4. This implies that we have five premolariform elements in the lower jaw, suggesting that one of the elements is in fact the canine. Premolars with a more central position of the tip (Type III, V, VII) are believed to be the upper premolars. The P^4 is easily recognizable due to its very large size. The somewhat enigmatic Type VIII antemolars, which have been found in Keseköy only, may represent the upper canine.

Type I (Pl. 4, fig. 1) (9). The outline of the occlusal surface is subelliptical. The premolar is much longer than wide. There is only one cusp. Its tip lies far to the front of the tooth. The centrocristid runs in the middle of the premolar over the tip of the cusp. The lingual flank of the cusp is straight; the labial side is slightly convex. The cingulum is well developed at the lingual and labial sides. At the front and at the back of the premolar, where the centrocristid reaches the side, the cingulum is interrupted. The premolar has two long, slender roots that are of about the same length and thickness.

Type II (Pl. 3, fig. 9) (1). The outline of the occlusal surface is subelliptical. The

Table 4. Measurements of *Suleimania ruemkae* gen. et sp. nov.

			Length		Width					Length		Width	
tooth	loc.	N	range	mean	range	mean	tooth	loc.	N	range	mean	range	mean
D_4	Ha1	2	2.00-2.10	2.05	0.92-0.94	0.93	D^4	Ke		—			
	Ki3A	2	1.80-1.99	1.90	0.86-1.00	0.93		Ha3	4	2.35-2.63	2.46	1.28-1.42	1.33
	Ki3B	1		1.87		0.93		Ha1	2	2.52-2.55	2.54	1.30-1.31	1.31
	Ki0″	7	1.76-1.87	1.82	0.83-1.05	0.92		Ki3A	—				
								Ki0″	4	2.21-2.52	2.32	1.18-1.30	1.24
								Ki0	—				
P_4	Ke	2	2.13-2.20	2.17	1.05-1.06	1.06	P^4	Ke	3	2.68-2.68	2.68	1.48-1.50	1.49
	Ha3	13	1.99-2.33	2.18	0.90-1.08	0.97		Ha3	9	2.41-2.87	2.70	1.38-1.65	1.52
	Ha1	12	1.96-2.17	2.04	0.83-0.98	0.92		Ha1	19	2.54-3.00	2.70	1.31-1.74	1.46
	Ki3A	2	2.08-2.16	2.12	0.87-0.91	0.89		Ki3A	2	2.47-2.65	2.56	1.34-1.52	1.43
	Ki0″	7	1.80-2.11	1.97	0.80-0.91	0.85		Ki0″	11	2.43-2.67	2.56	1.29-1.53	1.43
	Ki0	2	2.13-2.18	2.16	0.92-1.04	0.98		Ki0	7	2.56-2.97	2.79	1.46-1.69	1.54
M_1	Ke	1		2.80		1.77	M^1	Ke	2	3.83-3.85	3.84	2.09-2.13	2.11
	Ha3	12	2.85-3.19	3.03	1.76-1.98	1.90		Ha3	5	3.76-4.09	3.94	2.15-2.25	2.22
	Ha2	1		2.83		1.39		Ha1	7	3.60-4.07	3.89	2.64-2.83	2.75
	Ha1	8	2.73-3.01	2.84	1.76-1.96	1.83		Ki3A	—				
	Ki3A	1		3.06		1.82		Ki0″	3	3.66-3.72	3.68	2.02-2.06	2.04
	Ki3B	1		3.08		1.80		Ki0	—				
	Ki0″	6	2.63-3.05	2.76	1.58-1.80	1.67							
	Ki0	2	2.85-2.87	2.86	1.77-1.84	1.81							
M_2	Ke	—					M^2	Ke	—				
	Ha3	6	2.71-2.86	2.78	1.38-1.51	1.43		Ha3	9	2.13-2.32	2.25	2.62-2.87	2.74
	Ha1	6	2.63-2.86	2.76	1.49-1.62	1.39		Ha1	8	1.91-2.31	2.07	2.35-2.83	2.65
	Ki3A	—						Ki3A	—				
	Ki0″	7	2.46-2.72	2.59	1.22-1.45	1.35		Ki0″	9	1.65-2.26	1.99	2.24-2.70	2.48
	Ki0	3	2.68-2.92	2.84	1.34-1.46	1.38		Ki0	2	2.14-2.30	2.22	2.62-2.89	2.76
M_3	Ke		—										
	Ha3	8	1.21-1.30	1.27	0.66-0.79	0.73							
	Ha1	7	1.26-1.69	1.38	0.77-0.93	0.85							
	Ki3A	4	1.26-1.52	1.35	0.71-0.85	0.79							
	Ki0″	10	1.11-1.29	1.19	0.63-0.81	0.72							
	Ki0	1		1.07		0.72							

premolar is very narrow. It consists mainly of one large, blade-like cusp. The tip of this cusp lies just in front of the middle of the premolar. The labial side is convex; the lingual side is straight. There is a small cusplet directly in front of the main cusp and a second directly behind it. The sharp centrocristid runs over the tips of the three cusps. The premolar stands on two plank-shaped roots. The posterior root is somewhat thicker than the anterior one.

Type III (Pl. 4, fig. 4) (6). The outline of the occlusal surface is elliptical. The premolar consists mainly of a large blade-like cusp, with a small cusplet directly in front of it. The tip of the main cusp lies just in front of the middle of the premolar. The labial and lingual flanks are slightly convex. The posterocrista is sharp. It slopes down from the tip of the main cusp and ends horizontally. In unworn specimens the anterior side of the main cusp is rounded. In worn specimens there is a sharp anterocrista. The labial cingulum is weak. Two out of the six specimens have also a weak lingual cingulum. The type III premolar has two flat roots, which stand far apart.

Type IV (Pl. 3, fig. 8) (1). The outline of the occlusal surface is subelliptical. The premolar is somewhat longer than wide. There is one cusp, the tip of which lies in front of the middle of the premolar. The centrocristid runs over the tip. The labial flank is convex, the lingual flank is straight. The premolar is surrounded by a cingulum that is only interrupted at the front of the tooth. The cingulum is irregular, well developed in some places, but nearly absent in others. There are two roots that are elliptical in cross section. The posterior root is clearly thicker than the anterior one.

Type V (Pl. 3, fig. 10) (2). The outline of the occlusal surface is elliptical. The premolar has one cusp, the tip of which lies just in front of the middle of the tooth. The lingual and labial sides are convex. There is a very weak posterocrista at the back of the premolar. The posterocrista is not connected to the tip of the cusp. The anterior cingulum is very well developed. The premolar has two stout roots. The posterior root is thicker than the anterior one.

D_4 (1) — The outline of the occlusal surface is subelliptical. The milkmolar is arrow-shaped in labial view, with a posterior side that is clearly lower than the anterior side. The tip of the main cusp lies in front of the middle of the milkmolar. A sharp centrocristid runs over this tip. The centrocristid is forked near its posterior end. One of these ridges ends in the postero-lingual corner, the other one in the postero-labial corner of the D_4. The labial side is convex. A short second ridge runs from the tip of the protoconid backwards and ends near the lingual side of the tooth. The lingual flank of the main cusp is straight in front of this ridge and concave between the transverse ridge and the centrocristid. The lingual cingulum is weak along the straight flank, but well developed along the concave part. The antero-labial cingulum is well developed. The posterolabial cingulum is weak.

P_4 (13) — The outline of the occlusal surface is subelliptical. The tooth is much longer than wide. The protoconid is the only cusp. Its tip lies in front of the middle of the P_4. The sharp centrocristid runs just lingually of the axis, giving the premolar a blade-like appearance. Just in front of and behind the tip of the protoconid there are thickenings in the centrocristid. In unworn specimens these thickenings appear as small cusplets. There is a weak lingual cingulum. The premolar has two strong roots.

M_1 (12) — The outline of the occlusal surface is subtriangular. The trigonid is considerably narrower and somewhat shorter than the talonid. The protoconid is the highest cusp. It is connected to the metaconid and paraconid by notched ridges. The metaconid is somewhat lower than the protoconid; the paraconid is lower than the metaconid. The very small parastylid lies in front of the paraconid. The cusps of the talonid are of the same height as the metaconid. The hypoconid is very large. The oblique cristid ends close to the protoconid, at about one-thirds of the protoconid-metaconid crest. The entocristid is well developed. The talonid basin is bordered by a small and low metacristid. The entocristid and metacristid are not connected. Directly behind the entoconid lies a small entostylid. A weak labial cingulum borders the re-entrant valley. In 5 out of the 12 specimens there is a weak anterior cingulum. There are no other cingulums. The molar has two strong roots with a triangular cross-section.

M_2 (6) — The outline of the occlusal surface is subrectangular. The trigonid is somewhat shorter and wider than the talonid. The protoconid is very high. The two arms of the protoconid are sharp. The low parastylid lies directly in front of the paraconid. It lies on an anterior cingulum, which is broad on the lingual side and narrows labially. The cusps of the talonid are lower than the metaconid. The oblique cristid ends lingually of the middle of the protoconid-metaconid crest. The entocristid is well developed; the metacristid is very small. The entostylid is well developed in 1 out of the 6 specimens. In the others it is small to very small. The molar has two strong roots with a triangular cross-section.

M_3 (8) — The M_3 is very small. The outline of the occlusal surface is subelliptical. The molar consists of the trigonid only. The highest cusp is the protoconid. It is connected to the paraconid and to the metaconid by sharp ridges. The posterior arm of the protoconid is shorter than its anterior arm. The metaconid is lower than the paraconid. The M_3 has a broad anterior cingulum. It has only one root.

I^1 (4) — The crown is rectangular in labial view. The antero-labial corner is worn in 1 out of the 4 specimens, giving the crown a more triangular outline. There is a small pinnacle on the labial side of the crown that disappears quickly with wear. The enamel is thickened along the base of the crown. In medial view the crown is triangular. The enamel-dentine boundery curves up sharply on the medial side. The inner face of the crown is concave. Unlike the labial face, the enamel is not thickened near the base. The incisor has one strong, straight root.

D^4 (5) — The outline of the occlusal surface is subelliptical. The anterolingual and posterolingual sides are fairly straight. The paracone is the largest cusp. Its tip lies in front of the middle of the tooth. A slightly curved posterocrista runs from the tip of the paracone to the back of the tooth. In one out of the five specimens there is a small cusplet at the posterior end of the posterocrista. The small protocone lies on the lingual side of the paracone, directly lingual from the tip of the latter cusp. A well-developed ridge slopes from the tip of the protocone downward and ends at the back of the tooth. Directly in front of the paracone lies the parastyle. It is well developed and crescent-shaped in two out of the five specimens. In the other three it is less pronounced. There is a well-developed cingulum at the labial side of the tooth, which is only interrupted directly off the tip of the paracone.

P^4 (10) — The outline of the occlusal surface is subelliptical. The postero-lingual side is straight. The tooth consists mainly of the very large paracone. The tip of this cusp lies in front of the middle of the tooth. The straight posterocrista runs from the tip of the paracone to the back of the tooth. In front of the paracone lies a well-developed parastyle. The parastyle is small in two out of the ten specimens, well developed in the others. The postero-lingual cingulum is strong; it starts lingually of the tip of the paracone and ends at the back of the tooth.

The premolar has four strong roots: one in front, one at the back and a labial and lingual root in the middle of the premolar.

M^1 (7) — See the description of the holotype. Two out of the seven specimens have a short transverse ridge between the anterior arm of the protocone and the base of the paracone. The protoconule can only be observed in unworn specimens.

M^2 (10) — The outline of the occlusal surface is subtriangular. The lingual part is completely made up by the large protocone. In the anterior arm of this cusp, which ends against the base of the paracone, a very faint protoconule is discernable. The posterior arm of the protocone lies against the small, crescent-shaped hypocone. There is a small bulge in the outline of the tooth at the place of the hypocone. The posterior and anterior arms of the hypocone end closely together at the base of the metacone. The paracone is the largest and highest cusp. Its anterior arm is somewhat longer than the posterior arm in some specimens. In other specimens the two arms are of the same length. The metacone is clearly lower than the paracone. The posterior arm of the metacone is about half the length of the anterior arm. The mesostyle is widely spaced. The M^2 has three plank-shaped roots: one below each of the main cusps.

Other localities — The material of *Suleimania ruemkae* from the various localities apart from Harami 3 is listed in Table 5.

Premolar — Type I. Eight premolars from Harami 1 and eight from Kilçak 0″ are assigned to this group. The cingulums are less developed than in Harami 3. This may be related to the smaller width of the premolars in Harami 1 and Kilçak 0″. The specimens from Kilçak 0″ are also shorter than in the type locality.

Type II. Two premolars from Kilçak 0, three from Kilçak 0″ and Harami 1 are assigned to this group. In size and general morphology they agree well with the single premolar from Harami 3. However, the anterior and posterior cusplets are much weaker developed and may even be absent.

Type III. A specimen from Kilçak 0 agrees with the premolars from this group in Harami 3 in having a rounded anterior side of the main cusp and a sharp posterocrista. However, the cingulums are weaker developed than in the type locality and the anterior cusplet is missing.

Type VI. A small premolar from Kilcak 3B belongs to a morphotype that is not present in the assemblage of Harami 3. It is interpreted as a lower premolar. The outline of the occlusal surface is elliptical. In labial view the crown is quadrangular. The tip of the premolar lies in front of the middle of the premolar. The faint centrocristid runs over the tip. A weak posterior cingulum and a very weak lingual cingulum are

Table 5. Numbers of elements of *Suleimania ruemkae* gen. et. sp. nov. from localities other than the type locality.

loc.	D_4	P_4	M_1	M_2	M_3	D^4	P^4	M^1	M^2
Keskeköy		2					2	2	
Harami 2			1						
Harami 1	2	12	8	8	7	2	3	9	10
Kilçak 3B	1		2					1	
Kilçak 3A	2	2	1		4		2	3	3
Kilçak 0″	8	8	6	7	10	6	13	6	9
Kilçak 0	1	3	3	3			7	1	

present. The two roots are circular in cross-section. The posterior root is somewhat thicker than the anterior one.

Type VII. Two premolars from Kilçak 3A also belong to a type that has not been found in the Harami 3 assemblage. They are believed to represent upper premolars. The outline of the occlusal surface is elliptical. The premolar is much longer than wide. The tip of the main cusp lies in the centre of the premolar. The centrocrista is very sharp. In labial view the posterocrista is strongly concave. There is a very small anterior cusplet and a somewhat larger posterior cusplet. The centrocrista runs over these cusplets. The roots are not preserved, but judging from the rootcanals the two roots stand far apart.

Type VIII. This element is known by two specimens from Keseköy only. The outline of the occlusal surface is elliptical. The crown is triangular in labial view. The tooth is only somewhat longer than wide. The only cusp is conical. Its tip lies just in front of the centre of the tooth. A blunt ridge runs over the tip in one of the two specimens. The anterior flank of the cusp is rounded in the other, so that this specimen only has a ridge on the posterior side. The tooth has two roots, which are circular in cross-section. The element is tentatively interpreted as the upper canine.

D_4 — The posterocristid is not divided near its end in the D_4 from Kilçak 3B and in three of the eight D_4 from Kilçak 0″. As in Harami 3, the lingual ridge of the protoconid may run to the side (the specimens from Harami 1, Kilçak 0 and one of the eight specimens from Kilçak 0″), or may run backwards parallel to the posterocristid (the specimen from Kilçak 3B, seven of the eight specimens from Kilçak 0″. The two D_4 from Kilçak 3A differ from those in the other assemblages in having two long arms which run from the tip of the protoconid backwards. In one of the two specimens, the lingual arm connects to a cusplet that lies at the back of the milkmolar, the labial arm ends just short of this cusplet. In the other specimen a ridge, starting between the two arms, connects to the posterior cusplet.

P_4. — The anterior thickening in the centrocristid is less developed than in Harami 3. It is absent in one out of the three P_4 from Kilçak 0. None of the P_4 from Kilçak 0″ has a posterior thickening in the centrocristid. The lingual cingulum, if present, is weak and confined to the antero-lingual side of the premolar.

M_1 — The protoconid and metaconid stand close together in the M_1 from the various Kilçak localities, making the trigonid narrower than in Harami 3. The oblique cristid ends against the base of the protoconid in the two specimens from Kilçak 0. In Kilçak 0″ and Kilçak 3B it ends somewhat more lingually. The width of the trigonid and the direction of the oblique cristid in Harami 1, Harami 2 and Keseköy are comparable to that of the type locality. In Kilçak 3A and 3B the metacristid is separated from the metaconid by a notch. A — very — weak anterior cingulum is generally found in the Kilçak localities. Only 1 of the 6 specimens from Kilçak 0″ lacks this feature. Only two of the eight M_1 from Harami have an anterior cingulum. This cingulum is absent in the other six, as well as in the M_1 from Harami 2 and Keseköy.

M_2 — As a rule, the entostylid is poorly developed or even absent. Well-developed entostylids can be found in two of the three specimens from Kilçak 0 and two out of seven M_2 from Kilçak 0″.

M_3 — The M_3 from the various assemblages resemble those from Harami 3 closely.

D^4 — The development of the cingulums in the six D^4 from Kilçak 0″ is considerably weaker than in Harami 3, particularly on the lingual side. The parastyle is only a small cusp. In 1 of the 6 specimens the tip of the paracone lies in the centre of the milk molar, and not in front of the middle, as in the other D^4. The development of cingulums on the only complete D^4 found in Harami 1 resembles that of Kilçak 0″. The tip of the paracone in this D^4 also lies in the centre.

P^4 — The tip of the paracone lies in the middle of the P^4 in all localities older than Harami 3. Only in Keseköy and Harami 3 itself the tip lies in front of the middle. The two P^4 from Keseköy also agree with Harami 3 in having a well-developed parastyle and a strong postero-lingual cingulum. In the other localities the parastyle is small. The postero-lingual cingulum is generally well developed, but it is weak in two of the seven specimens from Kilçak 0, 3 of the 13 from Kilçak 0″, both specimens from Kilçak 3A and in two of the three specimens from Harami 1.

M^1 — The anterior arm of the protocone usually connects to the paracone (Kilçak 3A, Keseköy) or ends just short of it (Kilçak 0″, Harami 1). This arm connects to the parastyle in two of the six M^1 from Kilçak 0″. The anterior arm of the protocone is split into two ridges in the specimen from Kilçak 0, the one from Kilçak 3B and one of the nine specimens from Harami 1. In these cases a thick ridge connects to the paracone, and a narrower one runs in the direction of the parastyle. The protoconule is small and can be observed in two unworn specimens only, one from Kilçak 0″ and one from Harami 1. The development of the hypocone varies. This cusp is very well developed in Kilçak 0, Kilçak 3A and Kilçak 3B. The development of the hypocone in the other localities resembles that of Harami 3. A widely-spaced mesostyle, resembling the configuration found in Harami 3, is found in the specimen from Kilçak 3B, as well as in two of the nine specimens from Harami 1 and two of the six specimens from Kilçak 0″. In the other specimens the mesostyle is well divided.

M^2 — An indistinct protoconule is found in two of the ten specimens from Harami 1 only. The development of the hypocone varies. The hypocone is well developed in all specimens from Kilçak 0 and Kilçak 3A, but only in three out of nine of the M^2 from Kilçak 0″ and in five out of ten specimens from Harami 1. The arms of the paracone in the Kilçak 0″ assemblage seem somewhat longer than those from the other localities. They stand close together, leaving only a narrow valley in between. Two of the M^2 from Harami 1 stand out by having very short arms of the paracone. The division of the mesostyle is most pronounced in the type locality. In the other localities the two cusps of the mesostyle even touch near their bases in some cases.

Remarks — Some of the differences between the various assemblages of *Suleimania ruemkae* can be interpreted as an evolutionary trend. However, the differences are not very clear-cut. There seems to be an increase in size through time, especially in the M_1/M^1. Morphological differences are the stronger development of cingulums on the P^4 and a somewhat less developed hypocone of the M^1 in the younger localities. The trigonid of the M_1 seems to become wider in time. However, these trends are not consistent. The hypocone of the M^1 in Kilçak 0″, for instance, resembles that of the younger localities. Since there is no clear gap in size or morphology between the various assemblages, all of them have been assigned to a single species.

At first sight, *Suleimania ruemkae* might be identified as a dimylid. The M^1 with its quadrangular outline and slightly inflated cusps can be easily confused with the M^1

of primitive dimylids. The M_3 has lost its talonid and resembles the M_3 of the Oligocene dimylid *Exaeonodus*. The M^3 is absent. Dimylidae are, however, not the only insectivores in which the M^3 and M_3 are reduced. The shrew *Amblycoptus* also lacks the last molars. In addition to the reduced last molars and the morphology of the upper molars, *S. ruemkae* shares the presence of a functional milk dentition with the Dimylidae. Within the Talpidae this feature is only found in the shrew-moles (Uropsilinae and Urotrichini sensu Hutchison, 1968).

Other features suggest that *Suleimania ruemkae* is a talpid rather than a dimylid. The oblique cristid of Dimylidae always ends against the protoconid, whereas this ridge ends against the protoconid-metaconid crest in *Suleimania* as it does in Talpidae. Although the hypocone of the M^1 is large in comparison to other Talpidae, it is considerably smaller than the large cone-shaped hypocone of Dimylidae. Although the P^4, M^1 and M_1 show a tendency to inflate their cusps, this inflation is much less pronounced than in the exaenodont dentitions of Dimylidae. Furthermore, the tendency is restricted to the above mentioned elements. In contrast, the M_2 is characterized by sharp ridges. The premolars too have very sharp cutting edges, whereas Dimylidae are defined as having blunt premolars with inflated cusps. All these features indicate that *Suleimania* is best classified as a talpid. The resemblence to Dimylidae is considered to be the result of convergence.

The combination of the characters mentioned above does not allow a classification of *Suleimania ruemkae* in any of the known subfamilies (Uropsilinae, Talpinae, Desmaninae, Gaillardinae). Therefore a new subfamily has been erected for this peculiar species.

The inflation of the P^4, M^1 and M_1 can be seen as an indication that *Suleimania ruemkae*, like dimylids, may have fed on molluscs. It is, however, unlikely that molluscs were its main diet. The premolars and M_2 still have sharp ridges, which suggests that the species also fed on nimbler prey, such as (water) insects and/or small vertebrates. Furthermore, the long paralophid of the M_1 and the long posterolingual flank of the P^4 provide a shearing action rather than a crushing action, as we would expect in true mollusc eaters. As a result of the reduction of the last molars, the cutting edge of the P^4 and M_1 lies relatively close to the condyle, which provides a powerful shearing apparatus. Such a strong cutting edge would have been useful for instance when eating small vertebrates as frogs and lizards.

The Suleimaninae is the first extinct subfamily of moles recognized in Eurasia. The discovery of an extinct stock of talpids confirms that the diversity of the family was once much higher than it is today. This is also the case for the talpids of North America (Hutchison, 1968).

Conclusions

Four different genera of Talpidae, *Desmanodon*, *Theratiskos*, *Geotrypus* and *Suleimania*, were found in Lower Miocene strata from Anatolia. This means that the Talpidae were the most diverse insectivore family in the Early Miocene of that area. In southern Germany too, talpids are the most diverse insectivore group in Early Miocene times (Ziegler, 1985; 1990a). Talpid diversity in southern Germany is higher than in Anatolia, but this holds true for all insectivore families.

Two of the genera found show a connection with the European insectivore faunas. *Geotrypus* is a common element in Late Oligocene/ Early Miocene insectivore faunas from Europe. *Desmanodon* appears in Europe sometime during the Early Miocene (Van den Hoek Ostende, 1997), but the closely related genus *Paratalpa* was already found in Europe during the Late Oligocene. The other two genera, *Theratiskos* and *Suleimania*, are thus far known from Anatolia only. Possibly these genera have their origin in Asia.

Acknowledgements

I am grateful to the Mineral Research and Exploration General Directorate of Turkey (M.T.A.) in Ankara for their support and promoting international collaboration in studying the fossil mammal faunas of Anatolia. Various versions of the manuscript were read by Hans de Bruijn, Albert van der Meulen, Thijs Freudenthal, and Johan Meulenkamp. Their comments and discussions were of great value. Jaap Luteijn made the drawings; the SEM photographs were made by Wil den Hartog.

References

For References see Part 8 in this volume.

Manuscript received 30 September 1998.

Plate 1

Figs. 1-7. *Theratiskos mechteldae* sp. nov. from Keseköy.
1: D_4 sin., Ke 6901.
2: Mandible sin. with M_1, Ke 6941.
3: Mandible sin. with P_4-M_2, Ke 6975, holotype; a: occlusal view; b: labial view.
4: D^4 sin., Ke 7163.
5: Maxillary fragment sin. with P^4 and M^1, Ke 7224.
6: M^2 sin., Ke 7304.
7: M^3 sin. Ke 7366.

Figs. 8-16. *Theratiskos rutgeri* sp. nov. from Harami 1.
8: P_4 sin., Ha 1 3811.
9: M_1 sin., Ha 1 3853.
10: M_2 sin., Ha 1 3894.
11: M_3 sin., Ha 1 3936.
12: D^4 sin., Ha 1 3981.
13: P^4 sin., Ha 1 3997.
14: M^1 sin., Ha 1 4028.
15: M^2 sin., Ha 1 4057, holotype.
16: M^3 sin., Ha 1 4108.

All specimens × 12.5.

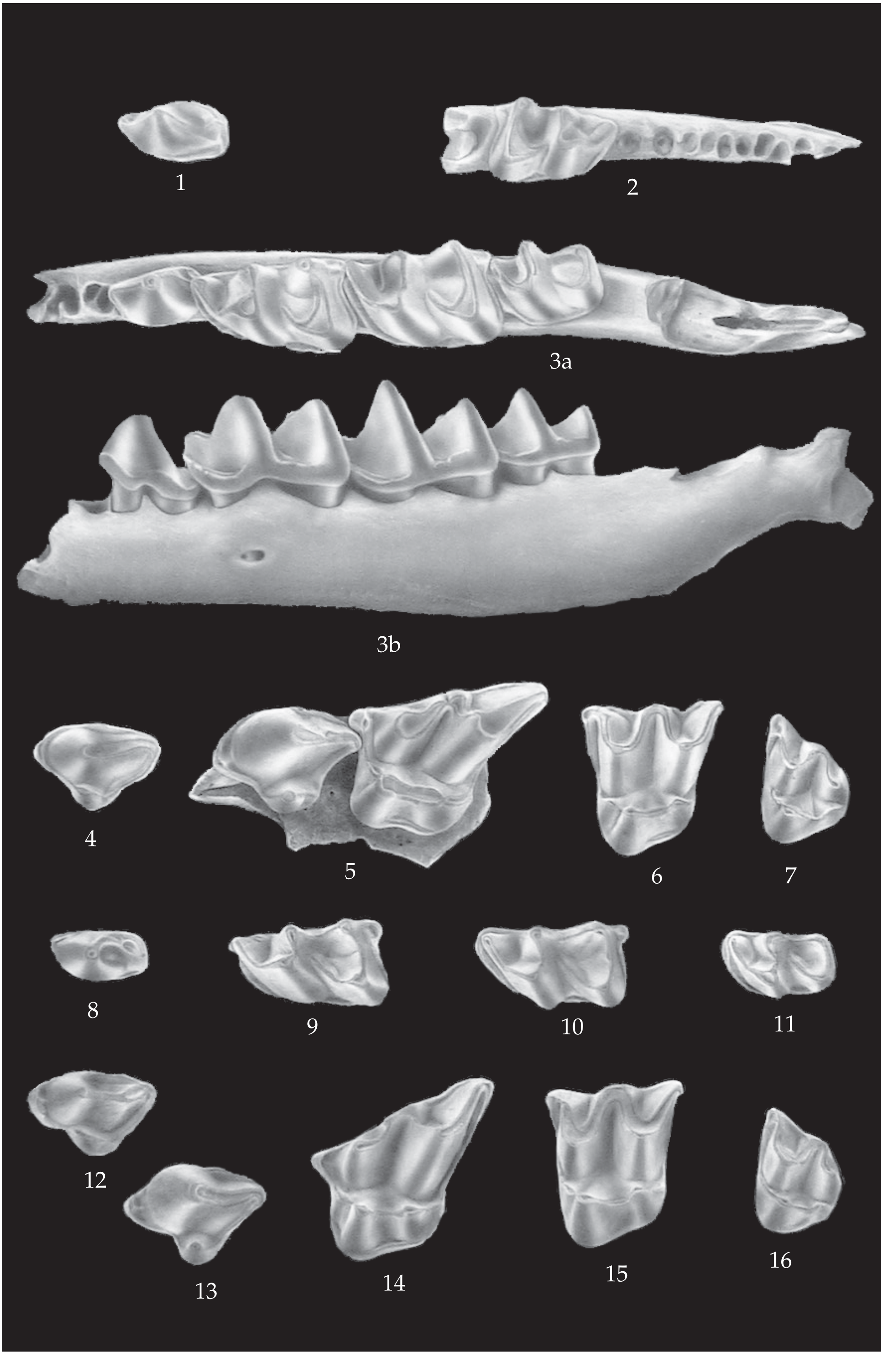
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Plate 2

Figs. 1-7. *Geotrypus haramiensis* sp. nov. from Harami 1 and 3.
1: Mandible sin. with P_1-M_3, Ha 3 781, holotype; a: occlusal view; b: labial view (× 6.2).
2: P_4 sin., Ha 3 782.
3: Humerus, Ha 3 876 (× 4). a: posterior view; b: anterior view.
4: M^2 sin., Ha 3 787.
5: M^3 sin., Ha 3 788.
6: M^2 sin., Ha 1 3801.
7: M^3 sin., Ha 1 3802.

Specimens × 12.5 unless indicated otherwise.

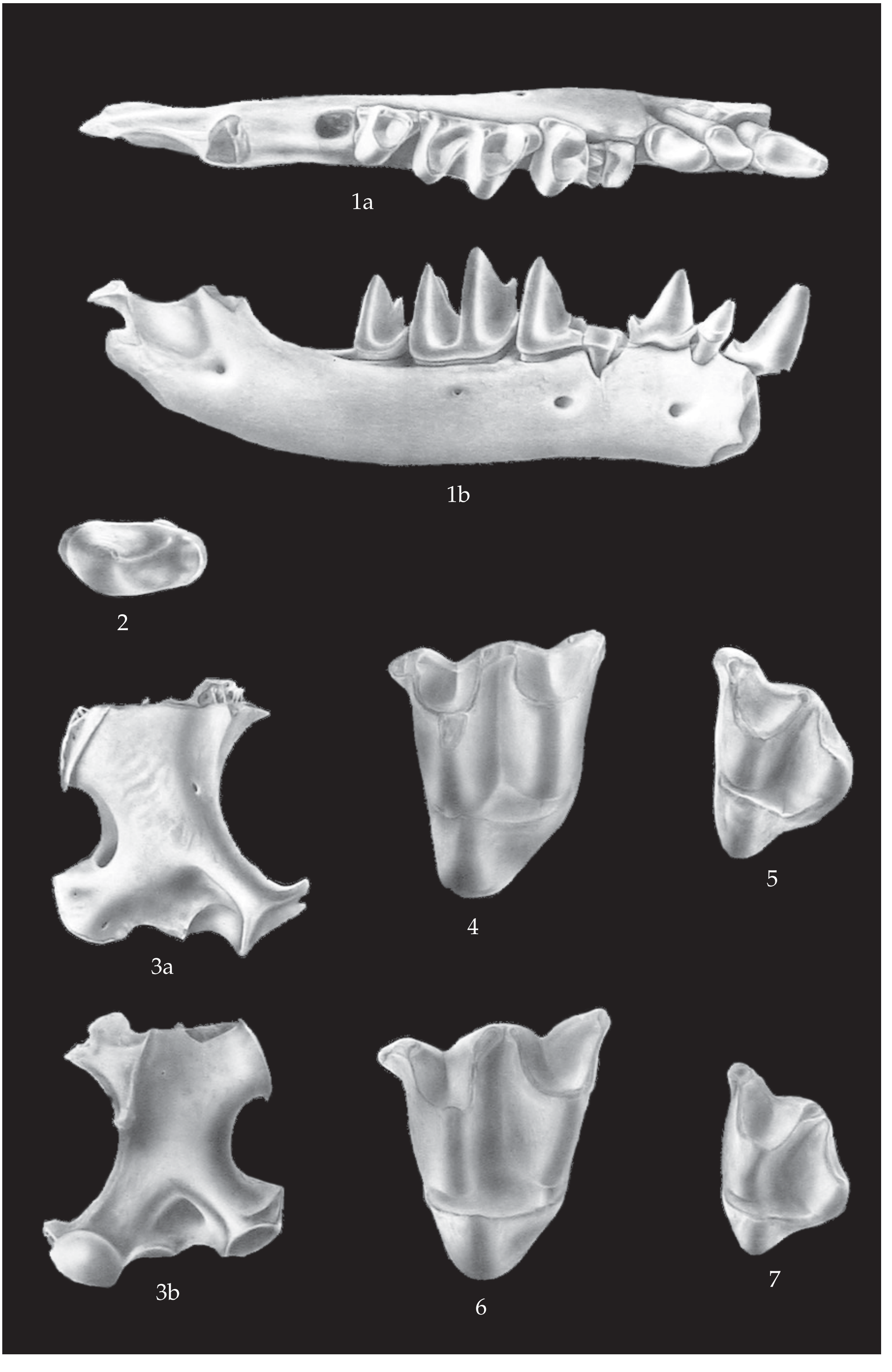
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Plate 3

Figs. 1-6. *Geotrypus kesekoeyensis* sp. nov. from Keseköy.
1: M_1 sin., Ke 6703.
2: M_2 sin., Ke 6704.
3: P^4 dext., Ke 6706.
4: M^1 sin., Ke 6708.
5: M^2 sin., Ke 6712, holotype.
6: M^3 sin., Ke 6715.

Figs. 7-10. *Suleimania ruemkae* gen. et sp. nov. from Harami 3.
7: I^1 dext., Ha 1, 3631.
8: Premolar Type IV, Ha 3 696; a: occlusal view; b: labial view.
9: Premolar Type II, Ha 3 691; a: occlusal view; b: labial view.
10: Premolar Type V, Ha 3 699; a: occlusal view; b: labial view.

All specimens × 12.5.

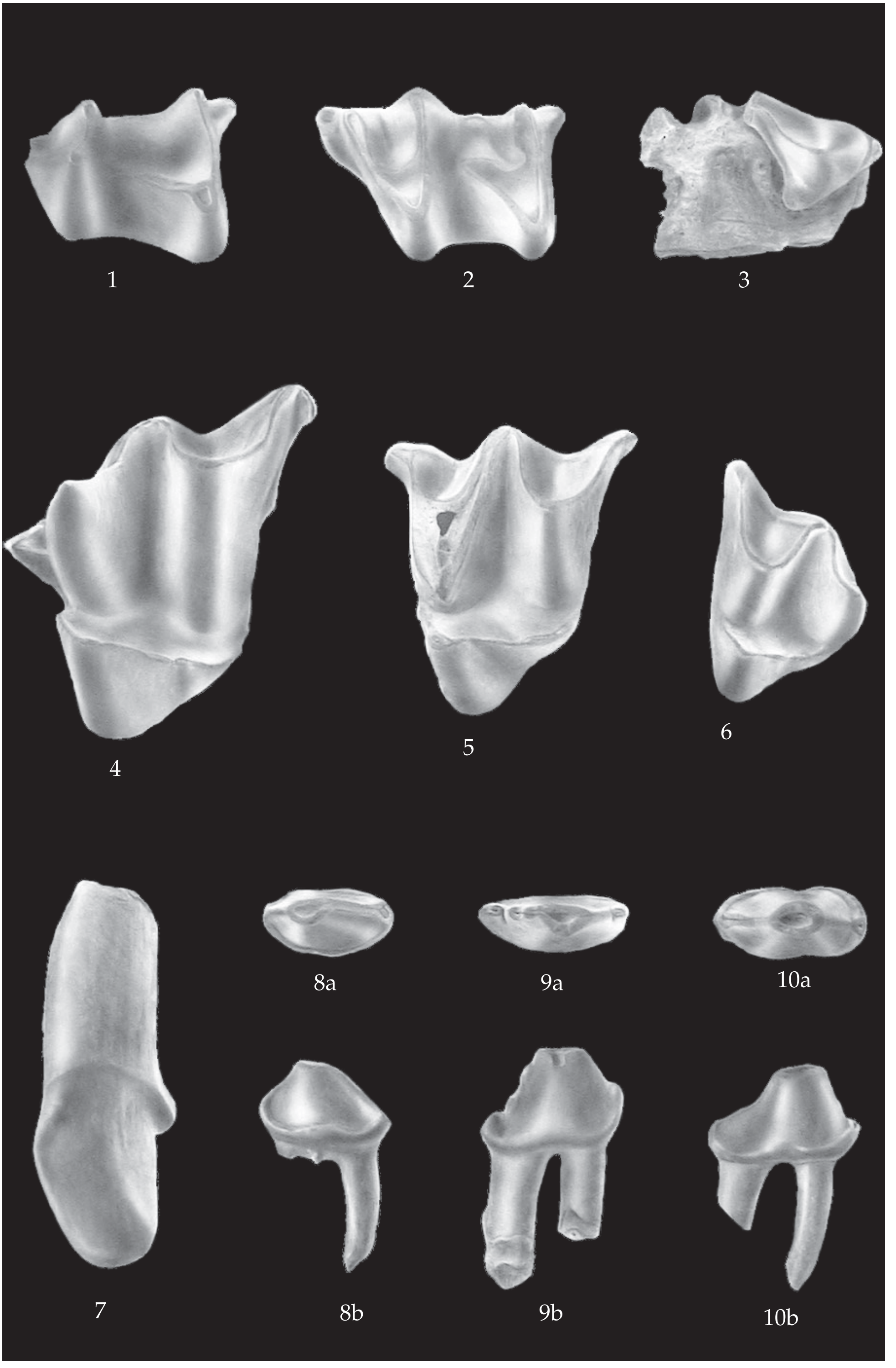
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Plate 4

Figs. 1-8. *Suleimania ruemkae* gen. et sp. nov. from Harami 1 and 3.
1: Premolar Type I with part of mandible, Ha 3 686; a: occlusal view; b: labial view.
2: D_4 sin., Ha 1 3644.
3: D_4 dext., Ha 3 706; a: occlusal view; b: labial view.
4: Premolar Type III, Ha 3 693.
5: P_4 sin., Ha 3 720.
6: P^4 sin., Ha 3 659.
7: D^4 sin., Ha 3 751.
8: D^4 sin., Ha 1 3734.

All specimens × 12.5.

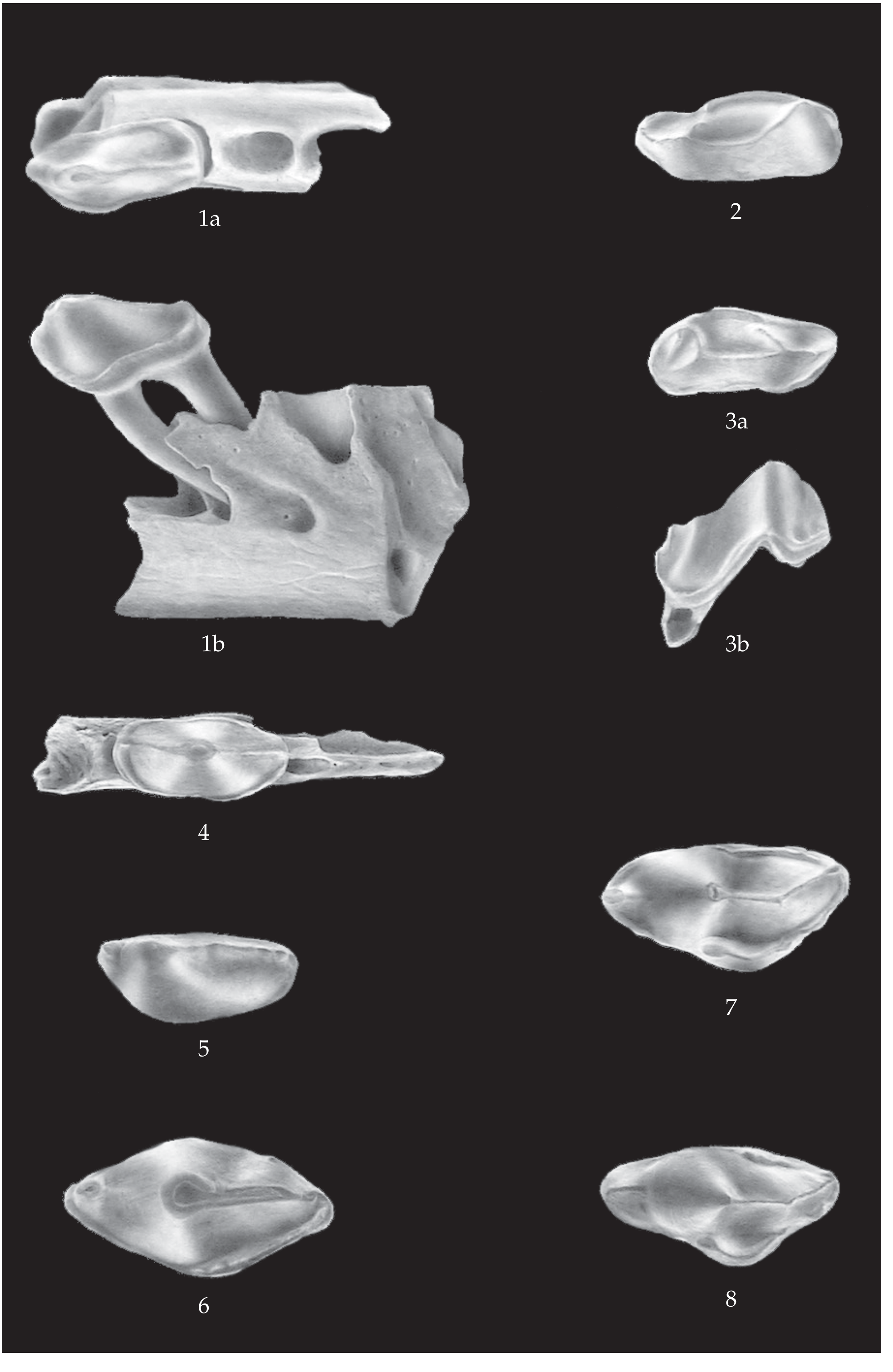
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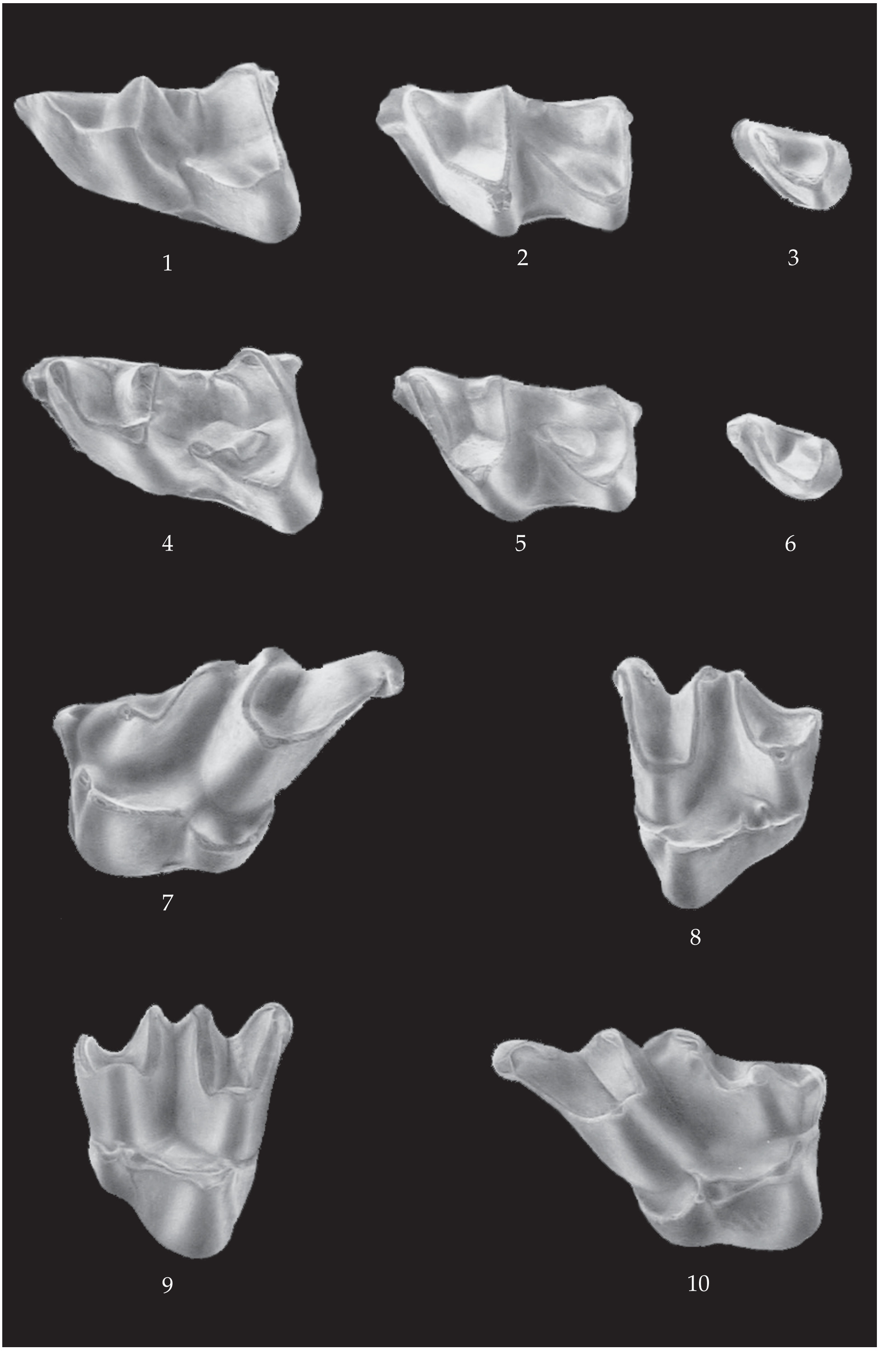
Plate 5

Figs. *Suleimania ruemkae* gen. et sp. nov. from Harami 1 and 3.
1: M_1 sin., Ha 1 3706.
2: M_2 sin., Ha 1 3713.
3: M_3 sin., Ha 1 3725.
4: M_1 sin., Ha 3 725.
5: M_2 sin., Ha 3 739.
6: M_3 sin., Ha 3 743.
7: M^1 sin., Ha 1 3761.
8: M^2 sin., Ha 1 3775.
9: M^2 dext., Ha 3 773.
10: M^1 dext., Ha 3 769, holotype.

All specimens × 12.5.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