Moles (Talpidae) from the late Middle Miocene of South Germany

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The moles from the South German fissure fillings Petersbuch 6, 10, 18, 31, 35, 48 include 14 species, four of which are new: *Leptoscaptor bavaricum* gen. et sp. nov., *Leptoscaptor robustior* gen. et sp. nov., *Myxomygale gracilis* sp. nov. and *Tenuibrachiatum storchi* gen. et sp. nov. Most samples are characterised by their high species diversity. *Talpa minuta* is the most common species in nearly all samples. *Leptoscaptor* is characterised by a slender humerus and by the loss of lower antemolars. It is interpreted as a Miocene offshoot of the Scalopini. *Myxomygale gracilis* represents the latest record of the genus. *Tenuibrachiatum storchi* has a slender humerus and one lower incisor is lost. The species is structurally ancestral to the extant *Urotrichus*. The genus *Pseudoparatalpa* Lopatin, 1999 is considered a synonym of *Paratalpa*. The talpids of the Petersbuch fissures are in line with a Middle Miocene correlation of MN 7+8 as already indicated by the cricetids. The remains of desmans in the Petersbuch 6 fissure filling indicate the proximity of water. The presence of Urotrichini in nearly all samples, albeit scanty, suggests a forestal environment within the range of the owls, which preyed on them.

Key words: Mammalia, Talpidae, moles, Miocene, Germany, Petersbuch.

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Introduction

Talpids in Miocene of Europe.—Our knowledge of the Miocene moles is limited. In South Germany the Lower Miocene moles from a couple of sites are sufficiently known. They have been published either in papers dealing only with talpids or in contributions with a broader scope. The most important sites are: Ulm-Westtangente (Ziegler 1990), Petersbuch 2 and the basal Upper Freshwater Molasse sites Rauscheröd, Rembach, and Forsthart (Ziegler 1985, Ziegler and Fahlbusch 1986). The only Middle Miocene site in South Germany with well-documented talpids is Steinberg in the Nördlinger Ries (Ziegler 1985). It yielded only one mole species, *Proscapanus sansaniensis*. Later mammal faunas are extremely rare in the South German Molasse area and the karstic fissure fillings of the Jurassic. Stromer (1928, 1940) reported on the sparse occurrence of species similar to *Talpa minuta*, *Proscapanus sansaniensis*, and *Scaptonyx edwardsi* from the Munich area. Their stratigraphic correlation is uncertain. It may be MN 7/8 to 9. The only talpid from the Hammerschmiede fauna (MN 9) is "*Desmanella*" *quinquecuspidata* Mayr and Fahlbusch (1975), which according to Engesser (1980: 92) is not *Desmanella*. Rümke (1985: 16) thinks that this species represents a primitive, hitherto undescribed desmanine genus. The insectivores from other Upper Miocene sites as Marktl and Giggenhausen, if present at all, are not known. Hambach 6 C in the Lower Rhine Embayment yielded the northwesternmost Miocene fauna in Europe, including five talpid species. It is correlative with MN 5 to 6 (Ziegler and Mörs 2000).

In the following section, the Miocene talpid record in the neighbouring countries known thus far is reviewed.

In Poland, the documentation of Miocene talpids is particularly poor. The MN 6-fauna of Opole 1 yielded a humerus of *Talpa minuta* (Andreae 1904, stratigraphy in Kowalski 1989). The A-horizon of Bełchatów, which is correlated with MN 7/8 or 9, yielded *Desmanella* sp. (Kowalski and Rzebik-Kowalska 2002).

The talpids from Devinska Nova Ves in Slovakia (MN 6) have been made known by Zapfe (1951), who described *Talpa minuta*, *Scaptonyx edwardsi*, *Scaptonyx* ?*dolichochir*, and two undeterminable talpids.

Feru et al. (1980) recorded a talpid similar to *Desmanella* from the Middle Miocene (MN 8) locality Comăneşti 1 in Romania.

In Austria the Lower Miocene sites Oberdorf in the western Styrian Basin and Obergänserndorf and Teiritzberg in the Korneuburg Basin yielded some talpids described by Ziegler (1998) and Rabeder (1998). From the Upper Miocene site Vösendorf (MN 9) in the Vienna Basin Rabeder (1985) listed *Desmanella* sp. The poor talpid record from Kohfidisch (MN 11) was published in Bachmayer and Wilson (1970, 1978). They recorded *Archaeodesmana pontica*, cf. *Desmanella crusafonti* and *Talpa* ?sp. The Eichkogel fauna (MN 11) yielded *Galemys* cf. *kormosi*, two undeterminable desmanine species, and various talpine species (Rabeder 1970).

From the Anwil fauna in Switzerland, which is correlated with MN 7+8, five species of talpids have been presented in a comprehensive paper on all mammals (Engesser 1972). The rich fauna from Nebelbergweg in Switzerland (MN 9) yielded only few isolated teeth of four talpid species (Kälin and Engesser 2001).

Sansan and La Grive are the most important Middle Miocene sites in France. The talpids from Sansan (MN 6) are documented in Baudelot (1972). The moles of the classic La Grive fauna (MN 7+8) have been updated by Hutchison (1974). Mein presented an up-to-date list of all mammals in de Bruijn et al. (1992: 112).

The Spanish talpid record is restricted mainly to the Late Miocene. There is no published evidence from the Middle Miocene, except a sample of *Desmanodon*/*Paratalpa* from La Col-C, which is correlated with MN 5 (Hoek Ostende 1997). The scarce Early Miocene talpids are published in van den Hoek Ostende (1997). The Late Miocene record is much better (see Gibert 1975; de Jong 1988; van Dam 1997).

The Greek talpid record also is very scarce. Two species from the Lower Miocene (MN 4) of Aliveri have been described by Doukas (1986). The Pikermi fauna (MN 12) yielded *Desmanella dubia* (Rümke 1976). In the Maramena fauna (MN 13) 4 talpid species have been recorded by Doukas et al. (1995).

Aim.—This study intends to fill the gap in our knowledge about Miocene talpids. The present paper provides a thorough documentation of the Middle Miocene talpids of Petersbuch 6-48. The composition of the talpid faunas will be discussed and compared to other Middle Miocene faunas elsewhere, followed by some ideas on the biostratigraphy and palaeoenvironment. This contribution presents the first detailed publication of talpids from this time and area.

The site.—Petersbuch, which yields the talpids described in this paper, is situated 10 km north of Eichstädt (topographic map 7033, Titting) and ca. 100 km northwest of Munich. The White Jurassic quarry of Petersbuch is known for its rich fossiliferous karstic fissure fillings, which have been exploited for more than 30 years. During that period more than 70 fissures yielded more or less rich Tertiary and Pleistocene mammal faunas. The first 30 fissures are situated in the quarry of the Schöppel Company. Fillings numbered from 31 onwards are located in the directly adjacent quarry of the Juma Company. The fissure fillings P6, 10, 18, 31, 35, and 48 yielded rich mammal faunas of late Middle Miocene correlation, including diverse talpid samples as well as other insectivores and bats. The bats and shrews of these fissure fillings have been presented by Ziegler (2003a, b). The other fillings yielded little material and/or faunas from other time slices. The first three fissures are located directly adjacent to one another in the southeast corner of the quarry (see Bolliger and Rummel 1994: fig. 2). The GPS coordinates of the fissures (position format Hddd°mm´mmm´´, standard for Germany WGS84, precision ±4 m) and the elevation above sea level are listed below.

fissure	Quarry (company)	latitude	longitude	elevation (m NN)
P6	Schöpfel	48°59´278´´	11°11´940´´	535
P10	Schöpfel	48°59´284´´	11°11´937´´	535
P18	Schöpfel	48°59´277´´	11°11´943´´	535
P31	Juma	48°59´431´´	11°12´049´´	540
P35	Juma	48°59´380´´	11°12´027´´	540
P48	Juma	48°59´385´´	11°12´021´´	518

Previous work on the Petersbuch fissure fill sites.—The first fissure P1 yielded a rich Pleistocene fauna, which was published by Koenigswald (1970). The Petersbuch 2 fissure, which was discovered in 1977, contained an exceptionally rich vertebrate fauna, detailed descriptions of which have been published in the years to follow, e.g., the talpids by Ziegler (1985) and glirids by Wu (1993). Beginning with the 1990s many fissures were discovered and exploited by M. Rummel, who over the years gathered a huge collection of fossil vertebrates. The complex formation of then known fissure fillings has been discussed by Bolliger and Rummel (1994). The faunal content of these fissure fillings is presented in preliminary faunal lists and the stratigraphic correlations are noted (Bolliger and Rummel 1994). The stratigraphic correlation of P6 and P18, as indicated mainly by rodents, is the uppermost part of the Middle Miocene corresponding to the unit MN 7/8 on the scale of the European Neogene mammal chronology (Rummel 2000). The fauna of the fissure P 31 was correlated with MN 7, P 10, and P 35 with MN 8 (Rummel 2000). For P 48 the correlation is MN 7/8 (personal communication by M. Rummel). As the faunas from the reference localities of MN 7 and MN 8, Steinheim, and Anwil respectively, show only minor differences in stage-in-evolution, both units have been united into one unit (de Bruijn et al. 1992). When quoting authors prior to 1992 or those who did not recognise this unification, we have to be aware that MN 7 and/or MN 8 mean MN 7+8. As already mentioned above, the bats and shrews of these fissure fillings have been presented by Ziegler (2003a, b).

Methods.—All measurements are given in mm. In the terminology of the dental and postcranial elements and in the measurements the works of Hutchison (1968, 1974: figs. 1–3) are widely followed. Differing from this author, the greater tuberosity of the humerus is called greater tubercle, translated from the Latin term tuberculum majus. The upper molars are not measured along or perpendicular to the base line. This procedure seems to me to be hardly reproducible. Instead the length is measured along the buccal margin (see Engesser 1980: fig. 35). When measuring the width of the lower teeth, the entoconid must be exactly vertical in occlusal view. Otherwise the tooth appears distinctly wider.

In the tables, the usual biometric parameters are given. The abbreviations are: n, number of specimens; R, range of

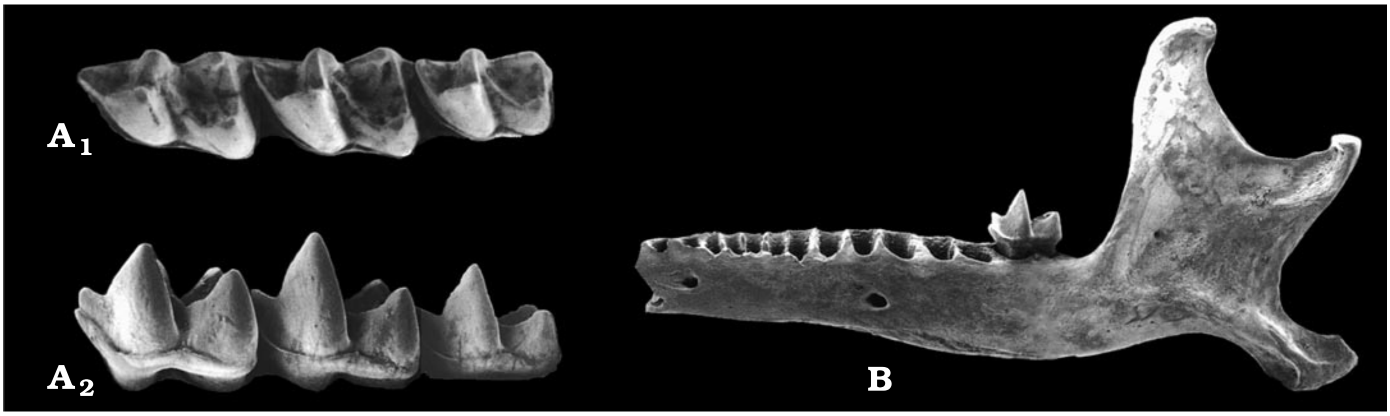

Fig. 1. *Mygalea antiqua*, Petersbuch 6. **A**. Left m1–m3, NHMA P6-1065.1, in occlusal (A_1) and buccal (A_2) views; ca. × 10. **B**. Left dentary with m3 and complete ascending ramus, NHMA P6-1065.2, buccal view; ca. × 5.

measurements, i.e., minimum and maximum value; m, arithmetic mean ± standard error of the mean (95% probability).

Abbreviations for the measurements of the teeth and postcranial elements are: L, length; W, width; a, anterior; Hcor, height of the coronoid; GL, greatest length; Bp, proximal breadth; BpwT, proximal width without teres tubercle; DS, diameter of the shaft; Bd, distal breadth; BdwE, distal breadth without epicondyles.

All the material is from the private collection of Dr. Michael Rummel (Weissenburg), abbreviated CRW. The figured specimens are now housed in the Naturmuseum Augsburg (Natural History Museum of Augsburg), abbreviated NHMA.

Systematic palaeontology

Family Talpidae Fischer von Waldheim, 1817
Subfamily Desmaninae Thomas, 1912
Genus *Mygalea* Schreuder, 1940

Type species: *Mygalea antiqua* (Pomel, 1848).

Mygalea antiqua (Pomel, 1848)

Fig. 1.

Material and measurements.—Petersbuch 6: NHMA P6-1065/1, left dentary fragment with m1–m3; Lm1–m3 (6.45), h of dentary below m1 (2.80), m1 (2.38×1.17×1.36), m2 (2.32×1.25×1.35), m3 (1.97×1.09×1.02); NHMA P6-1065/2, left dentary fragment with m3 and complete ascending ramus; h of dentary below m1 (2.70), h1 of coronoid (9.15), h2 of coronoid (7.80), m3 (1.86×1.04×0.95).

Description

Dentary.—The coronoid process, which is slightly bent posteriorly, forms a nearly right angle with the horizontal ramus. The masseteric fossa is moderately deep. The internal temporal fossa is deeply excavated. The mandibular foramen opens directly below the mylohyoid ridge, slightly posterior to the centre of the ascending ramus. The angular process is shovel-shaped with an internal concavity and a crest on the external side. The condylar process lies high above the level of the tooth-row. There are two mental foramina: one between the roots of m1, another beneath p1 or the posterior root of p2. There are 10 alveoles anterior to m1: two for p2–p4 each and one for i1, i2, c and p1 each. Consequently, the mandibular dental formula is 2-1-4-3. According to the alveoles the lower premolars decrease in size anteriorly, the i1 is procumbent.

Lower molars.—The size relation of the lower molars is m1>m2>m3. In the m1 the trigonid is distinctly narrower than the talonid, in the m2 only slightly, in the m3 it is somewhat wider. The protoconid is slightly higher than the hypoconid in the m1, but distinctly higher in m2 and m3. Most conspicuous in the lower molars is the strong cingulid, which extends from below the paraconid to the hypoconid. Postcingulids are somewhat weaker on m1 and m2 and rudimentary on m3. Lingual cingulids are absent. A short entostylid is developed in m1 and m2. The oblique cristid terminates at the posterior wall of the trigonid below the protocristid, slightly lingual to the protocristid notch. In the m2 a faint metacristid is developed.

Discussion

There are three *Mygalea* species in the Miocene of Europe. *Mygalea magna* Ziegler, 1990, the oldest and largest species, is only known from the type locality Budenheim or Hessler from the Calcareous Tertiary in the Mainz Basin. It is correlated with the Lower Miocene (Middle Agenian, MN 2a). This species has distinctly larger, primarily wider, teeth than the Petersbuch specimens and has the i3 retained.

Mygalea jaegeri (Seemann, 1938) is mainly known from faunas correlatable with MN 5, e.g., the type locality Viehhausen near Regensburg (Seemann 1938) and Sandelzhausen (Ziegler 1990, 2000). This species also has retained its i3 and it is smaller than the specimens under study.

In the evolutionary level, as indicated by the reduced number of lower incisors, both Petersbuch dentaries come closest to *Mygalea antiqua* from Sansan, where the i3 is lost. The position of the mental foramina is quite variable in the Sansan sample. In four dentaries the following combinations are present: (1) anterior part broken/ below anterior root of m1, (2) below p1 and anterior root of p3, (3) below c and p4/m1, (4) below p1 and p4. Compared to Petersbuch 6, the mental foramina are slightly shifted anteriorly in the Sansan sample. In two dentaries the m1 is larger than the m2, in another it is smaller. However, in overall size the lower molars are larger, mainly wider than ours. In spite of this small size difference, the Petersbuch 6 specimens are considered to represent *Mygalea antiqua*. This species is also recorded in the Swiss localities Zeglingen, Rümikon and Schwamendingen (Kälin 1993, all MN 6), and in the German sites Langenau (Sach and Heizmann 2001, MN 4) and Hambach 6C (*M.* cf. *antiqua*, MN 5/6, Ziegler and Mörs 2000). The Petersbuch 6 sample is the latest record of this species and its genus thus far.

Mygalea is allocated to the Desmaninae by most students except Rümke (1985: 16). She considers the subfamilial allocation not justified, unless the intermediate position of *Mygalea* can be demonstrated. I think this is not necessary. The humeri of all three *Mygalea* species are known and show clear desmanine affinities. In the most advanced species, *M. antiqua*, the i3 is absent. Hence it cannot be ancestral to any extant desmanine. The genus may be a desmanine side branch that became extinct in the early Late Miocene.

Subfamily Talpinae Fischer von Waldheim, 1817

Tribe Scalopini Gill, 1875

Genus *Leptoscaptor* nov.

Type species: *Leptoscaptor bavaricum* gen. et sp. nov.

Etymology: From Greek *leptos*, slender, asthenic; *skaptein*, to dig, to plug. Compared to other Scalopini, *Leptoscaptor* has a slender humerus.

Included species: *Leptoscaptor robustior* gen. et sp. nov.

Diagnosis.—Medium-sized scalopine mole. Tentative dental formula I?1/2, C1/1, P4/3, M 3/3. i2>i1>c. Lower canine incisor-shaped, single-rooted. i2 more procumbent than c. Lower premolars double-rooted, increasing in size posteriorly. m1<m2>m3. Oblique cristid joins metacristid in m2 and m3, no metastylid developed. Talonid lingually open in m1. Upper incisor enlarged. Upper canine single- or double-rooted. P1–P3 double-rooted, P4 with tiny parastyle, protocone in most P4 a small but distinct cusp. Mesostyles on upper molars divided, no lingual conules on M1 and M3, on M2 weakly developed para- and metaconules. Humerus more or less slender, head elliptical, directed parallel to shaft, brachialis fossa large but shallow, deltoid process short, teres tubercle long, crest-shaped, pectoral tubercle in midshaft position, scalopine ridge prominent, running diagonally from the head to the medial side of the lesser tuberosity, the trochlea is wide, separated by a narrow notch from the fossa for the m. flexor digitorum profundus ligament, olecranon fossa large.

Leptoscaptor bavaricum gen. et sp. nov.

Fig. 2.

Etymology: From Latin *bavaricum*, Bavarian. The species is recorded from the state of Bavaria, Germany.

Holotype: Left dentary fragment with c, p2–m1 and the alveoles of i1–i2, P10-608/6, fig. 2A.

Measurements of the holotype: lc–p4 (3.35), lp2–p4 (2.52), c (0.64×0.38), p2 (0.67×0.40), p3 (0.80×0.45), p4 (1.03×0.65), m1 (1.54×0.90×1.16); h of the corpus below the lingual side of m1 (1.80).

Type locality: Petersbuch 10 (details see p. 618).

Age: Uppermost part of the Middle Miocene (MN 8 according to Rummel 2000, means MN 7+8).

Paratypes (measurements see Tables 1, 2).—Petersbuch 10: NHMA P10-608/36, 37, 2 left dentary fragments with teeth; NHMA P10-624/1+3, 2 left maxilla fragments wilth teeth; NHMA P10-625D1+H4, 2 upper molars; NHMA P10-610.2+612, 2 left humerus fragments; CRW P10-608–611, 613, 624, 625, 102 dentary fragments with teeth, 27 maxilla fragments with teeth, 44 isolated teeth, 11 humerus fragments, 5 ulna fragments.

Referred material, *L. bavaricum* vel *robustior* (measurements see Tables 1, 2).—Petersbuch 6: CRW P6-1063, 5 dentary fragments with teeth; Petersbuch 18: CRW P18-752, 756, 5 dentary fragments with teeth, 2 maxilla fragments with teeth, 5 isolated teeth.

Diagnosis.—*Leptoscaptor* species with slender humerus and a single mental foramen in the vast majority of the dentaries.

Description of the holotype

Only the horizontal ramus of the dentary anterior to m2 with c and p2–m1 *in situ* is preserved. The mental foramen is situated beneath the anterior alveolus of p3; the symphysis extends posteriorly to c/p2. The dental formula is reduced, two antemolar teeth being lost: probably the i3 and the p1. The lost incisor is interpreted as i3, because it is the smallest one in those scalopines where it is still present, for example, in *Proscapanus* and *Scalopoides*. In the designation of the missing tooth between i2 and p2 as the p1 (Hutchison 1968: 63) is followed. Based on the alveoles, the i2 was distinctly larger than the i1, both being procumbent. All teeth are heavily worn. The canine is single-rooted, chisel-shaped and slightly inclined anteriorly. The p2–p4 are double-rooted, increasing in size posteriorly. The protoconid of p2 and p3 is centred over the anterior root, a small heel over the posterior one. The p4 is more inflated, the heel a veritable talonid with posterior cuspule. In m1 the talonid is distinctly wider than the trigonid. The oblique cristid extends lingually, but does not join the postero-lingual face of the metaconid. The only cingulid is a short ectocingulid below the hypoflexid. The entostylid is small.

Description of paratypes and referred material

Dentary.—Some other specimens show the alveoli of two incisors, the canine, three premolars, and three molars. The mandibular dental formula is 2i, 1c, 3p, 3m. There is some

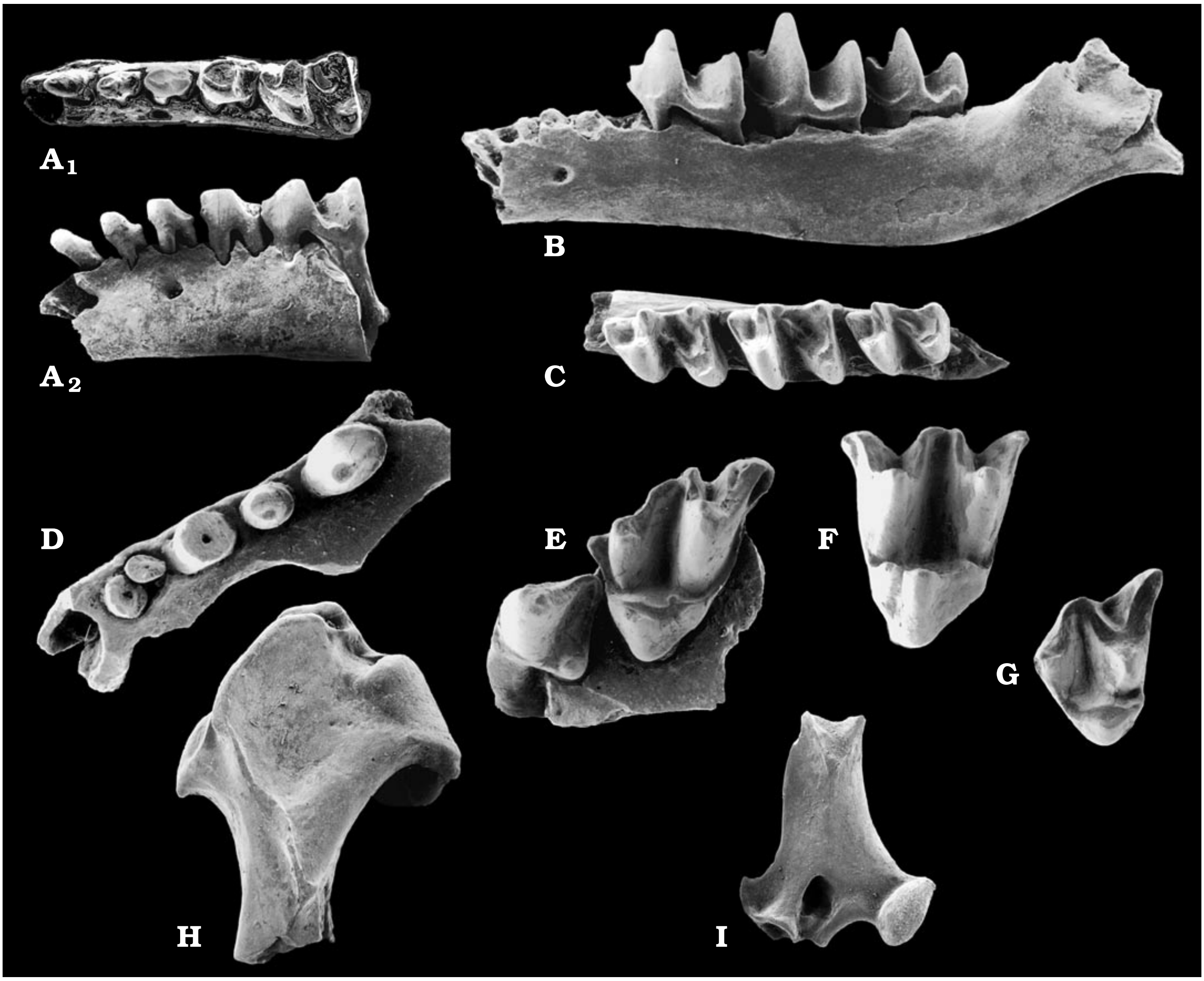

Fig. 2. *Leptoscaptor bavaricum* gen. et sp. nov., Petersbuch 10. **A**. Holotype, left dentary with c, p2–m1 and the alveoles of i1–i2, NHMA P10-608.6, in occlusal (A_1) and buccal (A_2) views; ca. × 10. **B**. Left dentary with m1–m3, NHMA P10-608.36, buccal view; ca. × 10. **C**. Left dentary with m1–m3, NHMA P10-608.37, occlusal view; ca. × 10. **D**. Left maxillary fragment with P1–P3 and the two roots of the canine, NHMA P10-624.1, occlusal view; ca. × 15. **E**. Left maxillary fragment with P4–M1, NHMA P10-624.3, occlusal view; ca. × 15. **F**. Left M2, NHMA P10-625D1, occlusal view; ca. × 15. **G**. Right M3, NHMA P10-625H4, occlusal view; ca. × 15. **H**. Left humerus, NHMA P10-612, proximal fragment, anterior view; ca. × 7.5. **I**. Left humerus, P10-610.2, distal fragment, anterior view; ca. × 7.5.

variability in the position of the mental foramen. In the Petersbuch 6 sample there are four dentaries with the mental foramen preserved. In one specimen there are two foramina, one below the posterior root of p2, the other beneath the posterior root of p4. In three further dentaries a single foramen is situated either beneath the anterior root of p3, or between the roots or under the posterior root of p3. In the Petersbuch 10 sample there is consistently one mental foramen: twice between the roots of p2 and p3, 24 times below the anterior root of p3, thrice between the roots of p3 and five times beneath the posterior root of p3. In the Petersbuch 18 sample there are four dentaries with the mental foramina preserved: one with one foramen between the roots of p4 and another between the roots of p2 and p3, one with the foramina under the anterior root of m1 and beneath p3/p4, respectively, and two dentaries with a single foramen below the posterior root of p4.

Lower dentition.—The i2 has a strong root, a laterally compressed crown with a mesial crest and no cingulids. It is distinctly larger than the canine. The p2 is similar to p3, but smaller. The size relation of the lower molars is consistently m2>m1>m3. In the m1 the trigonid is longer than in the m2, the talonid is distinctly wider than the trigonid. The oblique cristid terminates at the posterior wall of the trigonid well below the trigonid notch. As there is no metacristid the talonid is lingually open. The m2 has a very narrow trigonid, as it is known from *Proscapanus*. The trigonid is wider than the

Table 1. *Leptoscaptor*, sample statistics of the teeth (*L. bavaricum*, Petersbuch 10, *L. robustior*, Petersbuch 35, Petersbuch 48, *L. bavaricum–L. robustior,* Petersbuch 6, Petersbuch 18).

loc.	meas.	n	R	m	s	v
Petersbuch 6	Lp2–p4	1		2.71		
Petersbuch 10	Lp2–p4	1	2.45–2.72	2.58±0.05	0.083	3.21
Petersbuch 18	Lp2–p4	1		2.66		
Petersbuch 10	Lm1–m3	4	4.90–5.37	5.21		
Petersbuch 18	Lm1–m3	2	4.98–5.00	4.99		
Petersbuch 6	Hcor1	1		7.70		
	Hcor2	1		6.15		
Petersbuch 18	Hcor1			7.30		
	Hcor2			5.90		
Petersbuch 10	Li2	2	0.74–0.79	0.77		
	Wi2	2	0.42–0.49	0.46		
Petersbuch 6	Lcinf.	1		0.55		
	Wcinf.	1		0.43		
Petersbuch 10	Lcinf.	8	0.51–0.69	0.61	0.056	9.22
	Wcinf.	9	0.33–0.47	0.42	0.046	10.9
Petersbuch 6	Lp2	1		0.70		
	Wp2	1		0.42		
Petersbuch 10	Lp2	17	0.57–0.75	0.67±0.02	0.046	6.78
	Wp2	17	0.36–0.47	0.42±0.02	0.034	8.05
Petersbuch 18	Lp2	1		0.79		
	Wp2	1		0.50		
Petersbuch 6	Lp3	2	0.79–0.90	0.85		
	Wp3	2	0.49–0.56	0.53		
Petersbuch 10	Lp3	29	0.73–0.97	0.82±0.02	0.050	6.10
	Wp3	29	0.43–0.49	0.50±0.01	0.036	7.15
Petersbuch 18	Lp3	2	0.83–0.84	0.84		
	Wp3	2	0.47–0.59	0.53		
Petersbuch 48	Lp3	1		0.83		
	Wp3	1		0.45		
Petersbuch 6	Lp4	2	0.99–1.09	1.04		
	Wp4	2	0.60–0.68	0.64		
Petersbuch 10	Lp4	36	0.95–1.16	1.04±0.02	0.047	4.53
	Wp4	36	0.55–0.69	0.63±0.01	0.030	4.75
Petersbuch 18	Lp4	2	1.06–1.15	1.11		
	Wp4	2	0.58–0.71	0.65		
Petersbuch 35	Lp4	1		1.13		
	Wp4	1		0.63		
Petersbuch 48	Lp4	1		1.08		
	Wp4	1		0.58		
Petersbuch 6	Lm1	3	1.54–1.82	1.69		
	Wam1	3	0.94–1.03	0.98		
	Wpm1	4	1.09–1.27	1.18		
Petersbuch 10	Lm1	38	1.53–1.86	1.68±0.02	0.070	4.16
	Wam1	43	0.90–1.11	1.00±0.02	0.051	5.07
	Wpm1	43	1.10–1.37	1.19±0.02	0.054	4.51
Petersbuch 18	Lm1	4	1.65–1.82	1.75		
	Wam1	4	0.98–1.10	1.03		
	Wpm1	4	1.14–1.32	1.21		
Petersbuch 35	Lm1	4	1.74–1.98	1.82		
	Wam1	4	1.01–1.05	1.03		
	Wpm1	4	1.19–1.26	1.22		
Pet. 48	Lm1	1		1.87		
	Wam1	1		1.00		
	Wpm1	1		1.20		
Petersbuch 6	Lm2	4	1.85–1.95	1.92		
	Wam2	4	1.13–1.29	1.22		
	Wpm2	4	1.06–1.29	1.13		
Petersbuch 10	Lm2	35	1.66–2.02	1.90±0.03	0.085	4.44
	Wam2	40	1.11–1.36	1.24±0.02	0.060	4.82
	Wpm2	39	1.07–1.29	1.18±0.02	0.057	4.83
Petersbuch 18	Lm2	4	1.81–1.96	1.92		
	Wam2	4	1.14–1.36	1.22		
	Wpm2	4	1.12–1.20	1.16		
Petersbuch 35	Lm2	3	1.95–2.12	2.04		
	Wam2	3	1.27–1.28	1.27		
	Wpm2	2	1.15–1.19	1.17		
Petersbuch 6	Lm3	1		1.66		
	Wam3	1		1.07		
Petersbuch 10	Lm3	37	1.41–1.76	1.64±0.02	0.074	4.47
	Wam3	36	0.89–1.12	1.00±0.02	0.057	5.70
Petersbuch 18	Lm3	2	1.61–1.66	1.64		
	Wam3	3	0.93–0.98	0.96		
Petersbuch 35	Lm3	4	1.73–1.81	1.78		
	Wam3	4	1.01–1.10	1.06		
Petersbuch 48	Lm3	1		1.71		
	Wam3	1		0.97		
Petersbuch 10	LP1	2	0.63–0.80	0.72		
	WP1	2	0.48–0.51	0.50		
Petersbuch 10	LP2	2	0.54–0.54	0.54		
	WP2	2	0.42–0.43	0.43		
Petersbuch 10	LP3	4	0.82–0.91	0.87		
	WP3	4	0.56–0.64	0.59		
Petersbuch 18	LP3	1		0.64		
	WP3	1		0.46		
Petersbuch 10	LP4	16	1.38–1.63	1.46±0.04	0.073	4.96
	WP4	16	0.99–1.26	1.14±0.04	0.075	6.54
Petersbuch 18	LP4	2	1.36–1.42	1.39		
	WP4	2	0.98–1.13	1.01		
Petersbuch 35	LP4	2	1.47–1.66	1.54		
	WP4	2	1.21–1.32	1.27		
Petersbuch 10	LM1	29	2.04–2.50	2.27±0.04	0.113	4.97
	WM1	31	1.55–2.07	1.78±0.04	0.128	7.17
Petersbuch 18	LM1	3	2.34–2.44	2.40		
	WM1	3	1.66–1.74	1.69		
Petersbuch 48	LM1	1		2.36		
	WM1	1		1.72		
Petersbuch 10	LM2	7	1.69–1.87	1.80±0.07	0.065	3.64
	WM2	8	1.99–2.16	2.09±0.05	0.053	2.53
Petersbuch 18	LM2	1		1.66		
	WaM2	1		2.14		
Petersbuch 35	LM2	1		1.95		
	WaM2	1		2.04		
Petersbuch 48	LM2	1		1.88		
	WaM2	1		2.01		
Petersbuch 10	LM3	7	1.12–1.26	1.19±0.05	0.046	3.90
	WM3	7	1.55–1.80	1.65±0.08	0.082	4.93

talonid. The oblique cristid runs lingually to join the marked metacristid; the talonid is lingually closed. There is a prominent precingulid and a weak ectocingulid below the hypoflexid. The entostylid is small. The m3 is distinctly smaller than the m2, has a talonid reduced in width and no entostylid.

Table 2. *Leptoscaptor bavaricum* (Petetersbuch 10) and *L. robustior* (Petetersbuch 35, 48), sample statistics of the humeri.

Humerus	GL	Bp	BpwT	DS	Bd	BdwE	Bp*100/GL
Petetersbuch 10							
m		5.62	4.95	1.82	4.64	4.06	
min				1.70	4.62	3.94	
max				1.98	4.68	4.18	
n		1	1	10	3	7	
Petetersbuch 35							
m	10.5	6.35	5.70	2.61		5.29	60.5
min				2.41		4.98	
max				2.73		5.62	
n	1	1	1	9		9	1
Petetersbuch 48							
m	10.1	6.70	5.95	2.77	5.45	5.25	66.3
min				2.65		5.00	
max				2.90		5.45	
n	1	1	1	3	1	3	1

Maxilla.—Only two anterior fragments and some with one or two teeth are preserved. The two anterior fragments carry the double-rooted P1–P3 and the alveolus of the canine. In one specimen the canine is single-rooted but in the other double-rooted. Lingually to the canine alveolus of each fragment a foramen pierces the palate, probably the fissura palatina. In front of the canine alveolus there is one large incisor alveolus. The anteriormost part is broken. But on this small flake of bone broken off probably have been no incisor alveoli. Thus two incisors are eliminated, which ones cannot be determined. The maxillary dental formula is ?1-1-4-3. In one specimen the origin of the zygomatic arch above the metastyle of M2 is preserved; some other fragments show the lacrimal foramen above the anterior root of M1.

Upper dentition.—The antemolar size relation is I>>C~P3>P1>P2. P1–P3 are double-rooted and monocuspulate. The P3 has a small posterior cingulum. The only P4 of the Petersbuch 18 sample has a small protocone and a tiny parastyle, which is rather a small protuberance of the anterior cingulum. In the Petersbuch 10 sample in 15 P4 the parastyle is tiny with some transitions to a projecting parastyle in three specimens. The protocone is conical in 13 P4 and more or less fused with the lingual cingulum in 5 P4. The mesostyle is clearly divided in all molars. Para- and metaconule are hardly individualised in the M1. The preprotocrista is continuous with paracingulum, which joins a more or less projecting parastyle. Postproto- and postmetacrista run parallel to one another, the premetacrista parallel to the anterior margin. The four roots are situated above protocone, paracone, metastyle, and a very small one above and slightly labial to the centre. In the M2 para- and metaconule are somewhat better developed. The parastyle is completely fused with the preparacrista. Neither a para- nor a metacingulum is developed. On the M3 there are no lingual conules and no paracingulum. There are no labial and lingual cingula in the upper molars.

Humerus.—No complete humerus is preserved, but 12 distal fragments and one proximal from Petersbuch 10. The overall morphology and slenderness indicates a moderate stage of fossorial adaptation. The proximal epiphysis is wider than the distal one. The head is directed parallel to the shaft. The brachialis fossa is large but not very deep. The teres tubercle is moderately long and situated close to the pectoral crest. The pectoral tubercle is situated in mid-shaft position. The deltoid process is short. A prominent scalopine ridge runs from the head to the medial side of the lesser tubercle and separates two areas in different planes. The area delimited by pectoral crest, pectoral ridge and greater tubercle is slightly concave. The notch between head and lesser tuberosity is well defined. On the distal epiphysis there is a large olecranon fossa and a somewhat smaller supratrochlear fossa. The trochlea is broad, thus leaving only a narrow notch between trochlea and the fossa for the m. flexor digitorum profundus ligament.

Ulna.—Only the proximal part is preserved. The abductor fossa is deeply excavated. The proximal crest forms a large blade widely separated from the semilunar notch. A prominent processus anconaeus and smaller but distinct coronoid process delimit the well-defined semilunar notch.

Comparisons

Leptoscaptor shows clear scalopine affinities as defined by Hutchison (1968: 58): the enlarged i2, not enlarged p1 and upper canine, moderately to very broad humerus with a moderately deep brachialis fossa. The allocation with any other talpine tribe can be excluded with certainty. Consequently, with few exceptions, we can restrict our comparison to scalopine genera.

The only Recent Old World member of the Scalopini as defined by Hutchison (1968) is *Scapanulus oweni* Thomas, 1912, the Kansu mole, which lives in parts of China. It corresponds to *Leptoscaptor* in dental formula, the number of roots in the P1–P3 and in the divided mesostyles of the upper molars. However, *Leptoscaptor* differs from this species in:

- the absence of a metastylid on m2 and m3,
- the trigonid of the m1, which is not compressed anteroposteriorly,
- the double-rooted p2,
- the small but present parastyle on P4,
- the pectoral tubercle situated more in the midline of the shaft,
- the greater tubercle and head of the humerus not being twisted medially.

No specimen has been seen. The *Scapanulus oweni* criteria have been concluded from Storch and Qiu (1983: 119) and from Hutchison (1968: figs. 10D, 11).

Proscapanus Gaillard, 1899 (including *Alloscapanus* Baudelot, 1968) from the Early and Middle Miocene of Europe is distinguished from *Leptoscaptor* in:

- the complete lower and upper dental formula,
- the well-developed metastylids on m2 and m3,

- the more lingual termination of the oblique cristid on m1,
- the better-developed cingulids,
- the more robust humerus, which indicates a better fossorial adaptation.

"Scalopoides" agrarius (Skoczeń, 1980) from the Ruscinian of Poland and Germany, described by Skoczeń as *Scapanulus agrarius* and referred to "*Scalopoides*" by Dahlmann (2001), has similar measurements on the humerus (see Dahlmann 2001: table 8; Skoczeń 1980: table 11). However, if we compare the figures of the humeri of *S. agrarius* (Dahlmann 2001: fig. 7.4; Skoczeń 1980: pl. 7/4) to those of *Leptoscaptor* (see Fig. 2H, I) the latter is distinctly more slender. Furthermore, the Ruscinian species differs from *Leptoscaptor* in:

- the oblique cristid of m1 and m2 terminating more buccally,
- the absence of a metacristid on m2,
- the undivided mesostyle on M2 and M3,
- the prominent para- and metaconule on M2.

Scalopoides Wilson, 1960 from the Hemingfordian (Middle Miocene) to Clarendonian (Early Pliocene) and the Hemphillian (Late Pliocene) of the United States has a more robust humerus (cf. Hutchison 1968: fig. 55, table 15), thus indicating a more advanced fossorial adaptation. In the dentition it differs from *Leptoscaptor* in:

- the presence of the i3,
- the well-developed metastylid on m2 and m3,
- the weakly divided mesostyle on the upper molars,
- the better-developed metaconule and metacingulum on M1.

Scapanoscapter Hutchison, 1968 from the Barstovian (Late Miocene) of Oregon is known only from its dentition. In addition to its distinctly bigger size it differs from *Leptoscaptor* in having:

- a complete lower dentition,
- a not hypertrophied i2,
- lower molars with antero-posteriorly more compressed trigonids.

Domninoides Green, 1956 from the Lower Pliocene in South Dakota and from some Late Miocene sites in North America has a more reduced lower dentition and a more robust humerus (see Green 1956: fig. 4; Hutchison 1968: fig. 68).

cf. *Scalopoides* sp. from the Middle Miocene of La Grive is represented by a humerus and some additional similar humeri, referred to the genus by Hutchison (1974). This humerus (see Hutchison 1974: figs. 18, 19) is quite similar in slenderness and overall size to the humeri under study. With some reserve we can refer it to *Leptoscaptor*. However, there are no dental remains in the La Grive fauna similar to those of *Leptoscaptor*.

Leptoscaptor is readily distinguishable from all living North American scalopines. *Parascalops* True, 1894 and *Scapanus* Pomel, 1848 have a complete lower dentition (3i, 1c, 4p, 3m) and single-rooted p1–p3. Furthermore, their broader humeri indicate a distinctly better fossorial adaptation. *Scalopus* Desmarest, 1804 also has a broader humerus, a greatly reduced dentition and hypsodont teeth.

Yanshuella Storch and Qiu, 1983 from Late Turolian or Ruscinian of Inner Mongolia and from the Hemphillian of Oregon is distinguished from *Leptoscaptor* in:

- more robust humerus,
- in the presence of three upper and lower incisors,
- in the single-rooted p2,
- the presence of a small metaconid on p4,
- the better developed cingula on all teeth,
- the oblique cristid terminating more buccally on m2 and m3,
- the undivided mesostyle on the upper molars.

Yunoscaptor Storch and Qiu, 1991 from the Late Miocene of the Yunnan Province, China, so far represented by its type species *Y. scalprum* only, is in fossorial adaptation quite similar to *Leptoscaptor*. The Chinese genus differs from ours in (cf. Storch and Qiu 1991):

- the larger overall size,
- the complete set of three lower incisors with an enlarged i1,
- the single-rooted p2,
- the higher-crowned lower molars,
- the undivided mesostyles on the upper molars,
- the head of the humerus, which is directed medio-distally.

Mongoloscapter Lopatin, 2002 is a monospecific scaptonychine genus from the Oligocene Shand Gol Formation of the Tatsin Gol locality in Mongolia. *Mongoloscapter zhegalloi* Lopatin, 2002 is known only from its type, a dentary fragment with m2–m3. This is an extraordinarily poor basis for the designation of a new genus. This specimen differs from *Leptoscaptor* in (cf. Lopatin 2002):

- its wider m2 and m3 with well-developed metastylid,
- the oblique cristid joining the metacristid.

Van den Hoek Ostende (2001) described the new talpid subfamily Suleimaninae with the only species *Suleimania ruemkae* Van den Hoek Ostende, 2001 from the Lower Miocene localities Harami, Kilçak, and Keseköy in Anatolia. This species is mainly known from isolated teeth. This large-sized species is distinctive by the loss of the M3 and the loss of the talonid in the m3, a character known from the erinaceines and the dimylid *Exoedaenodus*. Furthermore, this species differs from *Leptoscaptor* in:

- the sharp cutting edges of the premolars,
- the inflated cusps of the m1 and M1,
- the presence of a well-developed hypocone in the upper molars.

Hugueneya Van den Hoek Ostende, 1989 is a monospecific species from the Early Miocene of South Germany. The only species *H. primitiva* (Hutchison, 1974), in spite of being also a scalopine, cannot be confused with *Leptoscaptor*. *Hugueneya* differs from *Leptoscaptor* in (cf. Hutchison 1974: fig. 21, pl. 39):

- the presence of four lower premolars,
- the more inflated teeth,

- the more prominent metaconule and the more spaced mesostyles of the upper molars,
- the distinctly more robust humerus.

Discussion

Along with *Talpa minuta*, *Leptoscaptor bavaricum* represents the most common talpid in the samples of Petersbuch 6, 10, and 18. Petersbuch 10 yielded the most numerous sample of this species and the only one with postcranial bones. Therefore it was chosen as type locality though the dentaries are better preserved in Petersbuch 6 and 18. The association of lower and upper dentition and of the humerus fragments to the dental remains is without alternative and is certainly correct. The ulna fragments match the humerus fragments in size. The only noticeable difference between the three samples is the position of the mental foramen. It is more variable in the smaller samples than in Petersbuch 10. In the size of the teeth there are no significant differences between the three samples even though some specimens of Petersbuch 18 are slightly smaller (P3) or larger (p2) than the corresponding teeth of the Petersbuch 10 sample. In the talpid samples of Petersbuch 6 and 18 there are no postcranial remains left that can be associated with the teeth of *Leptoscaptor*. There is another species of *Leptoscaptor* with a somewhat more robust humerus, *L. robustior*. This species can unambiguously be identified in its type locality Petersbuch 35. As the fissures from Petersbuch 6, 10, and 18 are directly adjacent to one another, they probably all belong to one fissure system and all three fissure fills may result from the same filling process. Consequently, the three samples possibly represent only one population instead of three different ones. This spatial viewpoint argues in favour of an affiliation between the Petersbuch 6 and 18 samples with *L. bavaricum*. However, the position of the mental foramen is more variable in Petersbuch 6 and especially in Petersbuch 18, as it is characteristic of the Petersbuch 35 sample, which undoubtedly represents *L. robustior*. Therefore, we cannot exclude with certainty that either Petersbuch 6 or Petersbuch 18 or even both samples represent *L. robustior*. The fact that two species only can unambiguously be identified by their humeri is not unique to the genus *Leptoscaptor*. Regarding *Paratalpa*, an Oligocene to Agenian genus, and *Desmanodon*, which appeared in Europe in the Orleanian, there are even two different genera that are only distinguishable by their humeri (see discussion in van den Hoek Ostende 1989, Ziegler 1990). However, in talpids the humeri usually allow discrimination to the level of the tribe and the dentition is more distinctive.

Regarding the loss of two lower antemolars, *Leptoscaptor* is more advanced than the majority of the scalopine genera. Only the living *Scalopus* from North America has more reduced dentition with single-rooted premolars. For *Scapanulus* the data are somewhat contradictory. Storch and Qiu (1983: 119) mention the loss of two upper and lower antemolars of questionable homologies. Consequently, the dental formula could be as in *Leptoscaptor*. Hutchison (1968: 74), in contrast, mentions a complete lower dentition. Gerhard Storch told me that his antemolar count is correct (personal communication, 18th December 2002). Ziegler (1971: 59) gives the same conclusion as Storch and Qiu, referring to the original description by Thomas (1912: 397). Obviously, Hutchison's antemolar count is erroneous.

Concerning the number of roots in the lower premolars, *Leptoscaptor* is less advanced than all living scalopines. As *Scalopus* is too specialised in other characteristics and as the other extant species have more complete dentitions, *Leptoscaptor* cannot be ancestral to any extant genus. Obviously it is a Miocene offshoot that became extinct somewhat later.

Leptoscaptor robustior gen. et sp. nov.

Fig. 3.

Etymology: From Latin *robustior*, more robust. The humerus is more robust than in the type species *L. bavaricum*.

Holotype: Right humerus, NHMA P35-58/6, fig. 3A.

Measurements of the holotype: GL (10.5), Bp (6.35), BpwT (5.70); SD (2.56), BdwE (5.14), Bp*100/GL (60.5).

Type locality: Petersbuch 35 (details see p. 618).

Age: Uppermost part of the Middle Miocene (MN 8 according to Rummel 2000, means MN 7+8.)

Paratypes (measurements see Tables 1, 2).—Petersbuch 35: NHMA P35-57A1, right dentary fragment with teeth; CRW P35-57+58, 4 dentary fragments with teeth, left maxilla fragment with p4, 7 isolated teeth, 11 humerus fragments, right ulna fragments.

Referred material (measurements see Tables 1, 2).—Petersbuch 48: CRW P48-93–94, left dentary fragment with p3–p4, right maxilla fragment with M2, 3 isolated teeth, 3 humerus fragments.

Diagnosis.—Medium-sized species of *Leptoscaptor* with postcranial elements more robust than in the type species and with two mental foramina on the dentary.

Description of the holotype

Pectoral crest, deltoid process and the epicondylar spines are broken. The long axis of the elliptical head is directed parallel to the shaft. The marked scalopine ridged separates two areas in different planes. The brachialis fossa is moderately deep. The anterior aspect shows the pectoral process in midshaft position and a concave area delimited by pectoral crest, pectoral ridge, and greater tubercle. Above the distal epiphysis there is a wide olecranon fossa and a small supratrochlear fossa. The broad trochlea only leaves a narrow notch, separating trochlea and the fossa for the m. flexor digitorum profundus ligament.

Description of paratypes and referred material

Dentary.—There are five fragments of the horizontal ramus from Petersbuch 35, and one from Petersbuch 48. The consistent presence of two mental foramina is characteristic: below the anterior roots of p3 and p4 (once), beneath the posterior root of p2 and between the roots of p4 (twice), below the anterior root of p3 and under the posterior root of p4 (once) in

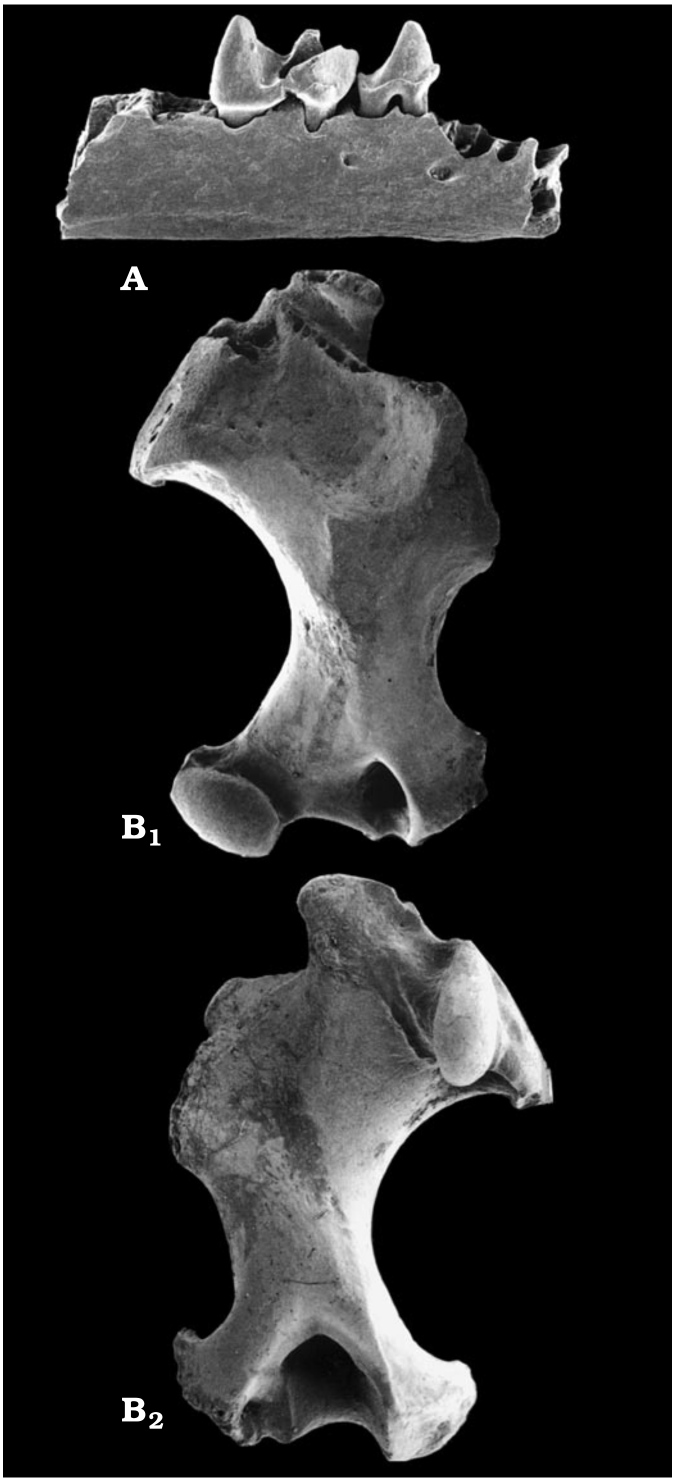

Fig. 3. *Leptoscaptor robustior* gen. et sp. nov., Petersbuch 35. **A**. Right dentary with p4–m1, NHMA P35-57A1, buccal view; ca. × 10. **B**. Holotype, right humerus, NHMA P35-58/6, in anterior (B_1) and posterior (B_2) views; ca. × 7.5.

the Petersbuch 35 sample. In the Petersbuch 48 specimen one mental foramen is situated beneath the anterior root of p3, another below the anterior root of p4. In two specimens the alveoles of the double-rooted p2–p3 and the single-rooted canine are preserved. The Petersbuch 48 dentary also preserves the canine alveolus and the two incisor alveoli, indicating that i2 was larger than i1.

Teeth.—In the morphology of the preserved teeth there is no difference to those of *L. bavaricum*.

Postcranial bones.—Aside from the type specimen there are 11 additional humerus fragments from Petersbuch 35 and three from Petersbuch 48, which correspond in robustness. The ulna fragment from Petersbuch 35 was referred because of matching size. It has a deep abductor fossa.

Comparisons

L. robustior is quite similar to the type species of the genus *L. bavaricum*. Only this species can be confused and needs to be differentiated. *L. robustior* differs in:

- the consistent presence of two mental foramina, which are situated slightly more posterior,
- a distinctly more robust humerus.

Discussion

In the small talpid sample from Petersbuch 35 there are only two species: *Proscapanus sansaniensis* and *Leptoscaptor robustior*. As both species differ markedly in size and robustness of the humerus they are easily distinguishable. Assuming that there are not two different species, one being represented by teeth only and the other exclusively by postcranial elements, the association of postcranial elements and dental remains in *Leptoscaptor robustior* is without alternative. In the Petersbuch 48 talpid fauna there are only three species, which also can be readily distinguished: *P. sansaniensis*, *Talpa minuta* and *L. robustior*. The difference in robustness of the nearly complete humeri from Petersbuch 35 and 48 lies well within the range of a population. The more robust humerus of *L. robustior* indicates a better fossorial adaptation than in *L. bavaricum*. Without humeri the *Leptoscaptor* species are hardly distinguishable. Nevertheless, I am convinced that they represent different biological adaptations (see also chapter discussion of *L. bavaricus*).

Proscapanus Gaillard, 1899

Type species: *Proscapanus sansaniensis* (Lartet, 1851).

Proscapanus sansaniensis (Lartet, 1851)

Fig. 4.

Material (measurements see Tables 3, 4).—Petersbuch 10: CRW P10-620–621, left dentary fragment with p1–p3, right humerus. Petersbuch 31: NHMA P31-163A1, 163C1, 163E3, 162B2, 164A1, 2 dentary fragments with teeth, 2 upper teeth, left humerus; CRW P31-163, 164, 4 dentary fragments with teeth, 2 maxilla fragments with teeth, 8 isolated teeth, 6 humeri, 5 ulnae, 3 radii. Petersbuch 35: CRW P35-55, 56, 5 isolated teeth, left humerus, left ulna fragment, right radius. Petersbuch 48: NHMA P48-89A1+B2, right dentary fragment with teeth, left M1; CRW P48-89, 90, right maxilla fragment with P4, 4 isolated teeth, 4 humeri.

Table 3. *Proscapanus sansaniensis*, sample statistics of the teeth.

loc.	meas.	n	R	m	s	V
Petersbuch 31	Lp1–p4	1		3.99		
Sansan	Lp1–p4	3	3.41–3.88	3.66		
Petersbuch 31	Lm1–m3	1		7.02		
Sansan	Lm1–m3	4	6.54–7.04	6.77		
Petersbuch 10	Lp1	1		0.83		
	Wp1	1		0.65		
Petersbuch 31	Lp1	1		0.78		
	Wp1	1		0.60		
Sansan	Lp1	7	0.80–0.87	0.82±0.02	0.024	2.95
	Wp1	7	0.59–0.70	0.63±0.04	0.045	7.05
Petersbuch 10	Lp2	1		0,90		
	Wp2	1		0,54		
Petersbuch 31	Lp2	1		0.86		
	Wp2	1		0.61		
Sansan	Lp2	9	0.54–0.92	0.79±0.09	0.113	14.4
	Wp2	9	0.52–0.60	0.56±0.02	0.026	4.67
Petersbuch 10	Lp3	1		1.11		
	Wp3	1		0.65		
Petersbuch 31	Lp3	1		0.96		
	Wp3	1		0.65		
Sansan	Lp3	8	0.73–0.95	0.84±0.08	0.085	10.1
	Wp3	8	0.52–0.66	0.58±0.03	0.038	6.60
Petersbuch 31	Lp4	2	1.44–1.50	1.47		
	Wp4	2	0.87–0.86	0.84		
Petersbuch 48	Lp4	2	1.54–1.55	1.55		
	Wp4	2	0.84–0.91	0.88		
Sansan	Lp4	15	1.19–1.39	1.32±0.03	0.058	4.39
	Wp4	17	0.74–0.97	0.85±0.03	0.057	6.69
Petersbuch 31	Lm1	4	2.42–2.60	2.49		
	Wam1	4	1.16–1.26	1.22		
	Wpm1	4	1.40–1.49	1.46		
Petersbuch 48	Lm1	1		2.43		
	Wam1	1		1.41		
	Wpm1	1		1.44		
Sansan	Lm1	29	2.19–2.44	2.30±0.03	0.069	3.01
	Wam1	30	1.20–1.47	1.29±0.02	0.061	4.69
	Wpm1	31	1.33–1.63	1.45±0.02	0.068	4.68
Petersbuch 31	Lm2	4	2.64–2.67	2.65		
	Wam2	4	1.42–1.45	1.44		
	Wpm2	4	1.31–1.35	1.33		
Petersbuch 48	Lm2	2	2.58–2.62	2.60		
	Wam2	2	1.47–1.51	1.49		
	Wpm2	2	1.26–1.34	1.30		
Sansan	Lm2	23	2.27–2.68	2.48±0.04	0.098	3.97
	Wam2	23	1.38–1.63	1.51±0.03	0.062	4.08
	Wpm2	23	1.27–1.50	1.37±0.03	0.062	4.55
Petersbuch 31	Lm3	2	2.14–2.16	2.15		
	Wam3	2	1.21–1.21	1.21		
Petersbuch 35	Lm3	1		2.17		
	Wam3	1		1.30		
Petersbuch 48	Lm3	1		2.11		
	Wam3	1		1.16		
Sansan	Lm3	22	1.92–2.29	2.05±0.05	0.102	4.95
	Wam3	23	1.07–1.35	1.22±0.03	0.072	5.93
Petersbuch 35	LP3	1		1.17		
	WP3	1		0.82		
Petersbuch 31	LP4	1		1.78		
	WP4	1		1.45		
Petersbuch 35	LP4	1		2.02		
	WP4	1		1.76		
Petersbuch 48	LP4	1		1.88		
	WP4	1		1.65		
Sansan	LP4	16	1.68–1.96	1.87±0.04	0.076	4.16
	WP4	16	1.35–1.65	1.53±0.05	0.089	5.79
Petersbuch 31	LM1	3	2.98–3.08	3.03		
	WM1	3	2.40–2.57	2.50		
Petersbuch 48	LM1	2	2.98–3.00	2.99		
	WM1	2	2.00–2.14	2.07		
Sansan	LM1	12	2.61–3.02	2.86±0.09	0.134	4.40
	WM1	10	2.22–2.60	2.39±0.08	0.110	4.58
Petersbuch 31	LM2	3	2.37–2.62	2.49		
	WM2	3	2.49–2.67	2.56		
Petersbuch 35	LM2	1		2.25		
	WaM2	1		2.38		
Sansan	LM2	9	2.15–2.56	2.33±0.11	0.135	5.78
	WaM2	21	2.38–2.81	2.57±0.06	0.132	5.15
Petersbuch 31	LM3	3	1.43–1.52	1.46		
	WM3	2	2.01–2.05	2.03		
Sansan	LM3	16	1.25–1.63	1.42±0.05	0.099	6.94
	WM3	16	1.75–2.10	1.89±0.06	0.107	5.67

Description

Dentary—Only some more or less complete fragments of the horizontal ramus are preserved. The jaw slightly tapers anteriorly. The dentary fragment from Petersbuch 10 shows mental foramina below p4/m1 and beneath p2. In two specimens from Petersbuch 31 the anterior mental foramen is situated between the roots of p2 and p3, the posterior one under the trigonid of m1. In the dentary fragment from Petersbuch 48 there are three mental foramina, one situated between the roots of p1 and p2, and one below the anterior and posterior root of p4 each. All teeth anterior to p4 are single-rooted. According to their alveoles the three incisors are increasingly inclined anteriorly, i2 being larger than i1 and i3. The canine is only slightly inclined anteriorly.

Lower dentition.—p1 to p3 are slightly inflated and increase in size. There is an incipient anterior crest extending toward the apex of the protoconid. A faint posterior basal cuspule is developed. The p4 is rectangular in occlusal outline and has an antero-buccal and posterior cingulid, the latter culminating in a postero-lingual basal cuspule. The sizes of the molars are ranked in the following order, m2>m1>m3. The oblique cristid extends lingually to join the metacristid. In the m1 the paralophid is curved and leaves a long trigonid, whereas it is very short in m2 and m3. There is a marked precingulid in m2 and m3. In the Petersbuch 31 sample the pre- and ectocingulid of m1 are indistinct, whereas they are better developed in the Petersbuch 48 dentary. In the m1 the talonid is wider than the trigonid, in the m2 the trigonid is

Table 4. *Proscapanus sansaniensis*, measurements of some postcranials.

Humerus		GL	Bp	BpwT	DS	Bd	BdwE	Bp*100/GL
Petersbuch 10	m	16.5	11.7	9.6	4.75	10.6	9.5	70.9
	n	1	1	1	1	1	1	1
Petersbuch 31	m	14.7	10.9	9.35	4.28±0.20	9.6	8.80	74.6
	V				4.02			
	s				0.17			
	min	14.4	10.7	9.10	4.00	9.6	8.50	74.5
	max	14.9	11.1	9.60	4.50	9.6	8.90	74.7
	n	2	2	2	6	2	2	2
Petersbuch 35	m	14.8	10.7	9.00	3.90			72.3
	n	1	1	1	1			1
Petersbuch 48	m	14.5	10.6	9.30	4.20	9.4	8.6	75.7
	tomin	14.0			3.90	9.1	8.4	
	max	15.0			4.30	9.9	9.1	
	n	2	1	1	4	4	4	1
Sansan	m	13.53±0.19	4.46±0.24	9.78±0.28	3.98±0.11	8.85±0.28	8.00±0.26	72.5±1.4
	V	2.65	9.71	5.43	5.50	3.86	6.07	3.40
	s	0.358	0.433	0.531	0.219	0.342	0.486	2.465
	min	12.5	3.65	8.25	3.35	8.26	6.70	66.0
	max	13.9	5.15	10.4	4.25	9.42	8.50	76.0
	n	17	16	17	18	9	17	16

Radius		L1	L2
Petersbuch 31	m	10.7	9.5
	min	10.4	9.0
	max	11.0	9.9
	n	2	2
Petersbuch 35	m	11.7	9.9
	n	1	1
Sansan	m	9.92±0.56	8.78±0.50
	V	3.88	4.12
	s	0.385	0.362
	min	9.52	8.33
	max	10.4	9.2
	n	5	5

Ulna		GL
Petersbuch 31	m	18.0
	n	1
Sansan	m	16.9
	n	1

somewhat wider and in the m3 distinctly wider than the talonid.

Maxilla.—Two fragments from the Petersbuch 31 sample show the infraorbital foramen above the mesostyle of M1, the anterior opening of the infraorbital canal above the posterior root of M2 and the origin of the zygomatic arch above M3.

Upper dentition.—Only P4 to M3 are preserved. The P4 has an indistinct, hardly projecting parastyle. On the lingual talon there is no vestige of a protocone, but a lingual cingulum. The molars have four roots, the posterior one being the strongest and the central one the weakest. The M1 has a deeply divided mesostyle, a slightly projecting parastyle and indistinct para- and metaconule. The marked paracingulum joins the parastyle; the metacingulum tapers but extends to the postero-labial corner. The M2 also has a divided mesostyle. In some specimens the lingual conules are somewhat better developed than in the M1. Para- and metacingulum are either very thin or even absent. In the M3 the mesostyle is only superficially divided. There are only three M3 from the Petersbuch 31 sample, which are assumed to belong with *Proscapanus sansaniensis* because of their size. One has a marked paracingulum, in two M3 it is absent.

Postcranial bones—The humerus strongly resembles the specimens from Sansan in all morphological details and in gracility. The brachialis fossa is deeply excavated, the teres tubercle long, the supratrochlear fossa small, and the scalopine ridge marked and shelf-like.

In the ulna the most conspicuous character is the deep abductor fossa, which extends on the proximal moiety of the lateral side. The proximal crest delimits the large area of insertion for the triceps.

The radius has a capitular process projecting proximally. The distal joint is characterised by the large scaphoid articular facet.

Discussion

Proscapanus sansaniensis is based on an anterior fragment of a dentary with the four premolars from Sansan, described by Lartet (1851: 13) as *Mygale sansaniensis*. Gaillard (1899) described *Proscapanus sansaniensis* and selected as type the humerus from Sansan, once described as *Talpa sansaniensis* by Lartet (1851: 14). Ginsburg (1963) synonymized the type of *Mygale sansaniensis* with *Proscapanus sansaniensis*. The dentary fragment of *Mygale sansaniensis* is the valid type by page priority over the lectotype humerus of *Talpa sansaniensis*. *Alloscapanus auscitanensis* from Sansan was de-

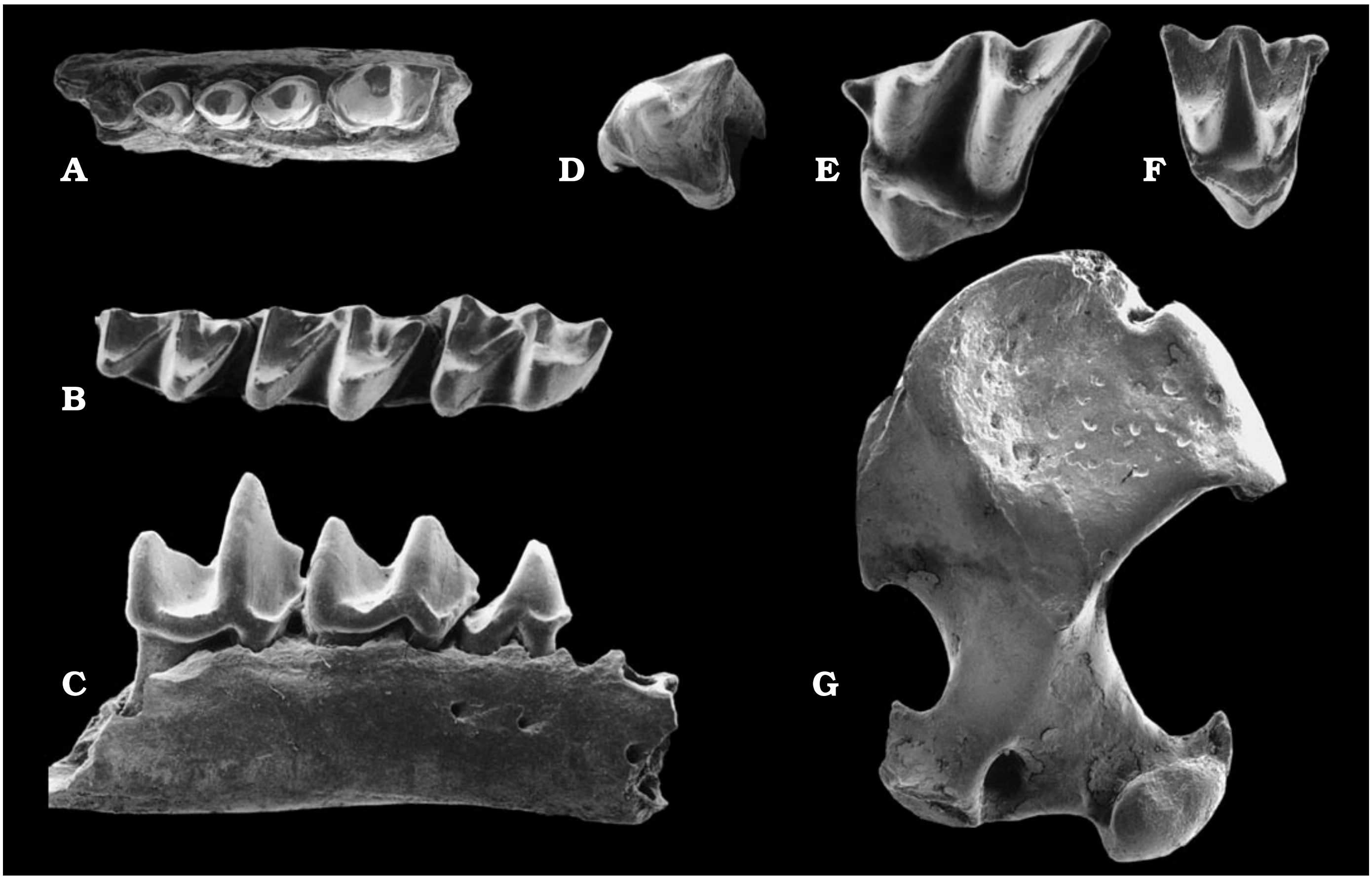

Fig. 4. *Proscapanus sansaniensis*. **A**. Left dentary fragment with canine root and p1–p4, Petersbuch 31, NHMA P31-163A1, occlusal view; ca. × 10. **B**. Right m1–m3, Petersbuch 31, NHMA P31-163B2, occlusal view; ca. × 10. **C**. Right dentary fragment with p4–m2, Petersbuch 48, NHMA P48-89A1, buccal view; ca. × 10. **D**. Left P4, Petersbuch 31, NHMA P31-163C1, occlusal view; ca. × 10. **E**. Left M1, Petersbuch 48, NHMA P48-89B2, occlusal view; ca. × 10. **F**. Right M2, Petersbuch 31, NHMA P31-163E3, occlusal view; ca. × 10. **G**. Left humerus, Petersbuch 31, NHMA P31-164A1, anterior view; ca. × 5.

scribed by Baudelot (1968). She referred to this species the type of *Mygale sansaniensis*. As this is not conformable with rules of the International Code of Zoological Nomenclature (for the current edition, see ICZN 1999), Hutchison (1974: 233) synonymized *Alloscapanus auscitanensis* with *Proscapanus sansaniensis*. Hutchison (1974) comments upon the somewhat confusing typology of the species in more detail.

The ample material of Sansan is the reference sample of *Proscapanus sansaniensis*. The Petersbuch specimens fit morphologically well with *Proscapanus sansaniensis* from the type locality Sansan. In most dentaries from Sansan the anterior mental foramen is situated between p1 and p2, and below p2, the posterior one under the posterior root of p4. In the dentary from Petersbuch 31 the mental foramina are slightly shifted posteriorly. The size differences between the teeth and bones of the Petersbuch samples on the one hand and Sansan sample on the other are more marked. This is not due to sample bias. In some teeth (p4–m2) the length measurements from Petersbuch exceed the size range of the larger sample from Sansan. This means that these teeth are more slender than in Sansan. Only the p1 from Petersbuch 31 is smaller than in the Sansan sample. In Sansan in three dentaries p1>p2, in the type dentary with p1–p4, p1, and p2 have the same length, but p1 is somewhat wider than p2. This means that p1 is enlarged with respect to p2 and p3 in Sansan, whereas in Petersbuch 31 the size relation is p1<p2<p3<p4. In the upper dentition the size differences are less obvious. Some P4 are wider, some M1 more slender than in the Sansan sample, and the M2 fit reasonably with Sansan. As much as can be concluded from a few measurements, the Petersbuch specimens correspond well in size *P. sansaniensis* from La Grive (cf. Baudelot 1972: table 13). However, the m1 are also wider in this sample. As there is no clear size trend visible and as there are no mentionable morphological differences, the description of a new species is considered neither necessary nor advisable. Obviously *Proscapanus sansaniensis* is a species with a large variability in size, as is already evident from the samples of the Upper Freshwater Molasse in South Germany, e.g., Sandelzhausen (cf. Ziegler 2000: fig. 2).

Proscapanus sansaniensis is a species with a wide temporo-spatial distribution. It is recorded from Germany, Switzerland and France, from sites correlative with MN 4 (Vieux Collonges, Mein 1958) to MN 9 (Nebelbergweg, Kälin and Engesser 2001). The northernmost occurrence is from Hambach in the Lower Rhine Embayment (Ziegler and Mörs 2000).

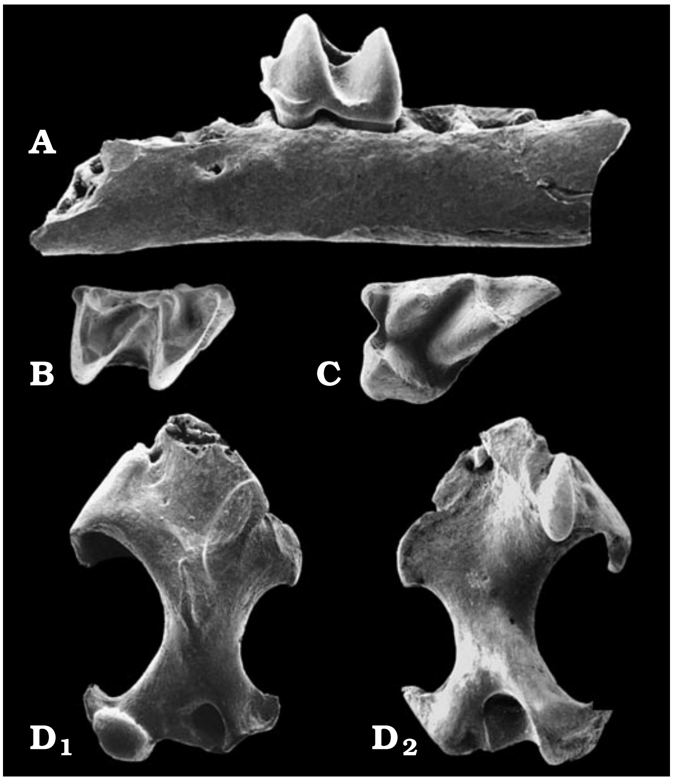

Fig. 5. *Proscapanus* sp., Petersbuch 31. **A**. Left dentary with m1, NHMA P31-169/1, buccal view; ca. × 10. **B**. Right m2, NHMA P31-169/3, occlusal view; ca. × 10. **C**. Left M1, NHMA P31-169/6; ca. × 10. **D**. Right humerus, NHMA P31-170/1, in anterior (D_1) and posterior (D_2) views; ca. × 5.

Proscapanus sp.

Fig. 5.

Material (measurements see Tables 5, 6).—Petersbuch 31: NHMA P31-169/1, 3, 6, P31-170/1, left dentary fragment with m1, 2 isolated teeth, right humerus; CRW P31-169/2, 4, 5, 7, P31-170/2–4, 4 isolated teeth, 3 radii.

Description

A formal description is considered superfluous, as the specimens are morphological quite similar to *Proscapanus sansaniensis*. Therefore I confine myself to noting the differences. In the dentary, the mental foramen is situated under the anterior root of p4. Nine alveoli anterior to m1 are preserved, two for the p4 and one for the three incisors, the canine, and the single-rooted p1–p3 respectively. However, I am not sure that in spite of the fracture really all alveoli are preserved. In the m1 the oblique cristid joins a very strong metacristid, which does not extend to the apex of the metaconid. The precingulid is faint. In the m2 and m3 the strong metacristid and precingulid are conspicuous. The M1 differs from *P. sansaniensis* in the more projecting parastyle and, most notably, in the undivided mesostyle. The humerus and radius fragments are reservedly assigned to the dental remains because of compatible size. I cannot exclude that some or all belong with the dentary of the indeterminate scalopine. The humerus has the characteristic shelf-like scalopine ridge and fits in all morphological details with the humerus *P. sansaniensis*. The radius fragments show no peculiarities.

Table 5. *Proscapanus sp.*, Petersbuch 31, sample statistics of the teeth.

meas.	n	R	m
Lm1	1		1.83
Wam1	1		1.10
Wpm1	1		1.28
Lm2	1		2.15
Wam2	1		1.26
Wpm2	1		1.25
Lm3	2	1.75–1.80	1.88
Wam3	2	1.13–1.14	1.14
LM1	2	2.76–2.79	2.78
WM1	2	1.94–1.96	1.95

Table 6. *Proscapanus* sp., Petersbuch 31, measurements of the humerus.

GL	Bp	BpwT	DS	Bd	BdwE	Bp*100/GL
9.38	6.25	5.31	2.17	5.35	4.80	66.6

Discussion

The above listed specimens are distinctly smaller than in *Proscapanus sansaniensis* and the undivided mesostyle is not compatible with this species. In size they would roughly fit with *P. intercedens* Ziegler 1985 from some Lower Miocene localities in South Germany (cf. Ziegler 1985). But in this species the mesostyle of the upper molars also is divided, albeit only superficially, and all lower premolars are double-rooted. This species can be excluded. As *P. intercedens* is considered to be a predecessor of *P. sansaniensis*, we do not expect it in faunas with late Middle Miocene correlation. *P. sansaniensis* is in most faunas accompanied by a smaller *Proscapanus*, e.g., in Sandelzhausen and in Vieux Collonges. *Proscapanus* sp. from Sandelzhausen would roughly fit in size but its M2 have divided mesostyles (Ziegler 2000: 92). *Proscapanus* sp. from Vieux Collonges is represented by humeri only, which are distinctly bigger than the specimen under study (cf. Mein 1958: 30). The small sample from Petersbuch 31 can be referred to *Proscapanus*, but yields no sufficient basis for the description of a new species.

Scalopini gen. et sp. indet.

Fig. 6.

Material and measurements.—Petersbuch 31: NHMA P31-168, left dentary fragment with p4–m1; h of dentary below m1 (2.10), p4 (1.20×0.79), m1 (2.07×1.16×1.36).

Description

Dentary.—There is only a short fragment of the horizontal ramus with the mental foramen below the posterior root of p4 and five crowded alveoli anterior to p4. As the third to fifth alveolus anterior to p4 are increasingly inclined, it is assumed that only a small anterior part of the dentary is broken off. Consequently, the antemolar dentition is reduced.

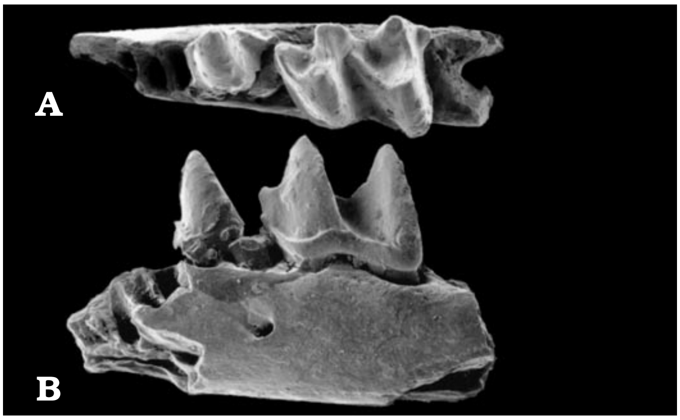

Fig. 6. Scalopini gen. et sp. indet., Petersbuch 31, NHMA P31-168, left dentary with p4–m1 in occlusal (**A**) and buccal (**B**) views; ca. × 10.

Lower dentition.—The cusp of the p4 is situated above the anterior root. There is a postero-lingual crest, a precingulid, and a postcingulid. In the m1 the oblique cristid extends far lingually but does not join the metacristid. Pre- and ectocingulid are continuous but not very strong. The postcingulid is weak and joins the small entostylid.

Discussion

The lower position of the mental foramen, the stronger horizontal ramus and the reduced antemolar dentition are not compatible with *Proscapanus* sp. from the same site. However, it cannot be excluded that some of the radius fragments referred to *Proscapanus* sp. belong with this dentary. In overall morphology both teeth show scalopine affinities, for example, the presence of a metacristid and the direction of the oblique cristid. The specimen does not fit with any talpid species in the European Miocene. Naturally, on the basis of this specimen no new species can be described. With some hesitation it is placed within the Scalopini.

Tribe Talpini Fischer von Waldheim, 1817

Talpa Linnaeus, 1758

Type species: *Talpa europaea* Linnaeus, 1758.

Talpa minuta Blainville, 1838

Fig. 7.

Material (measurements see Tables 7, 8).—Petersbuch 6: NHMA P6-1058B1, 1059/4, 6, 1060/1, 1062/2, 3, right dentary and right maxilla fragment with teeth, right P4, left hu-

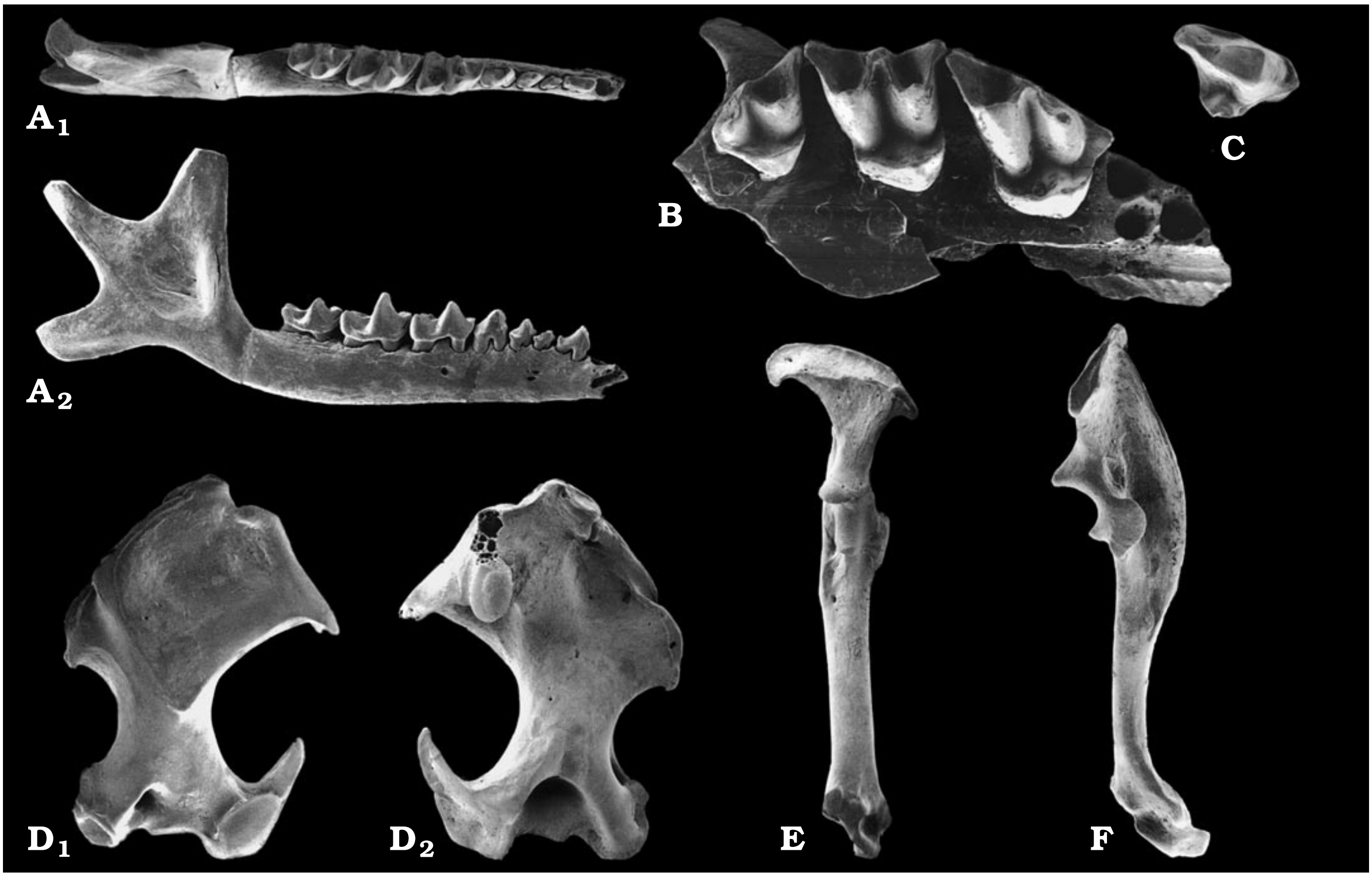

Fig. 7. *Talpa minuta*, Petersbuch 6. A. Right dentary with p1–m3, NHMA P6-1058B1 in occlusal (A_1) and buccal (A_2) views; ca. × 5. **B**. Right maxillary fragment with M1–M3, NHMA P6-1059/6, occlusal view; ca. × 10. **C**. Right P4, NHMA P6-1059/4, occlusal view; ca. × 10. **D**. Left humerus, NHMA P6-1060/1, in anterior (D_1) and posterior (D_2) views; ca. × 5. **E**. Left ulna, NHMA P6-1062/3, anterior view; ca. × 5. **F**. Left ulna, NHMA P6-1062/2, lateral view; ca. × 5.

Table 7. *Talpa minuta*, sample statistics of the teeth.

loc.	meas.	n	R	m	s	V
Petersbuch 6	Lp1–p4	1		3.25		
Petersbuch 6	Lm1–m3	1		5.44		
Petersbuch 6	Hcor	2	5.46–5.60	5.53		
Petersbuch 6	Lcinf.	1		0.59		
	Wcinf.	1		0.35		
Petersbuch 6	Lp1	3	0.90–0.93	0.92		
	Wp1	3	0.37–0.43	0.39		
Petersbuch 10	Lp1	6	0.89–1.06	0.96±0.09	0.074	7.71
	Wp1	6	0.38–0.46	0.43±0.02	0.028	6.57
Sansan	Lp1	3	0.80–0.88	0.84		
	Wp1	3	0.40–0.44	0.42		
Petersbuch 6	Lp2	2	0.62–0.65	0.64		
	Wp2	2	0.30–0.33	0.32		
Petersbuch 10	Lp2	3	0.59–0.71	0.67		
	Wp2	3	0.27–0.33	0.31		
Petersbuch 6	Lp3	2	0.82–0.83	0.83		
	Wp3	2	0.41–0.41	0.41		
Petersbuch 10	Lp3	2	0.73–0.73	0.73		
	Wp3	2	0.31–0.40	0.36		
Sansan	Lp3	1		0.60		
	Wp3	1		0.36		
Petersbuch 6	Lp4	6	1.11–1.23	1.17±0.06	0.054	4.61
	Wp4	8	0.52–0.63	0.58±0.04	0.042	7.25
Petersbuch 10	Lp4	20	1.14–1.33	1.24±0.03	0.055	4.43
	Wp4	20	0.56–0.70	0.62±0.02	0.039	6.29
Petersbuch 31	Lp4	1		1.33		
	Wp4	1		0.74		
Sansan	Lp4	13	0.97–1.15	1.07±0.04	0.058	5.45
	Wp4	13	0.54–0.66	0.58±0.02	0.033	5.75
Petersbuch 6	Lm1	6	1.68–1.88	1.79±0.08	0.067	3.77
	Wam1	6	0.94–1.11	1.01±0.07	0.057	5.64
	Wpm1	6	1.08–1.16	1.12±0.03	0.029	2.56
Petersbuch 10	Lm1	42	1.63–1.96	1.79±0.02	0.079	4.42
	Wam1	44	0.90–1.13	1.03±0.01	0.047	4.58
	Wpm1	42	1.04–1.32	1.17±0.02	0.061	5.23
Petersbuch 18	Lm1	1		1.69		
	Wam1	1		0.91		
	Wpm1	1		1.02		
Petersbuch 31	Lm1	4	1.78–1.90	1.85	0.049	2.67
	Wam1	5	0.97–1.08	1.04±0.06	0.044	4.28
	Wpm1	5	1.12–1.25	1.20±0.07	0.050	4.13
Petersbuch 48	Lm1	1		1.68		
	Wam1	1		0.90		
	Wpm1	1		1.07		
Sansan	Lm1	39	1.49–1.73	1.60±0.02	0.061	3.79
	Wam1	41	0.86–1.03	0.94±0.02	0.051	5.40
	Wpm1	38	1.00–1.21	1.09±0.02	0.053	4.91
Petersbuch 6	Lm2	6	1.93–2.15	2.05±0.09	0.076	3.72
	Wam2	8	1.08–1.21	1.14±0.04	0.050	4.40
	Wpm2	7	1.01–1.14	1.07±0.05	0.050	4.63
Petersbuch 10	Lm2	37	1.89–2.22	2.08±0.02	0.065	3.10
	Wam2	43	1.06–1.28	1.19±0.01	0.048	4.03
	Wpm2	38	1.00–1.22	1.10±0.02	0.047	4.30
Petersbuch 18	Lm2	5	1.96–2.10	2.04±0.08	0.061	2.99
	Wam2	5	1.02–1.28	1.15±0.13	0.095	8.30
	Wpm2	5	0.96–1.19	1.08±0.12	0.086	8.01
Petersbuch 31	Lm2	3	2.05–2.16	2.09		
	Wam2	3	1.21–1.23	1.22		
	Wpm2	3	1.12–1.15	1.14		
Petersbuch 48	Lm2	1		2.05		
	Wam2	1		1.10		
	Wpm2	1		1.00		
Sansan	Lm2	27	1.83–2.07	1.95±0.02	0.060	3.08
	Wam2	28	1.00–1.25	1.15±0.02	0.052	4.55
	Wpm2	26	0.92–1.13	1.05±0.02	0.048	4.59
Petersbuch 6	Lm3	11	1.75–1.92	1.83±0.03	0.047	2.59
	Wam3	11	0.86–1.03	0.97±0.04	0.053	5.47
Petersbuch 10	Lm3	47	1.71–1.96	1.80±0.02	0.058	3.22
	Wam3	47	0.82–1.13	0.97±0.02	0.056	5.79
Petersbuch 18	Lm3	5	1.77–1.90	1.83±0.07	0.050	2.75
	Wam3	5	0.89–1.02	0.95±0.07	0.051	5.33
Petersbuch 31	Lm3	3	2.05–2.16	2.09		
	Wam3	3	1.21–1.23	1.22		
Petersbuch 48	Lm3	4	1.75–1.88	1.81		
	Wam3	4	0.84–0.92	0.90		
Sansan	Lm3	23	1.58–1.92	1.67±0.03	0.073	4.41
	Wam3	23	0.77–1.11	0.90±0.03	0.061	6.73
Petersbuch 6	Lcsup.	1		1.20		
	Wcsup.	1		0.95		
ersbuch 10	Lcsup.	5	0.90–1.10	1.01±0.10	0.071	7.07
	Wcsup.	7	0.51–0.60	0.54±0.03	0.030	5.61
Petersbuch 31	Lcsup.	3	1.06–1.11	1.09		
	Wcsup.	3	0.52–0.55	0.53		
Sansan	Lcsup.	5	0.92–1.02	0.97±0.05	0.036	3.74
	Wcsup.	5	0.50–0.54	0.53±0.03	0.022	4.11
Petersbuch 6	LP2	1		0.52		
	WP2	1		0.42		
Petersbuch 6	LP3	1		0.77		
	WP3	1		0.49		
Petersbuch 6	LP4	3	1.47–1.58	1.52		
	WP4	4	1.02–1.09	1.05		
Petersbuch 10	LP4	12	1.47–1.73	1.61±0.05	0.048	4.84
	WP4	13	1.00–1.23	1.14±0.04	0.065	5.68
Petersbuch 18	LP4	2	1.31–1.58	1.45		
	WP4	3	0.97–1.12	1.04		
Sansan	LP4	5	1.28–1.47	1.37±0.10	0.070	5.14
	WP4	2	0.93–1.01	0.97		
Petersbuch 6	LM1	3	2.47–2.59	2.47		
	WM1	3	1.57–1.69	1.63		
Petersbuch 10	LM1	21	2.28–2.67	2.50±0.05	0.098	3.91
	WM1	22	1.50–1.89	1.69±0.05	0.114	6.72
Petersbuch 18	LM1	3	2.58–2.71	2.65		
	WM1	3	1.59–1.65	1.62		
Petersbuch 31	LM1	3	2.44–2.66	2.58		
	WM1	3	1.66–1.77	1.72		
Petersbuch 48	LM1	1		2.40		
Sansan	LM1	8	2.19–2.41	2.31±0.07	0.079	3.41
	WM1	9	1.45–1.66	1.54±0.05	0.064	4.16
Petersbuch 6	LM2	3	1.88–1.96	1.92		
	WM2	3	1.94–2.10	2.03		
Petersbuch 10	LM2	22	1.72–2.08	1.93±0.04	0.098	5.05
	WaM2	27	1.83–2.21	2.00±0.03	0.077	3.84
Petersbuch 31	LM2	10	1.78–2.02	1.90±0.06	0.076	4.03
	WaM2	11	2.00–2.21	2.10±0.06	0.080	3.82
Sansan	LM2	16	1.65–1.88	1.79±0.04	0.066	3.69
	WaM2	22	1.89–2.13	1.99±0.03	0.068	3.40
Petersbuch 6	LM3	2	1.18–1.24	1.21		
	WM3	2	1.75–1.75	1.75		
Petersbuch 10	LM3	11	1.10–1.36	1.20±0.06	0.088	7.37
	WM3	11	1.52–1.89	1.71±0.08	0.119	6.95
Petersbuch 31	LM3	1		1.23		
	WM3	1		1.79		
Sansan	LM3	16	1.08–1.40	1.18±0.04	0.079	6.71
	WM3	16	1.49–1.89	1.64±0.06	0.100	6.14

Table 8. *Talpa minuta*, measurements of some postcranials.

Humerus		GL	Bp	BpwT	DS	Bd	BdwE	Bp*100/GL
Petersbuch 6	m	10.53±0.21	7.82±0.09	7.06±0.13	2.67±0.05	7.16	5.85±0.15	74.36±1.13
	V	2.28	1.47	2.13	3.66		4.49	1.71
	s	0.240	0.115	0.150	0.055		0.263	1.268
	min	10.23	7.71	6.86	2.48		5.25	72.10
	max	10.93	8.04	7.31	2.90		6.25	76.20
	n	8	9	8	19	1	15	8
Petersbuch 10	m	10.90	7.36	6.77	2.51±0.05	5.58±0.11	6.22	75.40
	V				4.04	3.97		
	s				0.101	0.222		
	min		6.70	6.02	2.31	5.21		
	max		8.22	7.51	2.68	6.00		
	n	1	3	2	20	18	1	1
Petersbuch 18	m				2.50	6.70	5.77	
	min				2.47		5.48	
	max				2.52		6.05	
	n				2	1	2	
Petersbuch 31	m	10.31±0.19	7.64±0.23	6.84±0.26	2.61±0.04	5.98±0.23	5.60±0.08	73.5
	V	2.87	1.03	5.00	4.58	2.80	3.65	
	s	0.296	0.307	0.342	0.120	0.167	0.204	
	min	9.76	6.92	6.11	2.38	5.80	5.12	72.7
	max	10.80	8.10	7.22	2.93	6.25	5.96	74.2
	n	13	10	10	35	5	30	3
Petersbuch 48	m	10.75	8.11	7.18	2.76±0.14		6.12±0.18	76.5
	V				4.38		2.17	
	s				0.121		0.133	
	min	10.60	7.90	7.13	2.62		5.94	76.0
	max	10.90	8.23	7.20	2.95		6.28	77.0
	n	2	3	4	6		5	2
Sansan	m	9.37±0.17	2.08±0.05	6.84±0.10	2.44±0.03	5.72±0.25	5.12±0.06	73.01±1.21
	V	4.04	6.50	2.91	3.37	5.45	3.21	3.46
	s	0.378	0.135	0.199	0.082	0.312	0.165	2.525
	min	8.90	1.79	6.51	2.26	5.33	4.78	63.70
	max	10.66	2.32	7.25	2.60	6.37	5.50	76.00
	n	22	32	22	40	9	36	20

Radius		L1	L2
Petersbuch 31	m	8.84	7.77
	min	8.67	7.65
	max	9.08	7.95
	n	3	3

Ulna		GL
Petersbuch 6	m	14.27±0.55
	V	3.37
	s	0.480
	min	13.6
	max	14.8
	n	6
Petersbuch 10	m	12.5
	n	1
Petersbuch 31	m	13.5
	n	1

merus, 2 left ulnae; CRW P6-1058–1062, Petersbuch 6, 19 dentary fragments with teeth, 8 maxilla fragments with teeth, 18 humeri, 4 ulnae. Petersbuch 10: CRW P10-0601–607, 622-62, 6 dentary fragments with teeth, 3 maxilla fragments with teeth, 5 isolated teeth, 26 humeri, 13 ulnae. Petersbuch 18: CRW P18-0749–751, 6 dentary fragments with teeth, 3 maxilla fragments with teeth, 5 isolated teeth, 2 humeri. Petersbuch 31: CRW P31-0159–162, 3 dentary fragments with teeth, 2 maxilla fragments with teeth, 33 isolated teeth, 43 humeri, 8 ulnae, 3 radii. Petersbuch 48: CRW P48-0091, 92, 7 isolated teeth, 6 humeri.

Description

Dentary.—In general shape the dentary is similar to that of the extant *Talpa europaea*. The complete ascending ramus is only preserved in the Petersbuch 6 sample. It forms a nearly right angle with the horizontal ramus. The mandibular foramen is situated on the ventral margin of the mylohyoid ridge, roughly in the centre of the ascending ramus. The masseteric fossa is deeply excavated, the pterygoid fossa only moderately deep. The angular process is shovel-shaped with an internal concavity. The cylindrical condylus is situated high above the level of the tooth row. The coronoid process itself is rectangular. In the Petersbuch 6 sample the posterior mental foramen is located either under the anterior root of m1 (twice) or between its roots (four times), the anterior mental foramen below the posterior root of p2 (twice) or between p2 and p2 (twice) or under the anterior root of p3 (once). The incisor alveoli are not preserved.

Lower dentition.—The canine is incisor-shaped and slightly procumbent. All premolars are double-rooted, p2 and p3 overlap one another. p1 is distinctly larger than p2 and p3, but all are similar in shape. The cusp is centred over the anterior root and origin of a marked posterior crest, joining a posterior cuspule, and a less well-developed anterior crest. The buccal face is convex, the lingual side flat. A faint cingulid is restricted to the posterior part of the crown base. The p4 has a talonid and a trilateral crown with convex buccal and lingual faces and a concave posterior side. The postero-lingual crest joins the posterior cuspule. An anterior cuspule is also developed. The size relation between the molars is m1< or >m3<m2. Buccal cingulids are rudimentary and confined to the hypoflexid. The trigonid is lingual open. In the m1 the talonid is wider than the trigonid, the oblique cristid joins the middle of the protocristid or ends slightly labial to the middle. The most conspicuous feature is the faint ascending precingulid, which joins the paracristid. The protoconid of the m2 is the highest cusp in the tooth row. The trigonid is somewhat wider than the talonid. There is a marked precingulid and a tiny cuspule in front of the entoconid. The m3 is similar to a small m2 without entostylid and with a narrower talonid.

Maxilla.—Larger fragments of maxillae are preserved only in the Petersbuch 6 sample. The origin of the zygomatic arch lies above M3. The infraorbital foramen opens high above the middle of M1. The infraorbital canal runs in a deep groove. Its anterior and posterior opening are separated by a narrow bony bridge above the anterior root of M3. The same configuration is found in extant *Talpa*.

Upper dentition.—According to the alveoles there are three single-rooted incisors. Only two chisel-shaped I2 and I3 are preserved. The double-rooted canine has a mesio-lingual groove and a distal crest. P1–P3 are double-rooted, P2 is smaller than both the others. No P1 is preserved. P2 and P3 have an oval outline in occlusal view. There is a distal crest. A faint disto-buccal cingulum may be developed. The P4 has a more or less projecting parastyle and a conical protocone. A straight distal crest originates from the paracone. The upper molars have an undivided mesostyle and neither para- nor metaconule. In the M1 the marked paracingulum joins the projecting parastyle. The metacingulum is interrupted along the postmetacrista or reduced to a short spur above the metastyle. There are four roots, the strongest above the protocone, a mesio-distally compressed one above paracone and postmetacrista respectively, and a small round one on both the labial roots. M2 and M3 have three roots and neither para- nor metacingulum.

Postcranial bones.—Humerus, ulna, and radius are smaller than in the extant *Talpa*, but do not show any morphological differences. Therefore we can abstain from a formal description. Even in the gracility index, defined as Bp*100/Gl, they correspond to *T. europaea*. This means that both have similar fossorial abilities. However, the extant *Talpa europaea* is distinctly larger.

Discussion

With the exception of Petersbuch 35, which yielded only two talpid species, *Talpa minuta* is represented in all samples and it is the most common talpid in all samples. There are no morphological differences among the specimens under study and *Talpa minuta* from the type locality Sansan. The position of the anterior mental foramen from this locality is as variable as in the samples under study. In the Sansan sample the posterior mental foramen is consistently situated under the anterior root of m1 whereas it slightly varies in position in the Petersbuch samples. However, there is a distinct difference in size, the dentition and postcranial bones from Sansan being smaller than in Petersbuch. It is assumed that the size difference lies within the variability of a species and that the delineation of a new species or subspecies is not justified. *Talpa minuta* is one of the most common and most wide spread talpid species in the Miocene of Europe. It is recorded from faunas correlated with MN 3, e.g., Wintershof-West, to MN 9, for example, Nebelbergweg (Ziegler 1994; Kälin and Engesser 2001), from Slovakia in the East to Southeast France in the West.

Tribe Urotrichini Dobson, 1883

Urotrichus Temminck, 1841

Type species: *Urotrichus talpoides* Temminck, 1841.

?*Urotrichus dolichochir* (Gaillard, 1899)

Fig. 8.

Material and measurements.—Petersbuch 6: NHMA P6-1066, left dentary fragment with p4–m1 (trigonid), p4 (1.05×0.67), m1 Wa (1.03); NHMA P6-1067, right humerus, GL (7.60), Bp (3.64), BpwT (3.00), DS (1.30), Bd (3.86), BdwE (3.32), Bpx100/GL (48.0).

Description

Dentary.—There is only a short fragment of the horizontal ramus with two small mental foramina beneath the trigonid of m1 and a bigger one under the second alveolus anterior to p4. The third alveolus anterior to p4 is slightly inclined. This means that the fracture is near the real tip of the dentary and that the antemolar part is reduced. The cusp of the p4 is cone-shaped with a more or less flat lingual face and a postero-lingual crest. Close to the base of this crest there is a small accessory cuspule. The p4 is slightly heeled and has a precingulid and a postcingulid respectively. The m1 protoconid is somewhat higher than the p4. The paracristid is angular, the protocristid notched. The oblique cristid extends to below the protocristid notch and does not join the weak metacristid. There is a well-developed precingulid. The talonid is broken off.

Humerus.—The humerus is nearly complete. Only the epicondylar spines and the deltoid process are broken. It is slender in overall shape, which means only modest fossorial specialisation. Posteriorly the olecranon fossa is extensive, but shallow. The long axis of the head points latero-distally. The ridge running from the lesser tubercle to beneath the

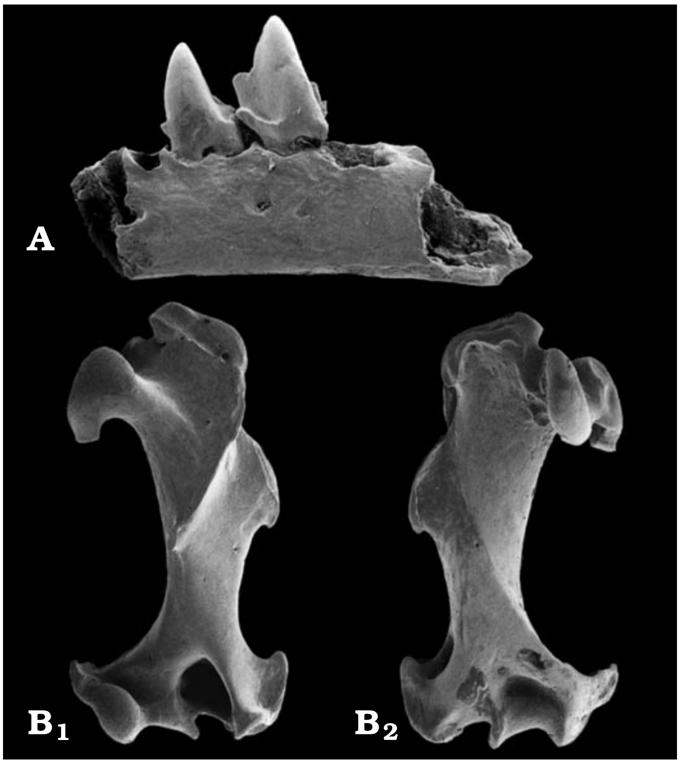

Fig. 8. ?*Urotrichus dolichochir*, Petersbuch 6. **A**. Left dentary fragment with p4 and m1-trigonid, NHMA P6-1066, buccal view; ca. × 10. **B**. Right humerus, NHMA P6-1067 in anterior (B_1) and posterior (B_2) views; ca. × 7.5.

head is weak and curved. The brachialis fossa is moderately deep. Anteriorly the pectoral tubercle terminates far laterally about half way down the shaft. Teres tubercle and lesser tubercle are separated by a wide sulcus, head and greater tubercle by a deep and narrow notch. The supratrochlear fossa is wide and deeply pocketed. There is a deep notch between the trochlea and the fossa for the m. flexor digitorum profundus ligament.

Discussion

Dentary and humerus have been lumped together, because they match in overall size, both represent urotrichines and both are the only talpid leavings in the Petersbuch 6 talpid fauna. It is considered more probable that dentary and humerus represent only one species instead of two. The humerus shows undeniable urotrichine affinities and fits well with ?*Urotrichus dolichochir* from La Grive in all morphological details and in gracility. The small size difference is not worth mentioning. The Petersbuch 6 specimen also resembles the humeri of ?*Urotrichus* cf. *dolichochir* from Sandelzhausen (cf. Ziegler 2000: 81).

The type humerus from La Grive was named *Scaptonyx ?dolichochir* by Gaillard (1899: 30) even though he noted the resemblance to the extant genus *Urotrichus*. As this species is not referable to *Scaptonyx* and in the absence of associated dental material Hutchison (1974: 226) referred the species tentatively to *Urotrichus* on the basis of the humeral morphology. He also considered the lectotype dentary of "*Scaptonyx*" *edwardsi* from the same site a possible candidate for the association with ?*Urotrichus dolichochir*. However, Hutchison (1974: 228) also wrote that the dentary may belong with the humerus of cf. *Scalopoides* sp. from La Grive. In fact, we do not know the dentition of ?*Urotrichus dolichochir*. The dentary fragment under study differs from *Scaptonyx edwardsi* in the duplication of the posterior mental foramen, in the presence of a postero-lingual cuspule on p4 and of a weak metacristid in m1. In order to resolve the problem whether any dentary belongs to any humerus, much more material is needed. In the present study both humerus and dentary are reservedly referred to ?*Urotrichus dolichochir*. They represent the second record of this species in Germany.

Myxomygale Filhol, 1890

Type species: *Myxomygale antiqua* Filhol, 1890.

Myxomygale gracilis sp. nov.

Fig. 9.

Etymology: From Latin *gracilis*, slender, lank; because of the gracile humerus.

Holotype: Right humerus, P10-615/2, fig. 9D.

Measurements of the holotype: GL (8.05), Bp (3.50), BpwT (3.15), DS (1.30), Bd (3.92), BdwE (3.46), Bp*100/GL (43.5).

Type locality: Petersbuch 10 (details see p. 618).

Age: Uppermost part of the Middle Miocene (MN 7/8, Rummel 2000).

Paratypes and measurements.—Petersbuch 10: CRW P10-614/1, left dentary fragment with m1–m2; m1 (1.47×0.89×1.07); m2 (1.69×1.09×–); NHMA P10-614/2, right dentary fragment with m2–m3; m2 (1.64×1.15×1.04); m3 (1.35×0.88×0.6); NHMA P10-614/3, right dentary fragment with m2–m3; m2 (1.65×1.09 ×0.97), m3 (1.37×0.84×0.60); NHMA P10-614/4, left maxilla fragment with M1, M1 (2.10×1.84); CRW P10-614/5, right M1 (2.03×1.77); CRW P10-615.1, left humerus fragment, DS (1.44), Bd (ca. 4.1), BdwE (3.40).

Diagnosis.—Small-sized *Myxomygale* characterised a mental foramen situated under the protoconid of m1, an oblique cristid, extending labially in m1, joining a marked metacristid in m2 and m3. M1 without parastyle and preparacrista, with deeply divided mesostyle. The humerus is urotrichine and slender with long ledge-like teres tubercle and a pectoral tubercle situated laterally.

Description of the holotype

Only the deltoid process and the epicondylar spines are broken off. In anterior view the humerus shows a long teres tubercle with a proximal end hidden by the marked pectoral ridge. The pointed pectoral tubercle extends further distally than the teres tubercle and is situated on the lateral margin of the shaft. It is visible in posterior view. The brachialis fossa is moderately deep. The sulcus between head and major tubercle is a narrow groove. There is a large, pocketed supratrochlear fossa, between trochlea and the fossa m. flexor digitorum profundus ligament a deep, concave notch. The posterior face shows the shallow olecranon fossa and the head with a long axis slightly directed disto-laterally. The ridge between head and lesser tubercle is short and tapers towards the lesser tubercle.

Description of the paratypes

Dentary.—Among the 4 short fragments of the horizontal ramus two show the posterior mental foramen beneath the trigonid of m1. The specimens yield no information concerning the antemolar dentition.

Lower molars.—The size relation is m2>m1>m3. In the m1 the oblique cristid runs rather bucally, extending to the posterior base of the protoconid. There is no metacristid. The precingulid does not extend to below the paraconid but is continuous with the ectocingulid. There is only a weak postcingulid hidden by the marked precingulid of the m2. The entostylid is broken off. In the m2 the protoconid is more elevated than in the m1 and the trigonid is distinctly narrower. The oblique cristid joins the marked metacristid. The precingulid is more marked than in the m1. The m3 differs from the m2 in the smaller size and in the reduced talonid without entostylid.

Maxilla.—One fragment with M1 shows the lacrimal foramen above the anterior root of M1.

M1.—There are neither preparacrista nor parastyle. The mesostyle is deeply divided. Para- and metaconule are only moderately differentiated. The preparaconuluscrista is continuous with the precingulum, which extends to the buccal margin. The postmetaconuluscrista joins the metacingulum which itself tapers in its mid part and ends in a marked short crest above the metastyle.

Humerus.—In addition to the type specimen there is one humerus with the proximal third and the point of the pectoral tubercle broken off. It yields no further information.

Comparisons

There are five species of *Myxomygale* known thus far most of which are only scarcely represented. They are listed in ascending order with respect to their stratigraphic range: the type species *Myxomygale antiqua* Filhol, 1890 from the Quercy (Oligocene), *Myxomygale vauclusensis* Crochet, 1995 from Saint-Martin-de-Castillon (Oligocene, MP 23, figures and measurements in Hugueney 1972: 53 f), *Myxomygale minor* Ziegler, 1990 from Ulm-Westtangente (Lower Miocene, MN 2a), *Myxomygale hutchisoni* (Ziegler, 1985) from Petersbuch 2 (Lower Miocene, MN 4), *Myxomygale engesseri* Doukas, 1986 from Aliveri in Greece (Lower Miocene, MN 4). The humerus is known, i. e. published, described and figured, only from *M. hutchisoni* (Ziegler 1985: fig. 8, tab. 3). Crochet (1995: 56) also mentions the humerus in the revised genus diagnosis of *Myxomygale*. However, it is not known to which species he refers. As much as is known from published evidence, the humerus is only preserved in *M. hutchisoni*. Perhaps Crochet knows unpublished humeri from *M. antiqua*.

M. gracilis differs from *M. antiqua* in:

- the distinctly smaller size,
- the size relation between m1 and m2 (m1<m2) and the weaker ectocingulids.

M. gracilis differs from *M. vauclusensis* in:

- the distinctly smaller size,
- the more anterior position of the mental foramen,
- the absence of a parastyle, the divided mesostyle and the less developed para- and metaconule of M1.

M. gracilis differs from *M. minor* in:

- the distinctly wider M1,
- the absence of a parastyle and the divided mesostyle in M1,

M. gracilis differs from *M. hutchisoni* in:

- the absence of a parastyle and the divided mesostyle in M1,
- the smaller and in particular more slender humerus, with a relatively longer teres tubercle and a less marked ridge running from the head to the lesser tubercle.

M. gracilis differs from *M. engesseri* in:

- the wider m2,
- the somewhat bigger M1 without parastyle and with continuous preparaconuluscrista and paracingulum respectively and deeply divided mesostyle.

?*Urotrichus dolichochir* (Gaillard, 1899) known from the type locality La Grive (Middle Miocene, MN 7/8) by the humerus only, and from Petersbuch 6, is rather similar, thus deserves to be mentioned.

M. gracilis differs from ?*U. dolichochir* in:

- the somewhat bigger humerus,
- the longer teres tubercle hidden proximally by the pectoral ridge.

In the Petersbuch 10 fauna there is another small urotrichine, which is not determinable beyond the tribe. It is represented by a humerus and tentatively associated dentition.

M. gracilis differs from Urotrichini gen. et sp. indet. I in the:

- smaller overall size,
- more posterior position of the mental foramen,
- m1 without metacristid and an oblique cristid running more buccally,
- more gracile humerus with the longer teres tubercle,
- lateral position of the pectoral tubercle,
- less marked ridge running from the head and tapering towards the lesser tubercle.

The Petersbuch 31 fauna yielded a small urotrichine, represented by humeri and dentition.

M. gracilis differs from Urotrichini gen. et sp. indet. II in the:

- less pronounced para- and metaconule, the absence of the parastyle and the divided mesostyle in M1,
- more gracile humerus with the longer teres tubercle and a weaker and discontinuous ridge between head and lesser tubercle.

Discussion

Myxomygale gracilis is the smallest talpid in the Petersbuch 10 fauna. The association of lower teeth, upper teeth, and hu-

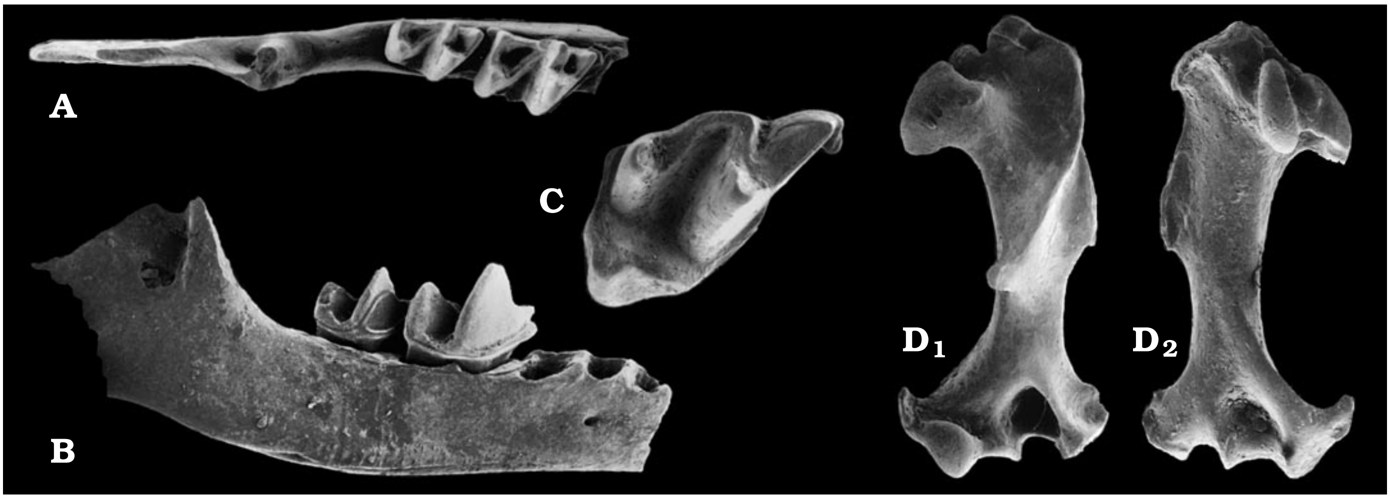

Fig. 9. *Myxomygale gracilis* sp. nov., Petersbuch 10. **A**. Right dentary with m2–m3, NHMA P10-614/3, occlusal view; ca. × 10. **B**. Right dentary with m2–m3, NHMA P10-614/2, buccal view; ca. × 10. **C**. Left M1, NHMA P10-614/4, occlusal view; ca. × 15. **D**. Holotype, right humerus, NHMA P10-615/2, in anterior (D_1) and posterior (D_2) views; ca. × 7.5.

merus is without alternative. However, the divided mesostyle in the M1 requires some comments on the generic allocation of the species. The upper dentition of the type species is unknown. In *M. vauclusensis* from Saint-Martin-de-Castillon Crochet (1995: 58, fig. 20) there are some M2 with a divided mesostyle. But Hugueney (1972: table 9b) listed a confluent mesostyle in M1 and M2 as character of this species. *M. minor* and *M. hutchisoni* has an undivided mesostyle even in unworn teeth. At last, *M. engesseri* has a heavily worn M1 and an unworn M2 with confluent mesostyle. Actually, I consider the shape of the mesostyle (deeply divided versus confluent) a character of generic relevance. On the other hand, I am rather convinced of the homogeneity of the sample under study. The lower dentition fits well *Myxomygale* and the humerus shows clear urotrichine affinities. Consequently, the generic allocation is acceptable with some reserve.

Obviously *M. gracilis* was a poor burrower. The genus so far was known from the sites with Oligocene to Early Miocene age. The new species extends the range to the end of the Middle Miocene. As most species are known only from small samples and as not all elements are known from all species—e.g., the humerus is known only from *M. hutchisoni* and *M. gracilis*—it is not possible to find any phylogenetic relationships between the species. The earlier species are not more primitive and the later ones not more advanced than the other at a time. Much more material and more complete dentitions are necessary.

Genus *Tenuibrachiatum* nov.

Type species: *Tenuibrachiatum storchi* gen. et sp. nov.

Etymology: From Latin *tenuis*, tenuous; *brachium*, arm; *tenuibrachiatum*, with tenuous arms; because of the slender humerus.

Included species: Type species only.

Diagnosis.—Small urotrichine mole. Tentative mandibular dental formula 2 i, 1 c, 4 p, 3 m. Incisors procumbent, i1>i2. All lower premolars double-rooted. m1<m2>m3. Oblique cristid terminates bucally in m1, joins the metacristid in m2 and m3. P4 with tiny parastyle and marked protocone. M1 and M2 with undivided mesostyle. Para- and metaconule weakly developed in M1, well differentiated in M2. Humerus typical urotrichine, slender, long teres tubercle, pectoral tubercle situated laterally, large, pocketed supratrochlear fossa. In anterior aspect the trochlea is broadening towards the capitulum.

Tenuibrachiatum storchi gen. et sp. nov.

Fig. 10.

Etymology: In honour of Dr. Gerhard Storch, Frankfurt, thus appreciating his outstanding contributions to our knowledge of the Tertiary small mammals.

Holotype: Left dentary fragment with p1, p4–m2 and the alveoles of i1, i2, c, p2–p3; NHMA P31-166 A1, Fig. 10A.

Measurements of the holotype: p1 (0.70×0.43), p4 (0.97×0.58), m1 (1.40×0.88×1.00), m2 (1.54×1.00×0.95), lingual height of the dentary below m1 (1.35).

Type locality: Petersbuch 31 (details see p. 618).

Age: Upper part of the Middle Miocene (MN 7 according to Rummel 2000: 157, means MN 7+8).

Paratypes and measurements.—Petersbuch 31: NHNA P10-166A2, right dentary with m1, m1 (1.40×0.85×0.91); CRW P31-166A3, right dentary with m1, m1 (1.40×0.78×–); NHMA P10-166A4, right m2 (1.56×0.97×0.90); CRW P31-166A5, right m2 (1.51×1.02×0.97); CRW P31-166C1, left m3 (1.41×0.88); CRW P31-166C2, left m3 (1.41×0.86); CRW P31-166C3, left m3 (1.44×0.89); CRW P31-166C4, right m3 (1.42×0.85); CRW P31-166C5, right m3 (1.33×0.82×0.68); CRW P31-166D1, left maxilla fragment with P4, P4 (1.34×1.12); NHMA P31-166D2, left maxilla fragment with P4–M1, P4 (1.29×1.03), M1 (1.87×1.38); CRW P31-166D3, left M1 (1.95×1.50); CRW P31-166D4, left M1 (–×1.50); CRW P31-166D5, right M1 (1.80×1.38); CRW

P31-166E1, left M2 (– ×1.57); NHMA P31-166E2, right M2 (1.42×1.64); NHMA P31-167/1, left humerus GL (7.74), Bp (>3.56), BpwT (>3.30), DS (1.44), Bd (3.94), BdwE (3.81); NHMA P31-167/8, right humerus GL (7.62), Bp (6.63), BpwT (3.33), DS (1.40), BdwE (3.58), Bp*100/GL (47.6); CRW P31-167/2–7, 9–11, 9 humeri.

Diagnosis.—As for the genus.

Description of the holotype

The horizontal ramus from the first incisor alveolus to the fracture behind m2 is preserved. The dentary was broken between p4 and m1 and was glued. It tapers anteriorly. The anterior mental foramen is situated under the anterior root of p2. The posterior foramen beneath the trigonid of m1 is filled with not removable sediment, thus hardly visible. The four alveoli of p2 and p3 are slightly overlapping. There are three alveoli anterior to p1: the first two nearly procumbent, the third slightly inclined anteriorly. They are interpreted as alveoli of i1, i2, and c, resulting in the tooth formula 2143. Alternatively they can be interpreted as i2, i3, and c, resulting in the same tooth formula, or as i1, i2, and i3. In the latter case the tooth formula was 3043. According to their alveoli the size relation is i1>i2>c. The symphysis extends to c/p1. The double-rooted p1 is oval in occlusal outline. Its cusp is situated above the anterior root. There is a weak posterior and lingual cingulid, respectively. The p4 has a postero-lingual and an anterior crest. It is surrounded by a weak cingulum. There is a tiny parastyle and a well-developed heel. In the m1 the oblique cristid terminates far labially, whereas in m2 it ascends and joins the marked metacristid. In the m1 there is only a vestige of a short ectocingulid below the hypoflexid, in the m2 a faint precingulid. Both have a well-developed entostylid.

Description of the paratypes

Dentary.—In two further fragments the posterior mental foramen is situated below the trigonid of m1; in one specimen, like in the type, the p3 is obliquely implanted. The slightly crowded p3 and p2 seem to be a consistent character of the species.

Lower dentition.—With respect to the lower dentition there is no additional information except for the m3. In the last molar the precingulid is more marked, the oblique cristid joins the metacristid. The reduced talonid has no entostylid. In size and morphology all five m3 fit well with one another. However, it cannot be excluded that one or more belong to Urotrichini gen. et sp. indet. II and/or to *Desmanella* sp., which is of roughly the same size. The well-developed precingulids of these m3 would argue in favour of the association with *Desmanella* sp. whose m1 and m2 have well-developed precingulids. However, *Desmanella* sp. is represented only by six specimens. It is unlikely, that all five m3 belong to this species.

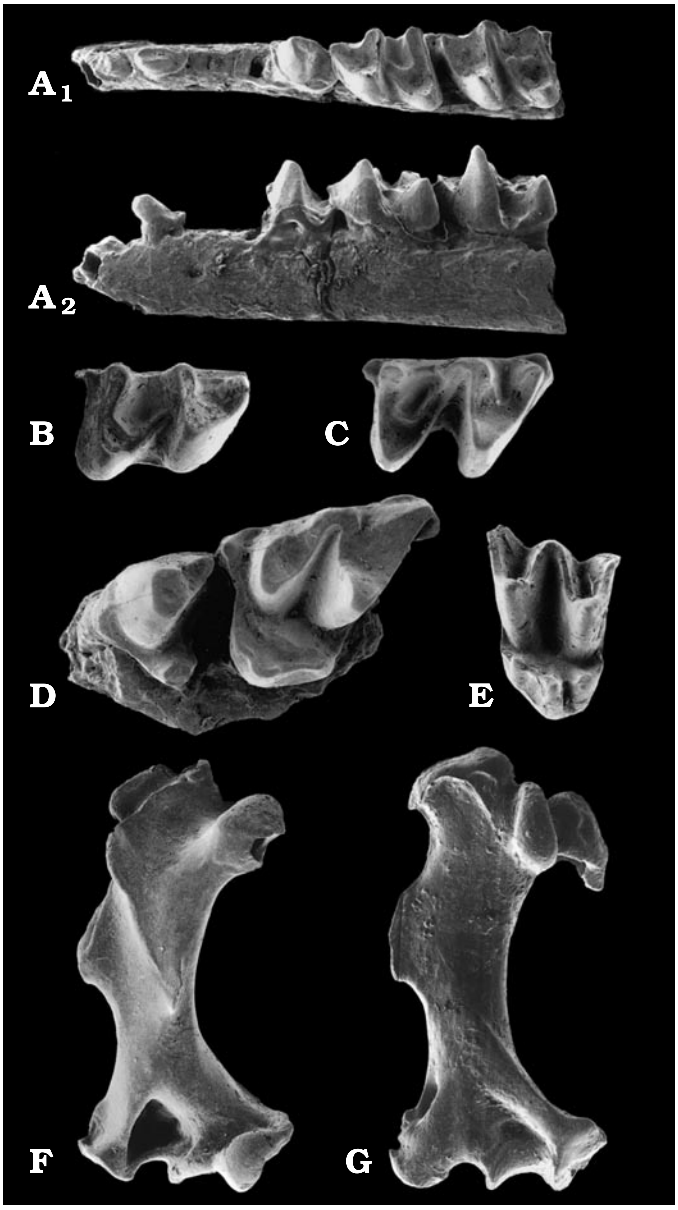

Fig. 10. *Tenuibrachiatum storchi* gen. et sp. nov., Petersbuch 31. **A**. Holotype, left dentary with p1, p4–m2, NHMA P31-166A1, in occlusal (A_1) and buccal (A_2) views; ca. × 10. **B**. Right m1, NHMA P31-166A2, occlusal view; ca. × 15. **C**. Right m2, NHMA P31-166A4, occlusal view; ca. × 15. **D**. Left maxillary fragment with P4–M1, NHMA P31-166D2, occlusal view; ca. × 15. **E**. Right M2, NHMA P31-166E2, occlusal view; ca. × 15. **F**. Left humerus, NHMA P31-167/1, anterior view; ca. × 7.5. **G**. Right humerus, NHMA P31-167/8, posterior view; ca. × 7.5.

Upper dentition.—The P4 has a tiny parastyle and a well-developed protocone. There is a weak precingulum and a more pronounced postcingulum. The M1 has an undivided mesostyle, hardly differentiated para- and metaconule respectively, a marked paracingulum, which joins the projecting parastyle and a weak metacingulum, which tapers distolabially. In the M2 there is a marked paraconule and a well-developed metaconule. Para- and metacingulum are absent. The mesostyle is undivided.

Humerus.—The associated humeri are the smallest and most gracile ones among the Petersbuch 31 talpid humeri.

There is a suite of urotrichine characters: large, pocketed supratrochlear fossa, deep, concave notch between trochlea and the fossa m. flexor digitorum profundus ligament, small and moderately deep brachialis fossa. In anterior view the trochlea is broadening towards the capitulum. The long axis of the elliptical head runs nearly parallel to the shaft. The marked ledge extending from the lesser tubercle to beneath the head is rounded. The olecranon fossa is shallow. The teres tubercle forms a long crest proximally not covered by the pectoral ridge. The pectoral tubercle is situated labially on the shaft. There is a deep groove between head and major tubercle. The passage of the biceps tendon between teres tubercle and pectoral crest is a bicipital notch.

Comparisons

As the material under study without any doubt represents a species of the tribe Urotrichini, the comparisons mainly refer to the fossil and extant species of this tribe. Storch and Qiu (1983: tabes 6 and 7) listed a suite of features characterising both the Recent genera *Urotrichus* Temminck, 1841 and *Neurotrichus* Günther, 1880.

The Recent *Urotrichus talpoides* Temminck, 1841 and *U. pilirostris* (True, 1886) differ from *Tenuibrachiatum storchi* in the:

- humerus with a long axis of the head directed disto-laterally,
- shorter, proximally angled teres tubercle (see Storch and Qiu 1983: figs. 20, 21),
- pectoral tubercle bent laterally, thus being visible in posterior view,
- dentary with a reduced antemolar region not tapered anteriorly,
- more posterior position of the mental foramina,
- at large more compact teeth (see Hugueney 1972: figs. 16, 17).

?*Urotrichus dolichochir* (Gaillard, 1899) from La Grive, originally described as *Scaptonyx* ?*dolichochir* on the basis of a humerus and tentatively assigned to *Urotrichus* by Hutchison (1974) shows striking resemblance to the Recent genus. In size and gracility it fits well with the humeri of *T. storchi*, but they differ in the same characters as the Recent species. The lectotype dentary of "*Scaptonyx*" *edwardsi* (Gaillard, 1899), which Hutchison (1974: 226, pl 38: 1.) "considered a possible candidate for the association with ?*U. dolichochir*", has a more reduced antemolar region and m1 and m2 with stronger precingulids.

?*Urotrichus dolichochir* from Petersbuch 6 is based on a humerus and an assigned dentary fragment (this paper, p. 634). The humerus fits well in size and gracility with the humerus of *T. storchi*, but the crest running from the lesser tubercle to beneath the head is distinctly weaker and forms no ledge, and the long axis of the head is pointed slightly more disto-laterally with respect to the shaft. The tentatively associated dentary fragment differs in having:

- a reduced antemolar region,
- a p4 with a disto-lingual cuspule,
- a m1 with a better-developed precingulid.

Urotrichus sp. from the uppermost Miocene locality Maramena in Greece is known from nine isolated upper molars (see Doukas et al. 1995). This species differs from *Tenuibrachiatum storchi* in (see Doukas et al. 1995: 51, table 5, pl. 5):

- the distinctly bigger size,
- the less differentiated lingual conules of M1 and M2.

Neurotrichus gibbsi (Baird, 1858), the Recent species of the genus and *Quyania chowi* Storch and Qiu, 1983 from the Neogene of Inner Mongolia differ from *Tenuibrachiatum storchi* in (see Storch and Qiu 1983: tables 6, 7):

- lacking two lower antemolars in *Neurotrichus* (? two premolars) and p1 in *Quyania*;
- having only 8 antemolar alveoles (p3 and p4 double-rooted) in *Neurotrichus* and 10 in *Quyania*,
- the presence of a metaconid on p4,
- the presence of a marked precingulid on m1,
- the more buccal termination of the oblique cristid of m2 and m3,
- the ectocingulid of P4 and the very short premetacrista of M1,
- the presence of an metacingulum and the weaker paraconule of m2.

Neurotrichus polonicus Skoczeń, 1980 from the Pliocene of Poland differs from *Tenuibrachiatum storchi* in:

- being distinctly bigger (see Skoczeń 1980: tables 5, 7),
- the morphological characters listed above for *N. gibbsi*.

Yanshuella columbiana (Hutchison, 1968) from the Hemphillan (Middle to Late Pliocene) of Oregon originally was tentatively assigned to *Neurotrichus*, thus being an urotrichine. Storch and Qiu (1983: 111) referred the species to the scalopine genus *Yanshuella*. This species, only known from the type dentary and some lower teeth, differs from *Tenuibrachiatum storchi* in having:

- distinctly bigger lower molars,
- m2 and m3 without metacristid and an oblique cristid terminating more labially,
- all lower antemolars between i1 and p4 and single-rooted p1–p3.

Myxomygale antiqua Filhol, 1890, the earliest urotrichine from the Oligocene in Europe, differs from *Tenuibrachiatum* in:

- its distinctly bigger size,
- having the complete set of lower antemolars, but single-rooted lower premolars,
- having lower molars with marked pre- and ectocingulids.

Myxomygale vauclusensis Crochet, 1995 from the Oligocene of Southern France differs from *Tenuibrachiatum* in:

- being distinctly bigger,
- having lower molars with marked pre- and ectocingulids,
- the projecting parastyle of P4,
- the presence of para- and metacingulum on M2.

Among the Miocene species of *Myxomygale* there are two with associated humeri. *M. hutchisoni* Ziegler 1985 from the Early Miocene of South Germany and *M. gracilis* sp.

nov. from Petersbuch 10. *M. hutchisoni* differs from *Tenuibrachiatum* in having:

- the complete set of lower antemolars, but single-rooted lower premolars,
- lower molars with marked pre- and ectocingulids,
- more robust humerus, which shows advanced fossorial adaptations.

M. gracilis differs from *Tenuibrachiatum* in having:

- lower molars with better developed pre- and ectocingulid respectively,
- M1 without projecting parastyle and with divided mesostyle,
- a slightly bigger humerus with a pectoral tubercle situated more laterally and being visible in posterior view.

Myxomygale engesseri Doukas, 1986, a poorly recorded species from the Lower Miocene of Greece, differs from *Tenuibrachiatum* in the:

- better developed cingulids of m2,
- less projecting parastyle of M1,
- hardly developed metaconule of M2.

Myxomygale minor Ziegler, 1990 from the Early Miocene of South Germany is mainly known from isolated teeth. It differs from *Tenuibrachiatum* in the:

- better developed cingulids of the lower molars,
- projecting parastyle of P4,
- better developed para- and metacingulum of M1 and M2.

Paratalpa Lavocat, 1951 is known from the Oligocene species *P. micheli* Lavocat, 1951, the Agenian *P. micheli saulcetensis* Hugueney, 1972, *P. brachychir* (von Meyer, 1846), and *P. meyeri* (Schlosser, 1887). They are all distinctly bigger, have a dentary with a more reduced antemolar region, lower molars with better-developed cingulids and further buccally terminating oblique cristids, upper molars with deeply divided and spaced mesostyles. The humerus, known from *P. micheli*, *P. brachychir*, and *P. meyeri*, is bigger, more robust and has a shorter teres tubercle.

Pseudoparatalpa Lopatin, 1999 is known from its type species, *P. shevyrevae* Lopatin, 1999, from the Lower Oligocene and *P. lavrovi* (Bendukidze, 1993) from the Lower Miocene of Kazakhstan (Lopatin 1999). This genus, scarcely represented only by some dental remains, differs from *Paratalpa* just in the structure of the p4-talonid and the m1-trigonid, in the position of the posterior mental foramen and in its larger size. These differences are sufficient to describe new species, but not to distinguish a new genus. Hence, *Pseudoparatalpa* is considered a junior synonym of *Paratalpa*.

Discussion

Both dentition and associated humeri show a suite of urotrichine characters, which leaves the tribal assignation beyond any doubt. I think the association of humeri and dentition is correct. The smallest are expected to belong to the smallest dentition. Additionally, it is assumed that the humeri have to be associated with the dentition that roughly corresponds in the number of specimens. The Petersbuch 31 fauna also yielded four dentary fragments and two m2 of *Desmanella*, which correspond in size to *Tenuibrachiatum*. The only *Desmanella* species with associated humeri is *D. engesseri* Ziegler, 1985 from the Early Miocene fissure fill Petersbuch 2 (Ziegler 1985: fig. 2). In this species the teres tubercle is distinctly shorter and forms no ledge. Consequently, we can be rather confident that the association of humeri – dentition for *Tenuibrachiatum* is correct.

T. storchi cannot be ancestral to the Recent *Neurotrichus* nor to *Quyania*. Both have all three lower incisors, whereas one is lost in *Tenuibrachiatum*. In anterior view the humerus of the later genera shows a narrow trochlea, which is connected to the capitulum by a thin bridge of the articular facets (see Storch and Qiu 1983: figs. 17–19). In the humerus morphology *Tenuibrachiatum* shows more affinities to *Urotrichus*. In the extant species the antemolar region is more reduced. *Tenuibrachiatum* is a possible candidate for the ancestry of *Urotrichus*. The ancestor of *Tenuibrachiatum* is expected to have the full set of lower antemolars and double-rooted lower premolars, hence one tooth (?i3) with one additional alveolus. Neither *Myxomygale* nor *Paratalpa* fulfil this qualification. In spite of the Oligocene to Early Miocene correlation of most species, both genera are more advanced with respect to the degree of reduction in the lower antemolar region. In dental morphology *Tenuibrachiatum* is somewhat closer to *Myxomygale*.

Genus *Desmanella* Engesser, 1972

Type species: *Desmanella stehlini* Engesser, 1972.

Desmanella cf. *stehlini* Engesser, 1972

Fig. 11.

Material and measurements.—Petersbuch 6: NHMA P6-1064, left dentary fragment with m1–m3, Lm1–m3 (4.19), m1 (1.53×1.00×1.03), m2 (1.59×1.04×1.02), m3 (1.26×0.80×0.62). Petersbuch 18: NHMA P18-754, left dentary fragment with p4–m3, Lm1–m3 (4.15), m1 (1.57×0.93×1.07), m2 (1.61×0.99×1.00), m3 (1.26×0.76×0.65). Petersbuch 31: NHMA P31-0165/1, left dentary fragment with p3+m2, p3 (0.49×0.45), m2 (>1.5×0.97×0.96); CRW P31-0165/2, right dentary fragment with p3–p4, p3 (0.42×0.40), p4 (0.97×0.69); NHMA P31-0165/3, right dentary fragment with p4–m1, p4 (0.92×0.67), m1 (1.46×0.95×1.08); NHMA P31-0165/4, left dentary fragment with m1, m1 (1.48×1.01×1.10).

Description

Dentary.—Only short fragments of the horizontal ramus are preserved. The specimen from Petersbuch 18 shows the posterior mental foramen between the roots of p4 and m1 and the anterior one under the third root anterior to p4, the p1 alveolus. In the small sample from Petersbuch 31 the anterior mental foramen is below p2 (twice) or between the roots of p1 and p2 (once) and the posterior one beneath the trigonid of m1. One specimen shows the complete set of antemolar alveoles. There is one alveolus each for i2, i3, c,

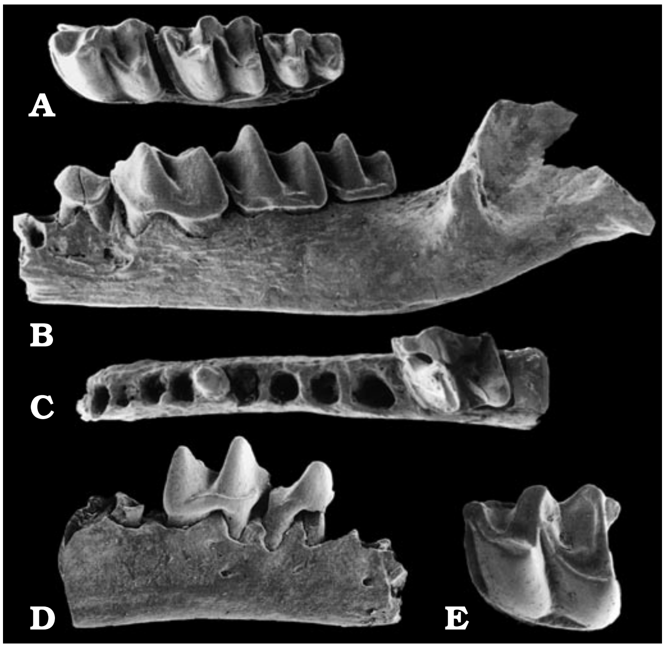

Fig. 11. *Desmanella* cf. *stehlini*. **A**. Left dentary fragment with m1–m3, NHMA P6-1064, Petersbuch 6, occlusal view; ca. × 10. **B**. Left dentary fragment with p4–m3, NHMA P18-754, Petersbuch 18, buccal view; ca. × 10. **C**. Left dentary fragment with p3 and m2, NHMA P31-165/1, Petersbuch 31, occlusal view; ca. × 10. **D**. Right dentary fragment with p4–m1, NHMA P31-165/3, Petersbuch 31, buccal view; ca. × 10. **E**. Left m1, NHMA P31-165/4, Petersbuch 31, occlusal view; ca. × 15.

p1, p2, and p3. Consequently, the lower tooth formula is 2-1-4-3.

Lower dentition.—The teeth anterior to p3 are not preserved. Their alveoli show that all are single-rooted. The likewise single-rooted p3 has a conical cusp with a posterior cingulid. The double-rooted p4 is oval in occlusal outline. The crown has a concave posterior face, a convex mesio-buccal side, and a flat mesio-lingual one. The posterior cingulid encompasses a short talonid.

The molars are slightly inflated and low-crowned. The size relation is m2>m1>m3. In m1 the oblique cristid joins the centre of the protocristid, in m2 and m3 it extends more lingually but does not join the weak metacristid. There is no well-developed metacristid in m1, but a weak, descending entocristid. A moderately developed cingulid runs from below the paraconid to the hypoflexid. The weak postcingulid joins the entostylid. The m2 and m3 are characterised by their short talonid. In m2 the protoconid is somewhat higher, the talonid narrower, and the oblique cristid joins the marked metacristid. The m3 has neither postcingulid nor entostylid.

Discussion

Desmanella stehlini, the genotype, was described for the first time by Engesser (1972) on the basis of six isolated molars from the Anwil fauna. The specimens under study fit well in morphology and length with the molars from the type locality, but they are narrower. The dentaries and teeth from Petersbuch 6+18 correspond well in size with those from Petersbuch 31, but differ in the slightly more posterior position of the mental foramen and in the somewhat weaker pre- and ectocingulid of m2. The position of the mental foramen is not known from *D. stehlini* from the type locality. For want of the upper dentition in our material the presence of important characters cannot be verified. Hence the determination is *Desmanella* cf. *stehlini*.

To date, the record of *D. stehlini* is extremely sparse. Kälin (1993) reported on five isolated teeth of *D.* aff. *stehlini* from Le Locle sous le Stand, Switzerland, which is correlatable with MN 7+8. Kälin and Engesser (2001) designated two isolated teeth from Nebelbergweg, a MN 9-fauna from Switzerland, *Desmanella* sp. Probably they also represent *D. stehlini*. The authors refrained from specific determination because of insufficient material. Crochet and Green (1982) referred 15 isolated teeth and a dentary fragment from Montredon, an Upper Miocene (MN 10) fauna from France, to *Desmanella* cf. *stehlini*. The genus *Desmanella* itself has a long stratigraphic range. The earliest records are from the Oligocene/Miocene transition in South Germany (Ziegler 1990), the latest is represented by *Desmanella gardiolensis* Crochet, 1986 from the Late Pliocene (MN 16) fauna Balaruc 2 in South France (Crochet 1986).

The subfamilial allocation of the genus is a matter of continuous dispute. *Desmanella* was referred to the Desmaninae (Engesser 1972), the Talpinae (Storch 1978) and by most students to the Uropsilinae (e.g., Rümke 1974, 1976; Engesser 1980; Ziegler 1985; Crochet 1986; and van den Hoek Ostende 2001). The whole story is reviewed and comprehensively discussed in Dahlmann (2001) and van den Hoek Ostende (2001). My arguments for an allocation with the Uropsilinae have been the associated humeri of *D. engesseri*, which are characterised by the absence of a bicipital tunnel. According to Campbell (1939), except from the Uropsilinae in all mole humeri the walls of the bicipital groove are fused to form a tunnel. However, in the Recent *Urotrichus talpoides* the bicipital groove is not fully ossified but rather closed by cartilage (Dahlmann 2001: 47). Another particularly important character of the uropsiline humerus is the rounded caput, which is elliptical in all other talpids. The humerus of *D. engesseri* has an elliptical caput (see Ziegler 1985: fig. 2b, 1994: pl. 1: 6, 7), hence they cannot belong to an uropsiline. I think, with respect to humerus morphology, *Desmanella* is better placed within the Urotrichini. Dental morphology and tooth formula is compatible with this allocation. The presence of a functional milk dentition, the main argument of the Uropsilinae advocates, is also known from some Urotrichini, for example *Urotrichus* Temminck, 1841 and *Quyania chowi* Storch and Qiu, 1983.

Urotrichini gen. et sp. indet. I

Fig. 12.

Material and measurements.—Petersbuch 10: NHMA P10-616/1, left dentary fragment with p3, p3 (0.93×0.53); NHMA P10-616/2, right m1 (1.78×0.87×1.01); NHMA

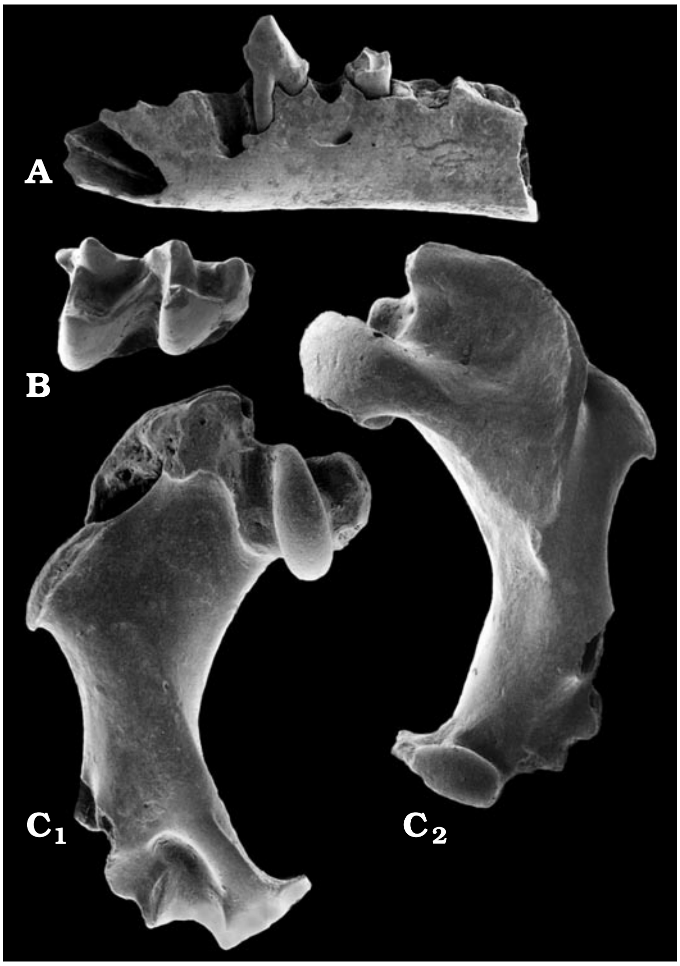

Fig. 12. Urotrichini gen. et sp. indet. I, Petersbuch 10. **A**. Left dentary fragment with p3, NHMA P10-616/1, buccal view; ca. × 10. **B**. Right m1, NHMA P10-616/2, occlusal view; ca. × 15. **C**. Right humerus, NHMA P10-617, in posterior (C_1) and anterior (C_2) views; ca. × 7.5.

P10-617, right humerus GL (10.3), Bp (6.17), BpwT (4.55), DS (2.03), Bp*100/GL (59.9).

Description

Dentary.—There is one dentary fragment with the alveoli of i1–m1, a double-rooted p3, and the talonid of p4. In this specimen a small posterior mental foramen is situated under the anterior root of p4, the anterior one beneath p2. There are five alveoli anterior to p3 for the single-rooted i1, i2, i3, p1, and p2. The incisors are increasingly inclined, i1 being the largest. The canine is assumed to be eliminated. In the p3 the crown is buccally convex and flat on the lingual side. It is surrounded by a cingulid which tapers lingually. From the p4 only the posteriormost part with the marked postcingulid is preserved.

m1.—There is one isolated specimen with a notched para- and protocristid respectively. The oblique cristid extends far lingually but does not join the metacristid. The precingulid is short; the ectocingulid restricted to the hypoflexid, the postcingulid is extremely weak and short.

Humerus.—The supratrochlear fossa, the fossa for the m. flexor digitorum profundus ligament with the medial epicondyle and the greater tubercle with the deltoid process are broken away. In spite of the fracture the deep notch between trochlea and the fossa, which characterises the urotrichines, is partly preserved. The pectoral tubercle extends halfway down the shaft and is situated in its mid, not laterally as in the other urotrichines. The brachialis fossa is only partly preserved; it was only moderately deep. Greater tubercle and head are separated by a deep groove. There is a notch between and lesser tubercle and teres tubercle.

Discussion

The humerus is the largest and most robust among the urotrichine humeri of all samples under study. It is associated with the biggest urotrichine dentary and the biggest urotrichine m1 of the Petersbuch 10 talpid sample. There is no more probable alternative to this association, nonetheless it is considered tentative. Neither humerus nor dental remains fit well with any known species or genus. In view of the uncertainties concerning the association and as the material is too scarce the description of a new taxon is not possible.

Urotrichini gen. et sp. indet. II

Fig. 13.

Material and measurements.—Petersbuch 31, P31-171/1–6: NHMA P31-171/1, left m2 (1.61×0.99×0.93); CRW P31-171/2, right m2 (1.77×1.05×1.08); NHMA P31-171/3, right M1 (2.06×1.47); NHMA P31-171/4, left M2 (1.90×1.87); CRW P31-171/5, right M2 (1.94×1.97); CRW P31-171/6, right M2 (1.57×1.85).

Description

Lower dentition.—In both m2 the metacristid does reach the cusp of the metaconid. It instead ends in a small metastylid below the metaconid. The oblique cristid joins the metacristid. There is a marked precingulid, a short ectocingulid beneath the hypoflexid and a vestigial postcingulid close to the entostylid.

Upper dentition.—The mesostyle of the M1 is nearly confluent in the moderately worn tooth. A slight notch shows that the mesostyle was divided in the unworn tooth. Paraconule and metaconule are differentiated. The prepara-

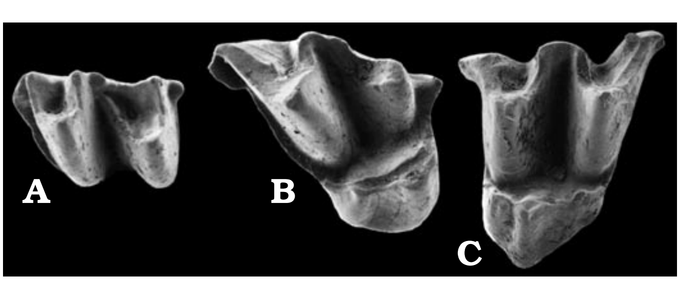

Fig. 13. Urotrichini gen. et sp. indet. II, Petersbuch 31. **A**. Left m2, NHMA P31-171/1, occlusal view; ca. × 15. **B**. Right M1, NHMA P31-171/3, occlusal view; ca. × 15. **C**. Left M2, NHMA P31-171/4, occlusal view; ca. × 15.

conuluscrista is confluent with the strong paracingulum, which itself joins the projecting parastyle. Postmetaconuluscrista and metacingulum are also confluent and terminate in the metastyle. In all three M2 the mesostyle is deeply divided. Paraconule and metaconule a more marked than in the M1. The preparaconuluscrista terminates at the mesial basis of the paracone, the postmetaconuluscrista at the distal basis of the metacone.

Discussion

The teeth cannot be referred to any other species of the Petersbuch 31 talpid fauna. They differ from *Tenuibrachiatum storchi* in the bigger size, the better developed precingulids of m2 and in the divided mesostyles of the M1 and M2. The marked lingual conules in the upper molars, especially in M2, is a distinct desmanine and urotrichine character. As desman teeth are more massive and differ in a suite of other characters, an affiliation with this subfamily can be excluded. It is assumed that all teeth form a homogeneous sample, in spite of the small M2 (no. 6). The teeth are too small for an association with the dentary of Scalopini gen. et sp. indet. Furthermore, the marked lingual conules of the upper molars better fit with the urotrichines. We cannot exclude that the teeth represent the same species as the indeterminable urotrichine from Petersbuch 10. As both samples have neither teeth nor postcranial elements in common this assumption cannot be corroborated. Hence, the determination is Urotrichini gen. et sp. indet. II.

Talpidae *incertae sedis*

Desmanodon Engesser, 1980

Type species: *Desmanodon major* Engesser, 1980.

Desmanodon sp.

Fig. 14.

Material and measurements.—Petersbuch 10, P10-618.1–6: NHMA P10-618/1, left dentary fragment with p4–m1; p4 (1.34×0.78), m1 (1.83×1.26×1.37); CRW P10.618/2, left m1 (1.81×1.16×1.31); NHMA P10-618/3, right dentary fragment with p2–p3; p2 (0.95×0.52), p3 (1.07×0.63); NHMA P10-618/4, right maxilla fragment with P4, P4 (1.99×1.88); CRW P10.618/5, right M1 (ca. 3.25×2.62); CRW P10.618/6, left M3 (1.28×2.50); NHMA P10-619/1, left humerus fragment, DS (2.67); NHMA P10-619/2, right humerus fragment, DS (2.39).

Description

Dentary.—There are only two short fragments of the horizontal ramus, one showing several pitting marks, which at the first glance look like foramina. On the other fragment p2 and p3 overlap each other.

Lower dentition.—The lower teeth are slightly amblyodont, i.e., they have inflated cusps. The premolars are double-rooted and increase in size from p2 to p4. The cusp is situated above the anterior root. In the p2 the cingulid is confined to the posterior half. The p3 has a postero-lingual crest and a weak anterior and posterior cingulid, respectively. The p4 is more heeled. In the m1 the talonid is longer and wider than the trigonid. The small trigonid-angle is conspicuous The oblique cristid runs quite buccally and extends to the posterior base of the protoconid. The paracristid is rounded. It forms an acute angle with the protocristid. There is only a weak precingulid, an ectocingulid confined to the hypoflexid and a somewhat more marked postcingulid.

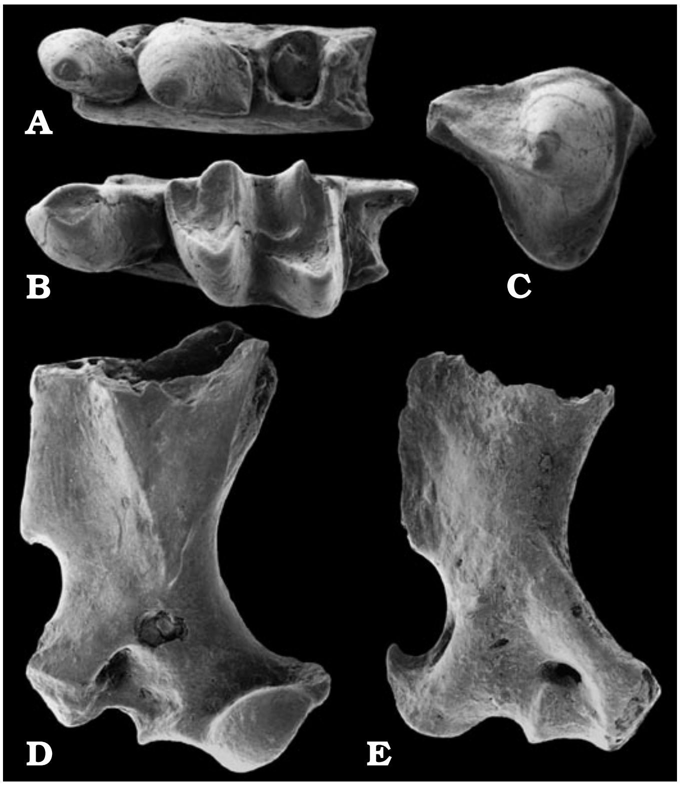

Fig. 14. *Desmanodon* sp., Petersbuch 10. **A**. Right dentary fragment with p2–p3, NHMA P10-618/3, occlusal view; ca. × 15. **B**. Left dentary fragment with p4–m1, NHMA P10-618/1, occlusal view; ca. × 15. **C**. Right P4, NHMA P10-618/4, occlusal view; ca. × 15. **D**. Left humerus, NHMA P10-619/1, anterior view; ca. × 7.5. **E**. Right humerus, NHMA P10-619/2, posterior view; ca. × 7.5.

Maxilla.—The maxillary fragment shows the lacrimal foramen above the posterior root of M1 and the alveoles of a triple-rooted P3.

Upper dentition.—The P4 is surrounded by a continuous cingulum. It has neither parastyle nor protocone, but an extended lingual heel. The postparacrista, which connects paracone and metastyle, is buccally concave. In the M1 the mesostyle is deeply divided and the protocone situated rather anteriorly. The parastyle is broken off. Preprotocrista and precingulum are separated by a notch, whereas postprotocrista and metacingulum are continuous. Para- and metaconule are hardly visible. The M3 is heavily worn. The only morphological detail, which survived wear, is the continuous paracingulum.

Humerus.—Both specimens are superficially corroded and preserved without their proximal parts. The most conspicuous character is the extremely long ledge-like teres tubercle. The broad shaft gives the humerus a compact appearance. The pectoral ridge and a lateral ledge include an acute-angled triangle. The pectoral tubercle extends further distally than the teres tubercle. The supratrochlear fossa is small. Between the trochlea and the fossa for the m. flexor digitorum profundus ligament there is a wide arc. The olecranon fossa is wide but not deep.

Discussion

The above listed specimens are pooled together because of their compatible overall size and because all teeth share the amblyodonty. The humeri are not referable to any other dentition. In the divided mesostyle and the anterior position of the protocone of M1, the short descending oblique cristid of m1 and in the inflated cusps of all teeth as well in the long teres tubercle of the humerus the sample fits well with *Desmanodon*, a genus well-represented in the Lower and Middle Miocene of Anatolia (Engesser 1980; van den Hoek Ostende 1997), the Lower Miocene of Greece (Doukas 1986), South Germany (Ziegler 1985; Ziegler and Fahlbusch 1986) and Spain (van den Hoek Ostende 1997). However, another diagnostic feature of *Desmanodon*, the marked metaconule of the upper molars, is missing. Therefore, the Petersbuch 10 sample is not referable to any known species of the *Desmanodon*. In *D. daamsi* van den Hoek Ostende, 1997 the metaconule is also poorly developed and even may be absent. However, in this species the trigonid is distinctly longer and the mesostyle of M1 is more spaced. As the majority of defining characters is present in the material under study, it can be assumed that the specimens represent a species of *Desmanodon*. Because of lack of sufficient material I refrain from describing a new species. The Petersbuch 10 sample represents the latest record of the genus in Germany.

Conclusions

Composition of the talpid samples (see Table 9).—Miocene talpid samples usually are more diverse than in the extant European fauna. In present-day Europe there is the Pyrenean desman, which is restricted to the northern part of the Iberian Peninsula, and five species of *Talpa*. In one area there do not live more than two talpid species at most, in most regions only one. Compared to the Neogene record, the extant talpid fauna is extremely impoverished. In Neogene European faunas we often find four to five talpid species, largely depending on sample size. In Petersbuch 2 and Sandelzhausen even seven talpid species have been recorded. With 11 talpid species the Early Pliocene site Wölfersheim yielded the most diverse talpid fauna known thus far (Dahlmann 2001). Some faunas more or less correlative with MN 7+8 are listed in Table 10.

Among the faunas under study the record of a desman is unique to Petersbuch 6. The preponderance of the Talpini is common to most of our samples. Their absence in Petersbuch 35 is due to small sample size, consequently incidental. The

Table 9. List of the talpid species of the six Petersbuch 6–48 fissure fills (n_s = number of specimens, n_c = number of most common element).

Species	Petersbuch 6		Petersbuch 10		Petersbuch 18		Petersbuch 31		Petersbuch 35		Petersbuch 48	
	n_s	n_c	n_s	n_c	n_s	n_c	n_s	n_c	n_s	n_c	n_s	n_c
Desmaninae												
Mygalea antiqua	2	2										
Talpinae												
Scalopini												
Leptoscaptor bavaricum gen. et sp. nov.			197	47								
Leptoscaptor bavaricum vel *robustior*	5	4			12	4						
Leptoscaptor robustior sp. nov.									26	12	8	3
Proscapanus sansaniensis			2	1			33	7	7	2	11	4
Proscapanus sp.							11	2				
Scalopini gen. et sp. indet.							1	1				
Talpini												
Talpa minuta	54	19	239	52	16	5	81	43			13	6
Urotrichini												
?*Urotrichus dolichochir*	2	1										
Myxomygale gracilis sp. nov.			7	3								
Tenuibrachiatum storchi gen. et sp. nov.							28	11				
Desmanella cf. *stehlini*	1	1			1	1	4	4				
Urotrichini gen. et sp. indet. I			3	2								
Urotrichini gen. et sp. indet. II							6	3				
Talpidae incertae sedis												
Desmanodon sp.			8	2								
∑	64	27	456	107	29	10	164	71	33	14	32	13

Table 10. Some sites correlative with MN 7+8 and their number of talpid species.

Site/Country	no of talpid species	Reference
France		
La Grive	5	de Bruijn et al. 1992
Switzerland		
Anwil	4	Engesser 1972
Germany		
Steinheim	1	Heizmann and Hesse 1995
Petersbuch 6	5	this paper
Petersbuch 10	6	this paper
Petersbuch 18	3	this paper
Petersbuch 31	7	this paper
Petersbuch 35	2	this paper
Petersbuch 48	3	this paper
Turkey		
Eskihisar	2	Engesser 1980
Sofça	1	Engesser 1980
Sari Çay	4	Engesser 1980
Mongolia		
Tunggur (Moergen II)	5	Qiu 1996

Table 11. Previous stratigraphic ranges (MN units) of the recorded taxa.

Species	Stratigraphic range of	
	species	genus
Desmaninae		
Mygalea antiqua	MN 5–6	MN 2, 5–6
Talpinae		
Scalopini		
Leptoscaptor bavaricum	new	new
Leptoscaptor robustum	new	new
Proscapanus sansaniensis	MN 4–9	MN 4–9
Talpini		
Talpa minuta	MN ?2, 3–9	2–Recent
Urotichini		
?*Urotrichus dolichochir*	MN 5, 7/8, 14–17	5, 7/8, 14–17, Recent
Myxomygale gracilis	new	Olicocene MN 7/8
Tenuibrchiatum storchi	new	new
Desmanella cf. stehlini	MN 7/8-10	Late Oligo–Pliocene
Talpidae incertae sedis		
Desmanodon sp.		MN 3-8

Scalopini are common to all samples, whereas the Urotrichini are rare.

Biostratigraphic considerations.—It is known that insectivores and especially talpids are not good stratigraphic guides. This is mainly due to the ignorance of lineages. Here the known stratigraphic ranges of the species are outlined in order to get a rough idea of the stratigraphy (see Table 11).

Mygalea antiqua, *Proscapanus sansaniensis*, ?*Urotrichus dolichochir* and *Desmanella stehlini* are species we expect in Middle Miocene European faunas. The other taxa are either new or not determinable to species level. *M. antiqua* (type locality Sansan, MN 6) so far has been rarely recorded in faunas correlative with MN 5 and MN 6. The earliest record is from the Randecker Maar in South Germany (Heizmann 1983). There are some finds from Switzerland, e.g., Zeglingen (Kälin 1993) and from the German site Hambach 6 C (Ziegler and Mörs 2000). The two specimens from Petersbuch 6 represent the latest record of *Mygalea antiqua*.

Proscapanus sansaniensis has been recorded in France, Switzerland and Germany. The earliest finds are correlative with MN 4, for example,Vieux Collonges (Mein 1958), and the latest ones from the Swiss Nebelbergweg (Kälin and Engesser 2001) correlate with MN 9.

Talpa minuta is one of the most common talpid species with the widest range. Most finds are only listed in faunal lists. The earliest record, *Talpa*? *minuta* from the Frankfurt Nordbassin (MN 2), is somewhat doubtful because of insufficient preservation (Stephan-Hartl 1972). The earliest unambiguous finds are from Wintershof-West (MN 3) in Germany (Ziegler 1994), the easternmost from the Czech localities Dolnice, Ořechov and Franzensbad (Fejfar 1974) and the latest and south-westernmost from the Vallesian (MN 9) localities Can Llobateres and Can Ponsic in Spain (Crusafont Pairó and Kurten 1976).

?*Urotrichus dolichochir* is recorded from La Grive (MN 7/8, type locality) and from distinctly younger localities. Two humeri from the Sandelzhausen fauna (MN 5) resemble this species in their preserved parts. However, some parts are missing and although humeri are important for recognition of tribal affinities in talpids, they are usually not sufficient for species determination. This species is also known from the Pliocene of Poland (Węże, Rębielice Królewskie, Podlesice, and Kadzielnia; see Skoczeń1980; Kowalski 1989). The presence of this species in a fauna is rather a hint for an at least late Middle Miocene correlation.

Desmanella stehlini and the closely related *D.* cf. *stehlini* are only known from faunas correlative with MN 7/8 as the type locality Anwil or from even younger faunas like Nebelbergweg (MN 9), both situated in Switzerland (Engesser 1972; Kälin and Engesser 2001). So far it was recorded from Switzerland, France and Spain. The recognition of this species in the faunas under study strongly indicates a minimum age corresponding to MN 7/8.

As the new species cannot be related to established lineages—these do not exist—they are biostratigraphically insignificant. A summary of the talpids is in line with a Middle Miocene correlation of MN7/8, as found for the cricetids (Rummel 2000).

Palaeoenvironmental aspects.—Desmans are strictly bound to water. This means that a lake or a rivulet was within the range of the owl that preyed on *Mygalea* and disgorged its pellets near the Petersbuch 6 fissure.

In the Recent fauna the Scalopini are restricted to North America, except the Kansu Mole *Scapanulus*, which lives in some Chinese states. From the present day distribution of this tribe no habitat preferences can be inferred.

The Talpini is an Old World tribe. The presence of *Talpa* in a fauna is not very informative for palaeoenvironmental and palaeoclimatologic questions.

Both the extant species of *Urotrichus* are forest dwellers avoiding the plains. *U. talpoides* also inhabits grasslands. Thus the presence of a species of this genus in a fossil fauna indicates a covered landscape.

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