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Heterosorex et Soricidae (Mammalia, Eulipotyphla) de la fissure Petersbuch 28 ; micro-évolution comme indicateur de mélange temporel ?

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ABSTRACT

The Bavarian fissure filling Petersbuch 28 (Germany, Lower Miocene, MN 3/4) yielded a diverse assemblage of shrews. *Soricella discrepans* Doben-Florin, 1964 and *Paenelimmoeus micromorphus* (Doben-Florin, 1964) show bimodal size distributions in some dental elements, which is interpreted as the result of a small time averaging. Two upper incisor types of *Miosorex desnoyersianus* (Lartet, 1851) were found, also indicating two populations of slightly different times. Apart from these, the fissure yielded *Heterosorex neumayrianus* (Schlosser, 1887), the only heterosoricid present, *Lartetium petersbuchense* Ziegler, 1989, *L. cf. prevostianum* (Lartet, 1851) and *Florinia stehlini* (Doben-Florin, 1964). The shrews confirm that Petersbuch 28 represents a time period near the MN 3/MN 4 transition. Thus, it fills the gap between the classical localities of Wintershof-West and Petersbuch 2. The two species of *Lartetium* Ziegler, 1989 are possible immigrants.

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R É S U M É

Le remplissage de la fissure bavaroise Petersbuch 28 (Miocène inférieur, MN 3/4, Allemagne) a livré une faune diversifiée de musaraignes. Les taxons *Soricella discrepans* Doben-Florin, 1964 et *Paenelimmoeus micromorphus* (Doben-Florin, 1964) présentent une distribution bimodale pour certaines variables dentaires que nous interprétons ici comme la conséquence d'un intervalle de temps prolongé d'accumulation des fossiles. De même, deux classes de taille d'incisives supérieures de *Miosorex desnoyersianus* (Lartet, 1851) ont été observées, suggérant également la présence de deux populations diachrones. En plus de ces espèces, le site a livré *Heterosorex neumayrianus* (Schlosser, 1887), l'unique hétérosoricidé représenté, *Lartetium petersbuchense* Ziegler, 1989, *L. cf. prevostianum* (Lartet, 1851)

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et *Florinia stehlini* (Doben-Florin, 1964). Ces soricidés confirment que l'âge de Petersbuch 28 correspond à un intervalle de temps proche de la transition MN3/MN4. Ce site comble ainsi une lacune entre les localités de Wintershof-West et de Petersbuch 2. Les deux espèces de *Lartetium* Ziegler, 1989 sont considérées comme de probables immigrants.

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1. Introduction

Soricids are very conservative in their molar morphology, differing in details only (Engesser, 2009; Van den Hoek Ostende, 2003). Important taxonomic characters, like the number of antemolars and the shape of the condyle, can only be observed on well-preserved specimens. From the view of a palaeobiologist, fissure fillings offer great opportunities in this respect. Bones and teeth can be more easily collected than in stratified sites and larger numbers of specimens can be obtained, allowing a better estimate of the variation within an assemblage. Moreover, the small mandibles and skull fragments are more readily preserved. Therefore, fissure fillings play an important role in shrew taxonomy (Doben-Florin, 1964; Reumer, 1984; Ziegler, 1989, 2003).

Unfortunately, fissure fillings are not ideal localities from a geological perspective. They lack any direct relationship with their surroundings, which precludes independent dating. Moreover, there is always the risk of a certain amount of time averaging in the fossil content.

The assemblage from Petersbuch 28 near Eichstätt, Bavaria (Germany), shows excellent preservation, which allowed us to demonstrate the presence of minuscule antemolars in two of its shrews (Klietmann et al., 2013). Moreover, the assemblage represents an interesting time frame. It belongs to the Mammal Unit MN 3 or MN 4, filling the gap between the MN 3 localities Stubersheim 3 and Wintershof-West, and the MN 4 sites Petersbuch 2 and Erkertshofen 1 and 2 (Rosina and Rummel, 2012). The insectivores from these localities have been extensively described by Doben-Florin (1964), Ziegler and Fahlbusch (1986) and Ziegler (1989, 1990a, 1990b). Between MN 3 and MN 4, a major change in the rodent faunas of Europe occurred, as the Cricetodontinae entered Europe (Van der Meulen et al., 2011).

Despite their frequent findings, shrews are mostly just described taxonomically or used as a whole group in ecological analyses (Van den Hoek Ostende, 2001b). Recently, some attempts have been made to assess the autecology of individual species, genera or tribes, usually using younger taxa (Furió et al., 2011; Rofes and Cuenca-Bescós, 2009, 2011; Van Dam, 2004). The ecological demands of the Miocene crocidorsicine shrews are not well understood, as they are commonly seen as a general indicator for “warm and moist” conditions, preferably woodlands (Reumer, 1989, 1995; Van den Hoek Ostende, 2001b).

The present paper deals with the shrews from Petersbuch 28. No new species were found, but the large number of well-preserved specimens revealed some previously unknown small, yet important changes, which are useful for the interpretation of the locality's age and for demonstrating how shrews can adapt to changing environmental parameters.

Furthermore, some preliminary conclusions about the ecology of the shrews from Petersbuch 28 can be drawn.

2. Material and methods

The terminology of the dental elements follows Reumer (1984), while morphological structures left unnamed by Reumer are named according to the terminology used for the talpids, following Hutchison (1974) and Van den Hoek Ostende (1989, 1997). The single exception is the hypocone ridge, which is named hypoloph as an analogy to the met-aloph.

The terminology of the astragalus and calcaneus follows Hooker (2001), if Latin names were unknown.

The teeth and bones were measured using a Leica M420 Microscope and a Mitutoyo measuring clock. Repeated measuring of some teeth gave a maximum error of 0.03 mm for the teeth and up to 0.05 mm for the bones.

The measurements of the teeth and mandibles follow Reumer (1984). The length of the lower molars was measured parallel to the lingual margin. The molars were positioned with the entoconid being exactly vertical, following the suggestion of Ziegler (1989). The trigonid and talonid widths were taken perpendicular to the length.

In addition to Reumer's (1984) method, measurements were made of both the greatest buccal length and the width perpendicular to it on the upper molars. The length of the triangular M3 was measured perpendicular to its straight anterior margin.

The P4 was measured using the greatest buccal length and the width perpendicular to it. Additional measurements were taken after De Jong (1988), using an imaginary connection of the posterolingual and posterobuccal endpoints as a reference line. The length was taken perpendicular to the reference line, the width parallel to it. The antemolars were measured along their main axis.

All upper incisors were measured using the method of Reumer (1984). However, correct positioning of the upper incisors is not easily achieved in the case of teeth with either damaged roots or differing angles between the crown and the root. Therefore, a new method was devised that can be used on damaged teeth as easily as on undamaged ones. For the new method, the incisors were measured in buccal or lingual view. The imaginary reference line equals the direction in which the apex and talon tips are pointing. The length was measured at a right angle to the reference line, the height parallel to it. Thus, the teeth were measured according to their functional position in the upper jaw. All upper incisors, except for the upper incisors of *Heterosorex neumayrianus*, were measured using the new method; thus, most of them were measured twice, once following Reumer (1984), once using the new method.

For the lower incisors, the maximum length and maximum height were measured in buccal view. The maximum width was measured in occlusal view. The length of the molar row (m1–m3) was measured in buccal view.

In addition to using the method of Reumer (1984), measurements were made of the greatest widths and heights of the upper and lower condylar facets. The height of the entire condyle perpendicular to the lower facet's width was also measured.

The measurements of the postcranial bones follow Van den Driesch (1976) and Klietmann (2013).

The drawings were done by graphic designer Norbert Frotzler in Vienna. The SEM photos were made using an FEI Inspect S electron microscope in low vacuum at a voltage of 10 kV.

Because the larger jaws exceeded the maximum size that the SEM could include in a single photo, multiple photos of the same jaw were taken and merged using Adobe Photoshop. The photos of the bones were taken using the Keyence VHX-S155 Profile Measuring Unit and the Keyence VHX 1000 Digital Microscope.

The calculations and diagrams were made using Microsoft Excel 2007 and PAST (Hammer et al., 2001). Mean, minimum and maximum values are given in mm. In cases where there were fewer than three specimens, individual values are given. The number of damaged specimens, which were excluded from the statistics, is shown in brackets next to the number of specimens. In the case of bones, all obtainable measurements were made, but in the case of damaged bones, some measurements were excluded.

The material used in this study is from either the private collection of M. Rummel (CMR) or the Naturmuseum Augsburg (NMA). All specimens shown in the figures are housed in the NMA.

Institutional abbreviations: CMR: Collection Michael Rummel; NMA: Naturmuseum Augsburg.

Abbreviations: n: number of specimens; (ex.): number of specimens excluded from the calculations; Param.: Measured parameter; L: Length; W: Width; H: Height; D: Depth; bucc: buccal; ling: lingual; ant: anterior; post: posterior; Tr: trigonid; Ta: talonid; par: parallel to the upper margin; HoM: height of mandible below the molar; CorH: Coronoid Height; LForM: Length to Foramen mentale; Mand: Mandible; PCond: Processus condylaris; Hum: Humerus; MDD: minimum diaphysis diameter; DiW: Distal width; TroW: Trochlear width; TroH: Trochlear height; CML: Caput maximum length; CaW: Caput width; ProxW: Proximal width; Linc: Length of incisura; MDPA: Minimum depth of Processus anconaeus; Calc: Calcaneus; MWTu: Minimum width of tuber; MaWFR: Maximum width of facies region; MaWFac: Maximum width of facies articularis cuboidea; LTuFat: Length of tuber above facies articularis talaris; MDTu: Minimum depth of tuber; Sust: Sustentaculum; MaLFat: Maximum length of facies articularis talaris; WFac: Width of facies articularis talaris; dj: de Jong; R: Reumer.

3. Systematic palaeontology

Infraclass: EUTHERIA Huxley, 1880

Order: EULIPOTYPHILA Waddell, Okada, Hasegawa, 1999

3.1. Family: HETEROSORICIDAE Viret and Zapfe, 1951

Genus: *Heterosorex* Gaillard, 1915

Heterosorex neumayrianus (Schlosser, 1887)

Fig. 1 A–G

Material: Two maxillary fragments, containing P4 and M1, six isolated upper incisors, six mandibular fragments with molars, one of them also with the incisor, eight isolated lower incisors, one mandible with only the incisor, eight mandibular fragments without teeth. Collection numbers: NMA 2012-79/2058-83/2058, CMR-P/28 - 1753, 1755-1759, 1761-1763, 1766-1771, 1773-1777, 1779, 1780, 3168-3171.

Diagnosis: Doben-Florin, 1964.

Description

A good description was given by Doben-Florin (1964), so only the most important features and the new results are presented here.

The **I** is fissident; the tips and ridges of the apex cusps are red.

The tree-rooted **P4** is sub-triangular. The parastyle and the protocone are small. There is no hypocone.

The nearly square **M1** has four roots. The lingual cusps are weak.

The tip and parts of the main ridge of the large **i** are red. The two or three cuspules on the main ridge are weak.

The **m1** has an open trigonid basin and a closed talonid basin. The oblique cristid ends at the posterolingual flank of the protoconid. The hypolophid joins either the entoconid tip or flank, so there is no postentoconid valley.

The **m2** is shorter than the m1; the paraconid is weak and trigonid shorter than in the m1. The oblique cristid reaches up to the posterobuccal wall of the metaconid.

The **m3** has a much narrower talonid with smaller cusps. The hypoconid is large, the entoconid weak.

The **mandible** has an extremely high ramus horizontalis. There are two small alveoli between the incisor and the molar row. The symphysis reaches below the m1 entoconid. The foramen mentale is usually below the protoconid of the m2, but is found under the hypoconid of the m1 in three specimens. The large, deep masseteric fossa is not subdivided by a horizontal bar.

The **processus condylaris** is at the height of the tooth row. The facies articularis superiora is posterobuccal to the larger facies condylaris inferiora. There is no interarticular area.

The rather large **calcaneus** has a long massive tuber. The facies articularis talaris is large. The sustentaculum tali is small, while its facet is large. The processus peroneus is small and situated at the distal end. The facies articularis cuboidea is large and narrow. The distal plantar tubercle is small.

The measurements of *H. neumayrianus* are given in Table 1.

Comparison: The size of the specimens, the deep masseteric fossa and the morphology and size of the upper incisors are typical for the Heterosoricidae (Viret and Zapfe, 1951). The genus *Heterosorex* Gaillard, 1915, is characterised by cusplated lower incisors whose posterior margin

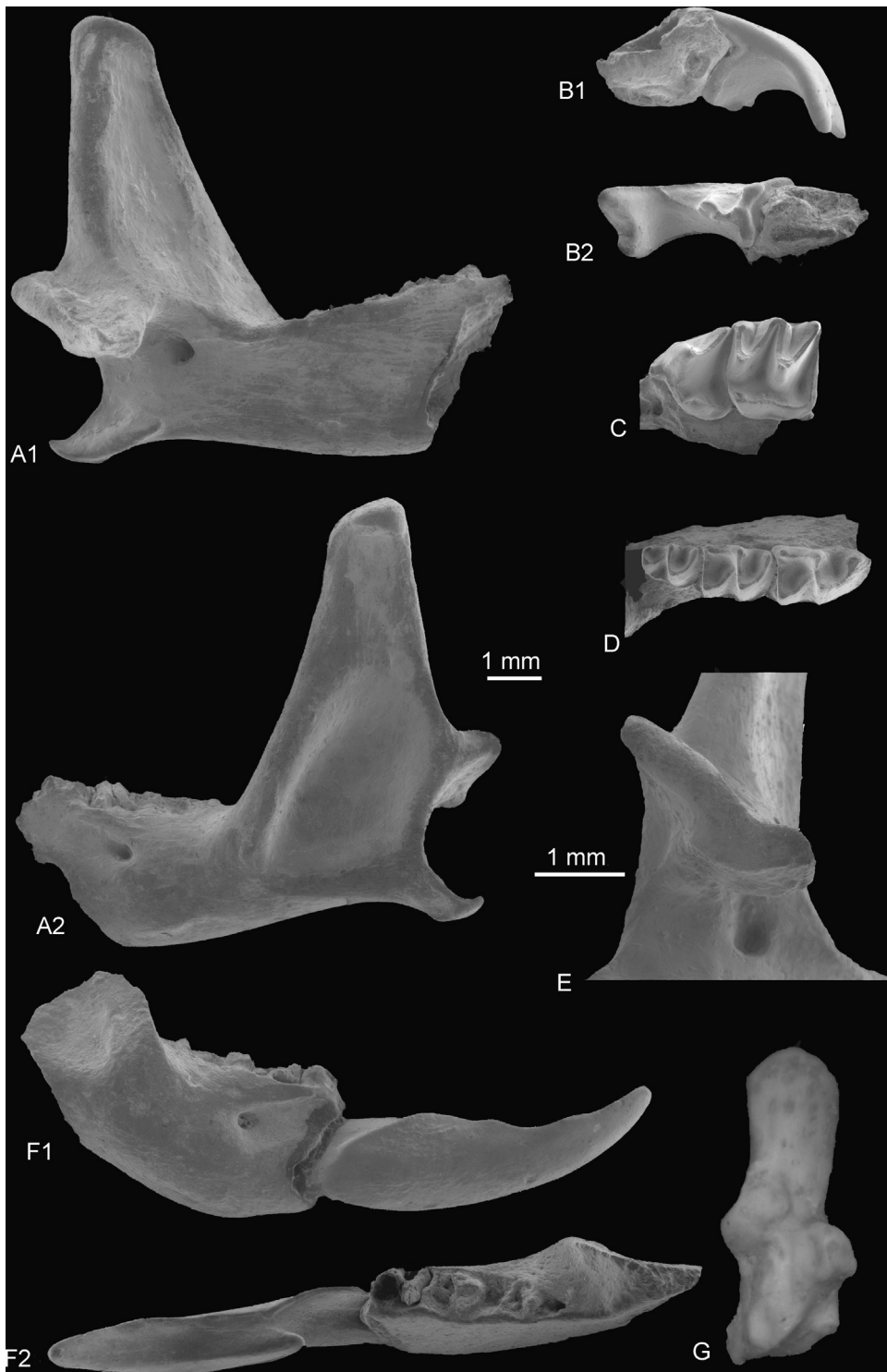


Fig. 1. *Heterosorex neumayrianus* (Schlosser, 1887) from Petersbuch 28 (Germany, Lower Miocene, MN 3/4). **A.** NMA 2012-82/2058: left mandible (1–lingual view, 2–buccal view). **B.** NMA 2012-80/2058: left I (1–lingual view, 2–occlusal view). **C.** NMA 2010-79/2058: left P4, M1 (occlusal view). **D.** NMA 2012-81/2058: right m1–m3 (occlusal view). **E.** NMA 2012-82/2058: left condyle (posterior view). **F.** NMA 2012-83/2058: right mandible with i (1–buccal view, 2–occlusal view). **G.** NMA 2012-139/2058: Right calcaneus (anteromedial view).

Fig. 1. *Heterosorex neumayrianus* (Schlosser, 1887) de Petersbuch 28 (Allemagne, Miocène inférieur, MN 3/4). **A.** NMA 2012-82/2058 : mandibule gauche (1–vue linguale, 2–vue labiale). **B.** NMA 2012-80/2058 : I gauche (1–vue linguale, 2–vue occlusale). **C.** NMA 2010-79/2058 : P4, M1 gauches (vue occlusale). **D.** NMA 2012-81/2058 : m1–m3 droites (vue occlusale). **E.** NMA 2012-82/2058 : condyle gauche (vue postérieure). **F.** NMA 2012-83/2058 : mandibule droite avec i (1–vue labiale, 2–vue occlusale). **G.** NMA 2012-139/2058 : calcaneus droit (vue anteromédiale).

Table 1

Measurements of teeth and bones of *Heterosorex neumayrianus* (Schlosser, 1887) from Petersbuch 28 (Germany, Lower Miocene, MN 3/4).

Tableau 1

Mesurés des dents et os de *Heterosorex neumayrianus* (Schlosser, 1887) de Petersbuch 28 (Allemagne, Miocène inférieur, MN 3/4).

	n (ex.)	Parameter	Mean	Min	Max	
I sup	5 (2)	L	4.13	3.97	4.26	
		H	1.83	1.77	1.92	
		W	1.41	1.40	1.43	
		L par	4.00	3.87	4.13	
		H par	1.77	1.76	1.77	
P4	2	L	1.79	1.51		
		W	1.65	1.49		
M1	2	L bucc	1.65	1.59		
		L ling	1.77	1.59		
		L max	1.62	1.57		
		W ant	1.95	1.70		
		W post	1.93	1.76		
i inf	9 (6)	W max	1.97	1.74		
		L	6.34	6.57	6.14	
		H	1.98	1.84	1.72	
		W	1.51	1.40	1.27	
		W Tr	1.14	1.09	1.21	
m1	5 (1)	W Ta	1.19	1.12	1.28	
		HoM	2.80	2.62	3.07	
m2	5	L	1.66	1.63	1.68	
		W Tr	1.02	0.97	1.07	
		W Ta	1.04	1.00	1.08	
m3	10	HoM	2.71	2.49	3.13	
		3 (1)	L	1.23	1.23	
			W Tr	0.77	0.84	
Mand	10	W Ta	0.53	0.54		
		HoM	2.50	2.05	2.80	
		m1-m3	4.39	4.49		
		LForM	4.39	4.06	4.73	
PCond	3	CorH	7.53	7.19	7.89	
		W inf	1.74	1.59	1.87	
		W sup	1.62	1.51	1.87	
		W total	3.01	2.74	3.31	
Calc	9 (6)	H	1.50	1.32	1.65	
		4	Max L	6.01	5.97	6.04
		9	MWTu	1.02	0.96	1.10
		6	MaWFR	2.59	2.39	2.95
		6	MaWFac	1.76	1.62	1.88
		8	LTuFat	2.27	2.16	2.40
		9	MDTu	1.52	1.44	1.65
		6	W Sust	1.05	0.99	1.12
		5	L Sust	1.12	1.04	1.21
		5	MaLFat	1.98	1.91	2.10
7	WFat	1.04	0.95	1.17		

reach below the trigonid of the m1 and the undivided fossa masseterica (Ziegler, 1998b).

The lack of a horizontal bar in the masseteric fossa and the presence of cuspules on the lower incisor exclude an assignment to *Dinosorex* Engesser, 1972. *Dinosorex* also has much larger lingual cusps on the M1, probably reflecting some trophic adaptation (Smith and Van den Hoek Ostende, 2006).

The specimens from Petersbuch 28 agree both metrically and morphologically with *H. neumayrianus* (Schlosser, 1887). Three subspecies are known for this species (Doben-Florin, 1964; Ziegler and Fahlbusch, 1986). In the oldest subspecies, *H. neumayrianus neumayrianus* (Schlosser, 1887), the foramen mentale is situated more anteriorly, and *H. neumayrianus subsequens* (Doben-Florin, 1964) has larger molars (Doben-Florin, 1964; Ziegler, 1989). The

youngest subspecies, *H. neumayrianus* aff. *subsequens*, as described by Ziegler and Fahlbusch (1986), appears to be most similar in size and morphology to the specimens from Petersbuch 28. Unfortunately, the lower antemolars were not preserved in Petersbuch 28; therefore the subspecies could not be determined with any degree of certainty.

The calcaneus was assigned to *H. neumayrianus* because it is similar in appearance to that of the recent shrew species *Suncus murinus* (Linnaeus, 1766), *Crocidura leucodon* (Hermann, 1780) and especially *Sorex araneus* (Linnaeus, 1758). It is much larger than the calcaneus of recent shrews, being nearer in size to that of a gymnure such as *Galerix aurelianensis* Ziegler, 1990, which was also found in Petersbuch 28 (Klietmann, 2013). However, it is smaller than the calcaneus of the gymnure *Galerix exilis* (de Blainville, 1839), a smaller relative of *G. aurelianensis*, and its facies articularis cuboidea and distal area are wider.

Ever since the description of the Heterosoricinae as a subfamily by Viret and Zapfe (1951), there has been a debate. Reumer (1987) raised the taxon to family level, arguing that Soricidae and Heterosoricidae evolved independently from the Nyctitheriidae. In some subsequent works, this view was endorsed (Kälin and Engesser, 2001; Reumer, 1998; Rzebik-Kowalska, 1998; Smith and Van den Hoek Ostende, 2006; Van den Hoek Ostende, 1995; Ziegler, 1989), while others retained the classification as a subfamily (McKenna and Bell, 1997; Storch and Qiu, 1991, 2004; Ziegler, 1998a, 2003, 2006a, 2006b; Ziegler and Storch, 2008). The descentance of all shrews from the Nyctitheriidae is still generally accepted (Ziegler, 2009). However, based on dental and postcranial characters, the Nyctitheriidae have been reinterpreted as being Archonta by Hooker (2001), which means that they might not be the ancestors of any eulipotyphlan taxon.

The taxonomic placement was chiefly influenced by two different, but correct considerations: Ziegler (2003) emphasized that soricids and heterosoricids are sister taxa in relation to all other eulipotyphlans. Reumer (1987) stressed that a subfamily Heterosoricinae would be the sister taxon to all other soricids.

Smith and Van den Hoek Ostende (2006) added the argument that the Heterosoricidae were already diverse and widespread when the first soricid was found.

The morphological differences are indeed compelling. The Heterosoricidae developed a large fossa on the buccal side of the mandible instead of on the lingual side, and also retained the zygomatic arch; it is therefore safe to assume that they developed their chewing musculature independently (Reumer, 1987). Furthermore, no indication of enlarging the chewing musculature on the lingual side has been found in heterosoricids. The molar and upper incisor morphology of contemporaneous soricids and heterosoricids is quite different. The incisor enlargement may have occurred before the division of soricids and heterosoricids, but it could also be a parallelism. The condyle is divided in a different way, so it was probably developed independently. The Soricidae and Heterosoricidae are almost certainly sister taxa, but the differences validate the differentiation into two families.

3.2. Family: SORICIDAE Fischer, 1814

Subfamily: CROCIDOSORICINAE Reumer, 1987

3.2.1. Genus: *Soricella* Doben-Florin, 1964

Soricella discrepans Doben-Florin, 1964

Fig. 2 A–I

Material: 153 maxillary fragments with teeth, seven of them also with the incisor, 47 isolated maxillary antemolars and molars, 27 isolated upper incisors, 567 mandible fragments (including a few specimens where only the angular process is damaged), 23 isolated mandibular antemolars and molars, 16 isolated lower incisors. Collection numbers: NMA 2012–84/2058–90/2058. CMR-P/28-1355, 1730, 1782–1795, 1797–1799, 1801, 1803, 1806, 1808, 1810–1821, 1826, 1827, 1830, 1833, 1835, 1836, 1839, 1841–1858, 1860–1881, 1883–1891, 1893–1904, 1906–1916, 1918, 1920–1923, 1925–1933, 1936–1944, 1946–1949, 1951–1956, 1958–1971, 1973, 1974, 1977–1985, 1990–1997, 1999–2005, 2007–2011, 2014, 2016–2033, 2036–2042, 2044–2052, 2054–2057, 2059, 2060, 2062–2066, 2068, 2069, 2071, 2074, 2076–2078, 2080, 2084, 2087, 2088, 2090–2095, 2097–2111, 2113, 2116, 2117, 2119–2156, 2158, 2160–2163, 2165, 2167, 2170, 2172–2182, 2184, 2186, 2187, 2189–2239, 2241–2251, 2253–2312, 2314, 2315, 2317–2326, 2328–2350, 2352–2361, 2363–2401, 2403, 2404, 2407–2474, 2476–2498, 2500–2515, 2517, 2518, 2520–2541, 2543–2546, 2548–2563, 2565–2602, 2604–2630, 2632, 2634–2648, 2650, 2651, 2653–2657, 2659, 2664–2667, 2673, 2674, 2679, 2681, 2689, 2697, 2707, 2713, 2715, 2769, 2776, 2781, 2783, 2785, 2787, 2789, 2791, 2792, 2794, 2797, 2831, 2867, 2868, 2871–2873, 2875, 2975, 3083, 3092, 3162–3165, 3172, 3180.

Original Diagnosis: Doben-Florin, 1964

Emended diagnosis

Middle sized soricid, teeth unpigmented. Bicuspluate inf., cuspules inclined to anterior direction. The first one is found near the tooth basis. Two antemolars are situated between the incisor and the p4; the p4 is double-rooted, the a2 is smaller than the a1. Molars decrease in size from the m1 to the m3. The m1 and m2 have a small, crest-like entostylid and the hypolophid is connected to the entoconid and entostylid. The m3 is relatively large and has a two-cusped talonid. There is a strong buccal cingulid. The I has two posterior tips, and there are four teeth between the incisor and the P4, all visible. The second tooth is smaller than the others, and the first one is the largest. Between the last one and the P4, a small gap remains. M1 and M2 show a concave posterior side and a weak hypocone; the trigon basin is closed by a small posterior enamel ridge. The condyle is fairly small with a wide, nearly straight, lingually confluent surface. The foramen mandibulae is located behind middle of the fossa temporalis. The foramen mentale is located below the a3. The fossa infraorbitalis is located between the P4 and M1. The posterior opening of the canalis infraorbitalis is located above the mesostyle of the M2. The foramen lacrimale is relatively high, lying above the mesostyle to metastyle of the M1. There are additional foramina on the labial side of the skull above the A2.

Description

An extensive description was given by Doben-Florin (1964); only the most important features and new results are presented here.

The I has a semicircular dorsal margin of the crown and a large apex tip. The cingulum becomes larger in the buccal direction and ends at the most dorsal point.

The size sequence of the **antemolars** is A1 > A3 > A4 > A2. The individual antemolars differ from each other mainly in size.

The P4 has a large posterior emargination. The protocone is larger, but lower than the parastyle. The tiny hypocone has a single ridge connecting to the cingulum in the posterior emargination.

The four-rooted M1 is nearly square with a concave posterior side. Protoconule and hypocone are weak; the hypoloph connects to the cingulum. Small transversal ridges connect the protocone ridges to the paracone and metacone.

The M2 has the parastyle as far buccal as the metastyle, and a smaller hypoconal flange than the M1.

The three-rooted M3 is triangular. The small metacone is an enlargement of its ridges. The hypocone is a tiny, conical cuspule at the posterior flank of the protocone. The trigonid basin is large and deep.

The bicuspluate crown of the i bends to the occlusal side. The main tip is very large. The cuspules' tips are pointing anteriorly. The large buccal cingulid reaches below the second cuspule.

The one-rooted a1 is sub-triangular. The large Y-shaped protoconid lies in the anterior third. The large cingulid surrounds the tooth except the anterior curve.

The a2 is shorter and higher. A small additional ridge starts on the buccal side and connects to the posterobuccal ridge in some specimens.

The a3 (p4) has two roots. It is higher than the other antemolars; the posterolingual ridge is more pronounced. In some specimens, the cingulid forms a small posterior cuspule.

The m1 has a wide trigonid basin. The talonid is a bit shorter, but wider than the trigonid; its basin is large, deep and closed, the hypoflexid short. The oblique cristid ends at the posterior flank of the protoconid in a distinct mesoconid. The hypolophid splits at its end. The posterior part connects to the entostylid. The small anterior part reaches the entoconid, so there is no postentoconid valley.

The m2 has a relatively wider and shorter trigonid than the m1.

The m3 is much smaller and has a talonid narrower than the trigonid. The hypolophid connects directly to the entoconid. There is no entostylid. In specimens CMR-P/28-2088, CMR-P/28-2342, CMR-P/28-2361 and CMR-P/28-2787, the hypolophid does not reach the entoconid, but ends at the entoconid posterior margin. Therefore, the talonid morphology resembles the m1 or m2 more than usual for the m3.

The symphysis of the **mandible** reaches the p4. The foramen mentale is positioned below the p4, in one case below the m1.

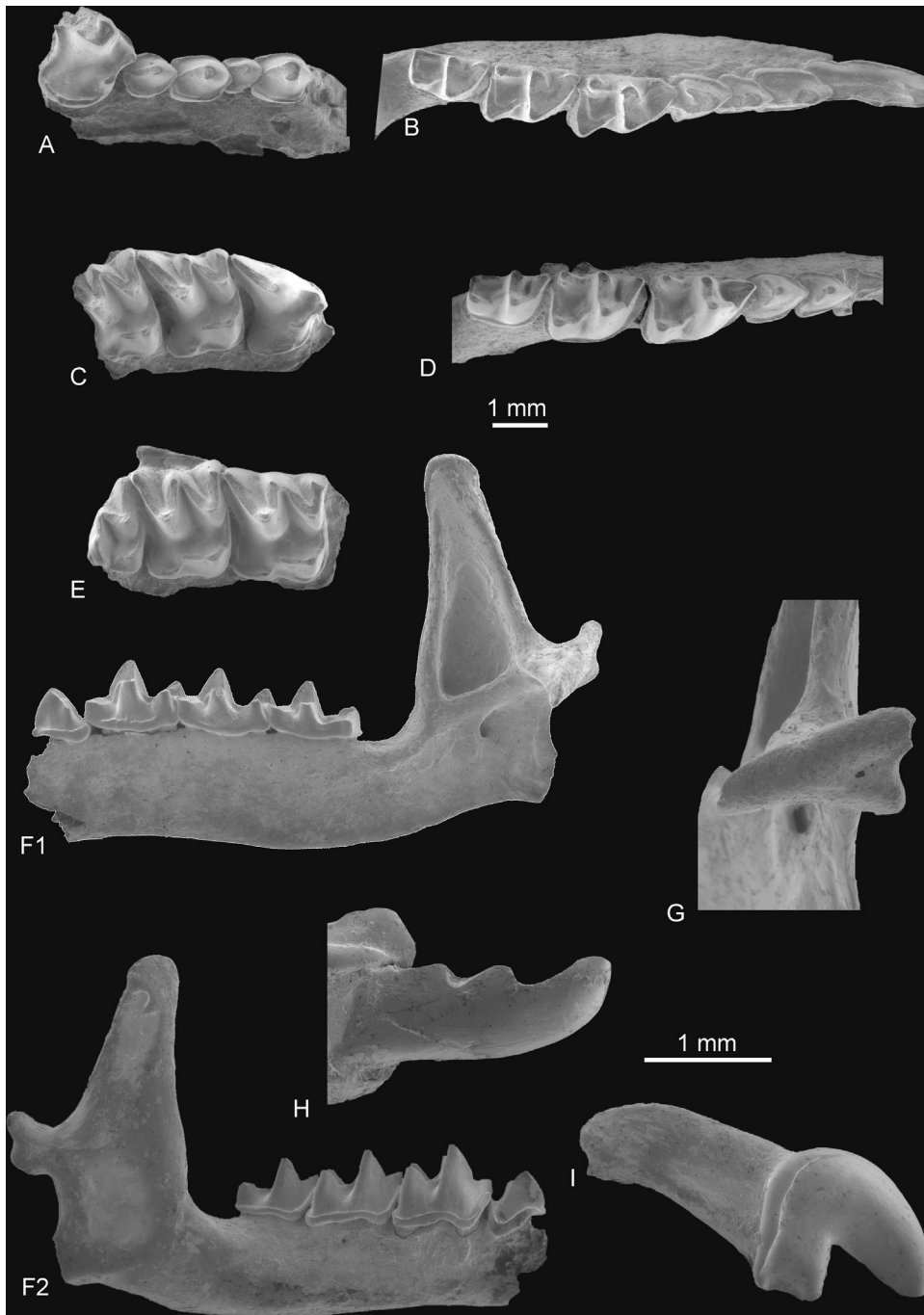


Fig. 2. *Soricella discrepans* Doben-Florin, 1964 from Petersbuch 28 (Germany, Lower Miocene, MN 3/4). All specimens are displayed as right. **A.** NMA 2012-85/2058: left A1–P4 (occlusal view). **B.** NMA 2012-88/2058: right mandible with i–m3 (occlusal view). **C.** NMA 2012-87/2058: left P4–M1 (occlusal view). **D.** NMA 2012-89/2058: right mandible with a2–m3 (occlusal view). **E.** NMA 2012-84/2058: left M1–M3 (occlusal view). **F.** NMA 2012-90/2058: right mandible with a2–m3 (1–lingual view, 2–buccal view). **G.** NMA 2012-90/2058: right condyle (posterior view). **H.** NMA 2012-88/2058: right i inf., a1 (buccal view). **I.** NMA 2012-86/2058: right I (buccal view).

Fig. 2. *Soricella discrepans* Doben-Florin, 1964 de Petersbuch 28 (Allemagne, Miocène inférieur, MN 3/4). **A.** NMA 2012-85/2058 : A1–P4 gauches, inverse (vue occlusale). **B.** NMA 2012-88/2058 : mandibule droite avec i–m3 (vue occlusale). **C.** NMA 2012-87/2058 : P4–M1 gauches, inverse (vue occlusale). **D.** NMA 2012-89/2058 : mandibule droite avec a2–m3 (vue occlusale). **E.** NMA 2012-84/2058 : M1–M3 gauches, inverse (vue occlusale). **F.** NMA 2012-90/2058 : mandibule droite avec p4–m3 (1–vue linguale, 2–vue labiale). **G.** NMA 2012-90/2058 : condyle droit (vue postérieure). **H.** NMA 2012-88/2058 : i inf., a1 droites (vue labiale). **I.** NMA 2012-86/2058 : I droite (vue labiale).

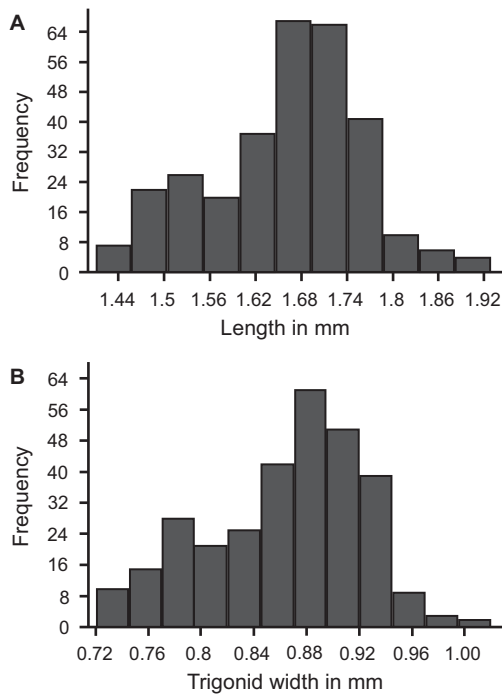


Fig. 3. Length and width of the m1 of *Soricella discrepans* Doben-Florin, 1964 from Petersbuch 28 (Germany, Lower Miocene, MN 3/4).

Fig. 3. Longueur et largeur de la m1 de *Soricella discrepans* Doben-Florin, 1964 de Petersbuch 28 (Allemagne, Miocène inférieur, MN 3/4).

The **processus condylaris** is much wider than it is high. Its facets include a small angle and are fused on the lingual side. There is only a small buccal interarticular area.

The measurements of *S. discrepans* are given in Table 2.

Comparison: *S. discrepans* Doben-Florin, 1964 is the only crocidosoricine shrew where the hypolophid connects directly to the entoconid, cancelling out the postentoconid valley. The number and relative size of the antemolars agree with Doben-Florin's (1964) description, as do the strong and stout incisors. The rich material enabled the presentation of a few additions to the original diagnosis by Doben-Florin (1964), so an emended diagnosis is given here.

S. discrepans is the most common shrew in Petersbuch 28. Its metric variability encompasses most of the variation found in different samples by Ziegler (1989). The unnamed species, *Soricella* sp. (Ziegler, 1989), is by far larger than the specimens from Petersbuch 28.

Interestingly, *S. discrepans* has the least crocidurine condyle of all crocidosoricines in Petersbuch 28. The condyle is very low and its facets are weakly separated.

The size distribution of the lower m1 suggests two slightly different populations (Fig. 3); the other lower molars are rather uniform in size. The smaller population encompasses the smallest specimens of *S. discrepans* known from Germany (Ziegler, 1989). A weak bimodal size distribution was also found in the P4 and the upper incisors. The two populations might be separated either in time or in space. A sexual dimorphism would most probably have been reported from other sites with many specimens.

Table 2

Measurements of the teeth and mandibles of *Soricella discrepans* Doben-Florin, 1964 from Petersbuch 28 (Germany, Lower Miocene, MN 3/4).

Tableau 2

Mesures des dents et mandibules de *Soricella discrepans* Doben-Florin, 1964 de Petersbuch 28 (Allemagne, Miocène inférieur, MN 3/4).

	n (ex.)	Parameter	Mean	Min	Max
I sup	35 (13)	L	1.50	1.28	1.65
		L Ta	0.64	0.55	0.76
		H	1.33	1.06	1.97
		L new	1.48	1.21	1.64
		L Ta new	0.66	0.53	0.77
		H new	1.39	1.15	1.64
		HTa new	1.20	0.90	1.39
A1	5	L	0.95	0.88	1.01
		W	0.75	0.65	0.81
A2	7 (1)	L	0.63	0.52	0.78
		W	0.57	0.54	0.62
A3	14	L	0.92	0.78	1.00
		W	0.69	0.58	0.79
A4	23 (2)	L	0.78	0.68	0.90
		W	0.65	0.57	0.73
		L bucc	1.63	1.36	1.78
		L ling	1.03	0.52	1.20
P4	100 (21)	W	1.47	0.40	1.70
		L dj	1.41	1.16	1.78
		W dj	1.69	1.28	1.94
		L bucc	1.50	1.30	1.69
		L ling	1.42	1.24	1.65
		L max	1.49	1.30	1.69
		W ant	1.55	1.33	1.74
M1	154 (20)	W post	1.74	1.47	1.93
		W max	1.68	1.40	1.86
		L bucc	1.39	1.25	1.52
		L ling	1.32	1.08	1.46
		L max	1.37	1.20	1.50
		W ant	1.70	1.54	1.85
		W post	1.66	1.47	1.81
M2	128 (41)	W max	1.71	1.56	1.88
		L	0.88	0.80	0.99
		W	1.42	1.26	1.60
		L	2.22	1.98	2.32
M3	25 (5)	H	0.66	0.57	0.78
		L	1.20	1.13	1.28
i inf	30 (8)	W	0.74	0.56	0.83
		L	0.87	0.72	1.04
a1	24 (6)	W	0.66	0.53	0.76
		L	0.97	0.82	1.09
a2	46 (7)	W	0.71	0.55	0.81
		L	0.97	0.82	1.09
a3 (p4)	96 (10)	W	0.71	0.55	0.81
		L	1.66	1.41	1.93
		W Tr	0.86	0.72	1.02
		W Ta	0.95	0.79	1.11
m1	356 (51)	HoM	1.53	1.03	1.99
		L	1.55	1.34	1.78
		W Tr	0.86	0.72	1.03
		W Ta	0.91	0.76	1.09
m2	404 (75)	HoM	1.57	1.10	1.96
		L	1.31	1.12	1.49
		W Tr	0.70	0.54	0.81
		W Ta	0.58	0.48	0.73
m3	291 (48)	HoM	1.59	1.24	2.00
		L	1.55	1.34	1.78
		W Tr	0.86	0.72	1.03
		W Ta	0.91	0.76	1.09
Mand	384 (114)	HoM	1.57	1.10	1.96
		L	1.31	1.12	1.49
		W Tr	0.70	0.54	0.81
		W Ta	0.58	0.48	0.73
PCond	24 (4)	HoM	1.59	1.24	2.00
		LForM	4.19	3.73	6.39
		CorH	6.00	4.48	6.83
		CorH	5.03	4.74	5.53
PCond	6	W inf	1.47	1.27	1.58
		W sup	1.62	1.22	1.91
		H	1.16	0.95	1.33
		H R	1.23	0.96	1.43

Because of a similar situation in *Paenlimnoecus micromorphus* (Doben-Florin, 1964), the favoured interpretation is a slight temporal mixing. Since the size difference was found in two occluding elements (P4/m1), it suggests that the evolutionary differences between the two populations affected the functionally most important part first.

Compared to the sample from Petersbuch 2 (Germany, Lower Miocene, MN 4), *S. discrepans* is slightly smaller in Petersbuch 28, but includes more size variation (Ziegler, 1989). The specimens from the type locality Wintershof-West (Germany, Lower Miocene, MN 3) are larger than the specimens from Petersbuch 28, Petersbuch 2 or Stuberseim 3 (Germany, Lower Miocene, MN3) (Ziegler, 1989).

3.2.2. Genus: *Lartetium* Ziegler, 1989

Lartetium petersbuchense Ziegler, 1989

Fig. 4 A–J

Material: 22 maxillary fragments with teeth, six isolated upper antemolars and molars, four isolated upper incisors, 126 mandibular fragments (including a few nearly complete mandibles), seven isolated lower molars, two isolated lower incisors. Collection numbers: NMA 2012–91/2058–98/2058, CMR-P/28-1309, 1351, 1802, 1805, 1859, 1934, 1975, 1986, 1987, 2006, 2034, 2035, 2053, 2082, 2083, 2085, 2086, 2089, 2115, 2118, 2157, 2183, 2316, 2327, 2362, 2475, 2499, 2516, 2519, 2542, 2547, 2564, 2603, 2658, 2660–2662, 2666, 2669–2672, 2675, 2677, 2680, 2682, 2683, 2685–2688, 2690–2696, 2698–2700, 2702, 2704–2706, 2708–2712, 2714, 2716–2733, 2736–2742, 2744–2756, 2758–2766, 2768, 2770–2775, 2777–2780, 2782, 2784, 2786, 2790, 2793, 2795, 2796, 2802, 2807, 2820, 2821, 2824, 2827, 2837, 2849, 2850, 2857, 2861–2864, 2942, 2956, 3031, 3048, 3075, 3080, 3093, 3101, 3178, 3179.

Diagnosis: Ziegler, 1989

Description

Since a good description has already been given by Ziegler (1989), only the most important or new traits are described here.

The dorsal outline of the **I** is straight. The talon tips are rounded. The cingulum is weak and does not reach the most dorsal point.

The **antemolar** size sequence is $A1 > A3 > A2 > A4$. The cingulum is relatively weak. Between the A4 and the P4, there is a visible gap.

The large **P4** has large and pronounced hypocone and protocone. The posterior emargination is large.

The **M1** is short and wide. The hypocone is large and dominates the hypoconal flange.

The **M2** has a large hypocone, but a small hypoconal flange; the hypoloph is weak or missing.

No **M3** could be assigned to *Lartetium*.

The crown of the **i** is robust and bicuspluate. The incisor is straight. The cuspules lack clear tips. The cingulid is weak.

The **a1** has a large, but weak cingulid.

The **a2** is smaller, but higher. The posterolingual ridge starts weak and becomes larger. The cingulid is weak on the lingual side.

The tiny **a3** has one root. The antemolar is tear-shaped. A large ridge runs to the posterobuccal corner.

The high **a4 (p4)** has two roots. The blunt posterior ridges reach up to half the height of the main cusp. The cingulid is rather weak.

The **m1** is wide. The entostylid does not extend posteriorly. The postentoconid valley is very narrow. The buccal cingulid is interrupted at the protoconid.

The **m2** has a slightly shorter and wider trigonid relative to the talonid.

The **m3** is smaller than the other molars. Its talonid is considerably smaller than the trigonid and the two talonid cusps are low.

The **mandible** has a symphysis reaching to the p4. The foramen mentale is situated below the p4.

The **processus condylaris** is high; its upper and lower facets are not completely divided. The buccal interarticular area is small. There is a dorsoventral groove sometimes isolating the buccal part of the lower facet.

The measurements of *L. petersbuchense* are given in Table 3.

Comparison: *L. petersbuchense* Ziegler, 1989, is characterised by the interrupted buccal cingulid of the lower molars, the presence of four lower antemolars and the posterior ridges on the p4 ending at half the tooth's height. The short and wide upper molars have large and high hypocones. The cuspules of the upper and lower incisors are narrow and lack clear tips, also a unique trait of *L. petersbuchense*. The genus is well defined and described by Ziegler (1989), yet it is very similar to *Oligosorex kretzoi*, 1959, a genus re-instated by Van den Hoek Ostende (2001a). When Ziegler defined *Lartetium*, *Oligosorex* was generally considered a junior synonym of *Crocidosorex lavocat*, 1951. Repenning (1967) had considered *Oligosorex* a synonym because of the rather poor diagnosis given by Kretzoi (1959). A thorough revision of the species of both *Oligosorex* and *Lartetium* would be necessary to clarify the relationship between them. Such a revision is beyond the scope of the present paper.

The Petersbuch 28 specimens are nearly similar in size to the specimens from Petersbuch 2 (Ziegler, 1989). Apart from the fissures in the Petersbuch quarry, *L. petersbuchense* has only been reported from Merkur-Nord (Czech Republic, Lower Miocene, MN 3) (Fejfar and Sabol, 2005). In the Petersbuch 28 material, a faint buccal cingulid remains on some m1 and m2, demonstrating that the reduction of the cingulid was still an ongoing development.

Despite being smaller than *S. discrepans*, *L. petersbuchense* has considerably larger upper and lower incisors (Tables 2 and 3). The interspecific morphological and metric variation is most probably linked to different feeding behaviour, but any interpretation given here would be mere speculation.

Lartetium cf. prevostianum (Lartet, 1851)

Fig. 5 D1–2

Material: 54 mandibular fragments with teeth, two of which include at least one antemolar anterior to p4, two isolated lower molars. Collection numbers: NMA 2012-99/2058, CMR-P/28-2168, 2701, 2767, 2865, 2882, 2888, 2895, 2902, 2907, 2910, 2913, 2922, 2925, 2927, 2928, 2930, 2934, 2935, 2940, 2944, 2945, 2949, 2954, 2959, 2963, 2972, 2974, 2976–2978, 2988, 2992, 2993, 3000,

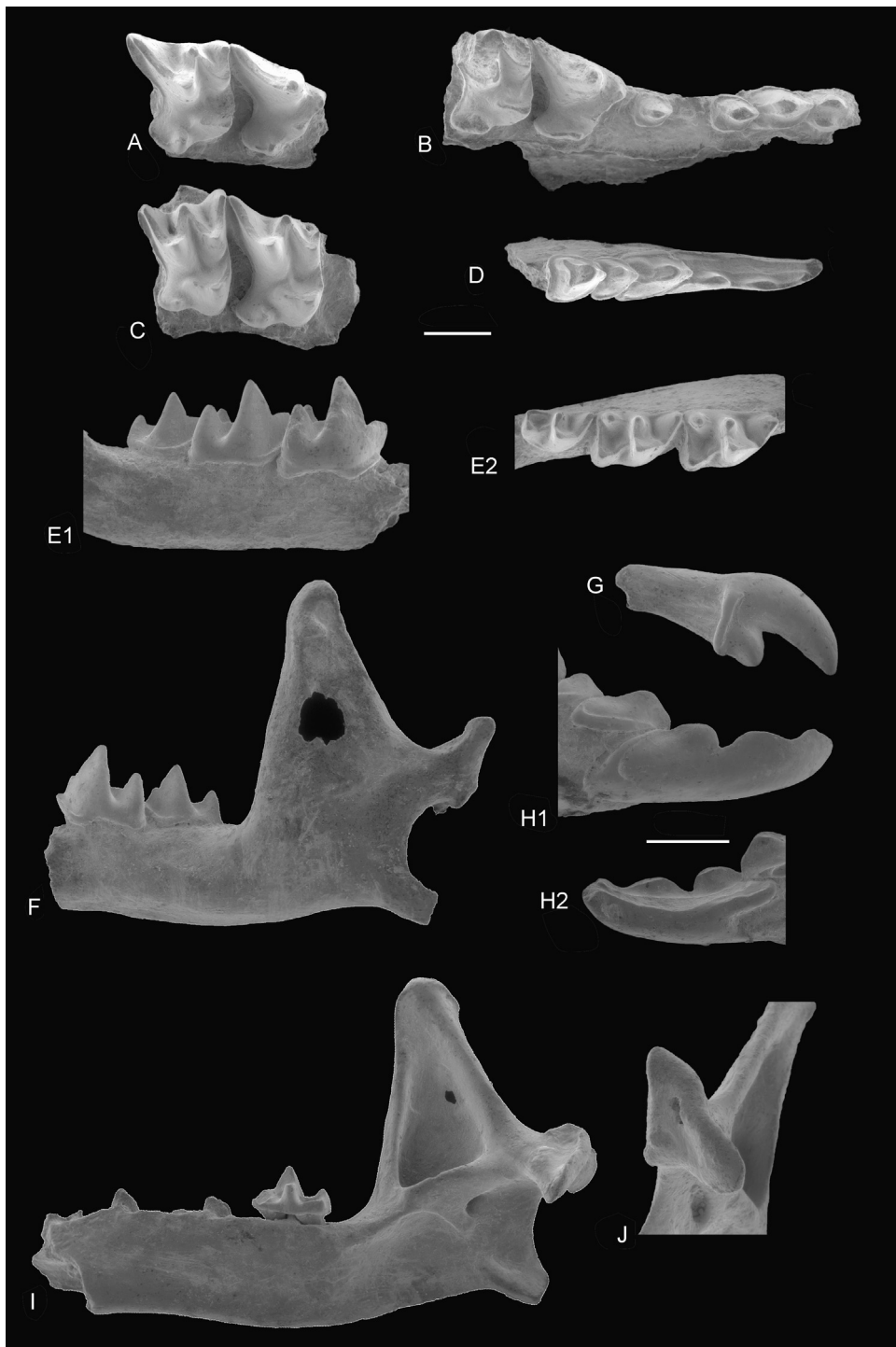


Fig. 4. *Lartetium petersbuchense* Ziegler, 1989 from Petersbuch 28 (Germany, Lower Miocene, MN 3/4). All upper teeth are displayed as dext. **A.** NMA 2012-92/2058: left P4, M1 (occlusal view). **B.** NMA 2012-91/2058: right I (damaged), A1, A2, A4, P4, M1 (occlusal view). **C.** NMA 2012-93/2058: left M1, M2 (occlusal view). **D.** NMA 2012-95/2058: right mandible with i-p4 (occlusal view). **E.** NMA 2012-97/2058: right mandible with m1–m3 (1–buccal view, 2–occlusal view). **F.** NMA 2012-98/2058: left mandible with m2, m3 (buccal view). **G.** NMA 2012-94/2058: left I (buccal view). **H.** NMA 2012-95/2058: right i inf., a1, a2 (1–buccal view, 2–lingual view). **I.** NMA 2012-96/2058: right mandible with m3 (lingual view). **J.** NMA 2012-98/2058: left condyle (posterior view).
Fig. 4. *Lartetium petersbuchense* Ziegler, 1989 de Petersbuch 28 (Allemagne, Miocène inférieur, MN 3/4). **A.** MA 2012-92/2058 : P4, M1 gauches, inverse (vue occlusale). **B.** NMA 2012-91/2058 : I, A1, A2, A4, P4, M1 droites (vue occlusale). **C.** NMA 2012-93/2058 : M1, M2 gauches, inverse (vue occlusale). **D.** NMA 2012-95/2058 : mandibule droite avec i-p4 (vue occlusale). **E.** NMA 2012-97/2058 : mandibule droite avec m1–m3 (1–vue labiale, 2–vue occlusale). **F.** NMA 2012-98/2058 : mandibule gauche avec m2, m3 (vue labiale). **G.** NMA 2012-94/2058 : I gauche, inverse (vue labiale). **H.** NMA 2012-95/2058 : i inf., a1, a2 droites (1–vue labiale, 2–vue linguale). **I.** NMA 2012-96/2058 : mandibule droite avec m3 (vue linguale). **J.** NMA 2012-98/2058 : condyle gauche (vue postérieure).

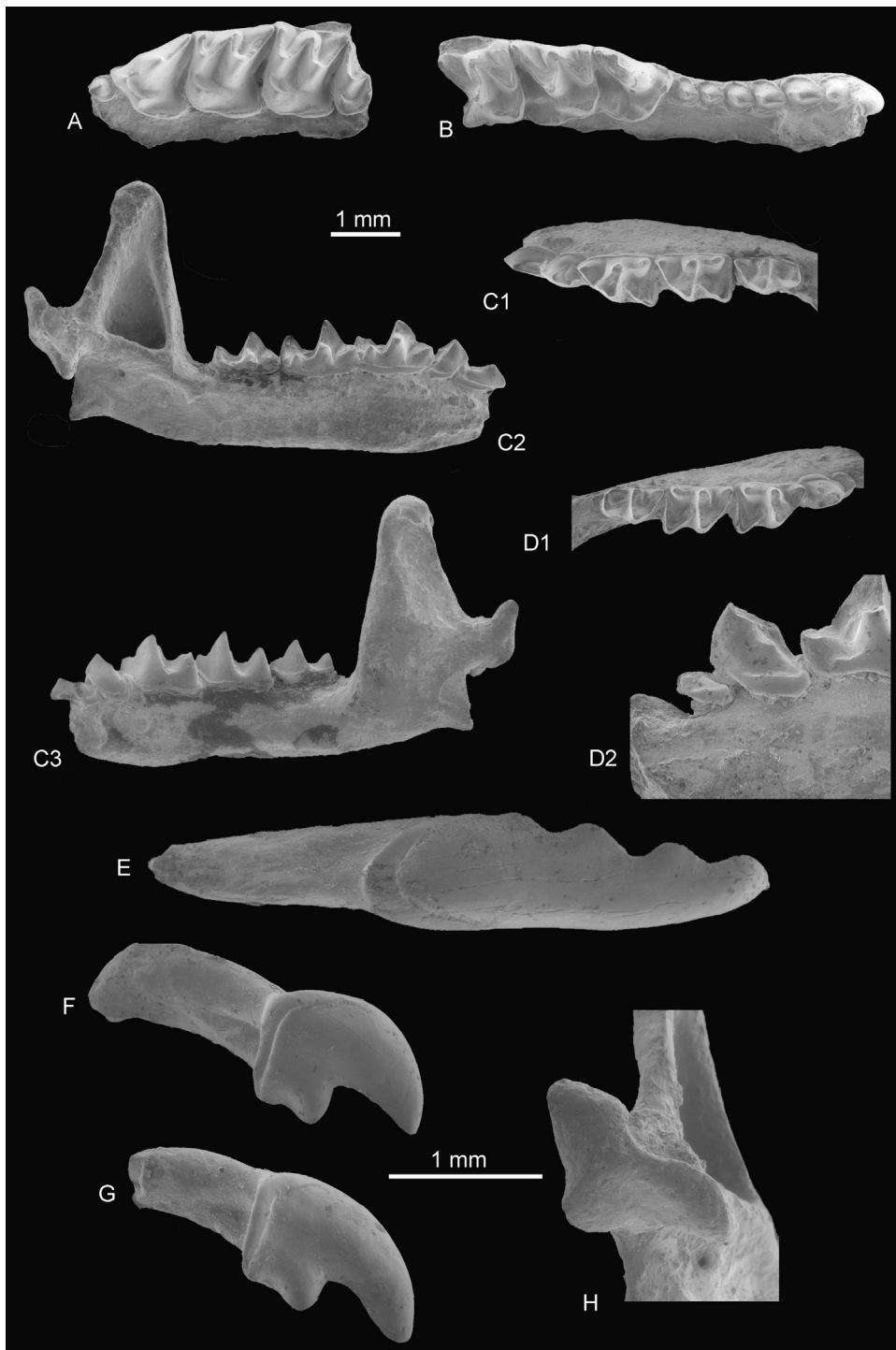


Fig. 5. *Miosorex desnoyersianus* (Lartet, 1851) from Petersbuch 28 (Germany, Lower Miocene, MN 3/4). **A.** NMA 2012-106/2058: left A5–M5 (occlusal view). **B.** NMA 2012-105/2058: right I–M2 (occlusal view). **C.** NMA 2012-110/2058: right mandible with a1–m3 (1–occlusal view, 2–lingual view, 3–buccal view). *Lartetium cf. prevostianum* (Lartet, 1851). **D.** NMA 2012-99/2058: right mandible with a2–m3 (1–occlusal view, 2–Detail of a2–p4, lingual view). *Miosorex desnoyersianus*. **E.** NMA 2012-109/2058: right i (buccal view). **F.** NMA 2012-107/2058: right I sup., type I (buccal view). **G.** NMA 2012-108/2058: right I sup., type II (buccal view). **H.** NMA 2012-110/2058: left condyle (posterior view).

Fig. 5. *Miosorex desnoyersianus* (Lartet, 1851) de Petersbuch 28 (Allemagne, Miocène inférieur, MN 3/4). **A.** NMA 2012-106/2058 : A5–M3 gauches (vue occlusale). **B.** NMA 2012-105/2058 : I–M2 droites (vue occlusale). **C.** NMA 2012-110/2058 : mandibule droite avec a1–m3 (1–vue occlusale, 2–vue linguale, 3–vue labiale). *Lartetium cf. prevostianum* (Lartet, 1851). **D.** NMA 2012-99/2058 : mandibule droite avec a2–m3 (1–vue occlusale, 2–a2–p4 en détail, vue linguale). *Miosorex desnoyersianus*. **E.** NMA 2012-109/2058 : i droite (vue labiale). **F.** NMA 2012-107/2058 : I droite, type I (vue labiale). **G.** NMA 2012-108/2058 : I droite, type II (vue labiale). **H.** NMA 2012-110/2058 : condyle gauche (vue postérieure).

Table 3

Measurements of the teeth and mandibles of *Lartetium petersbuchense* Ziegler, 1989 from Petersbuch 28 (Germany, Lower Miocene, MN 3/4). * = in two damaged specimens, W inf was measureable.

Tableau 3

Mesures des dents et mandibules de *Lartetium petersbuchense* Ziegler, 1989 de Petersbuch 28 (Allemagne, Miocène inférieur, MN 3/4). * = dans deux spécimens endommagés, on a pu mesurer W inf.

	n (ex.)	Parameter	Mean	Min	Max
I sup	5 (1)	L	1.57	1.52	1.62
		L Ta	0.73	0.64	0.83
		H	1.09	0.94	1.18
		L new	1.52	1.40	1.61
		L Ta new	0.71	0.65	0.76
		H new	1.33	1.04	1.51
		HTa new	1.11	1.01	1.19
A1	2	L	0.93	1.09	
A2	3 (1)	W	0.67	0.66	
		L	0.66	0.82	
A3	3 (1)	W	0.56	0.57	
		L	0.89	0.92	
A4	2	W	0.62	0.60	
		L	0.56	0.63	
P4	15 (2)	W	0.48	0.56	
		L bucc	1.73	1.63	1.82
		L ling	1.00	0.92	1.17
		W	1.33	1.28	1.39
		L dj	1.42	1.36	1.50
M1	22 (8)	W dj	1.70	1.55	1.86
		L bucc	1.45	1.34	1.52
		L ling	1.34	1.20	1.43
		L max	1.46	1.34	1.52
		W ant	1.44	1.34	1.51
M2	15 (5)	W post	1.82	1.76	1.93
		W max	1.67	1.61	1.76
		L bucc	1.25	1.14	1.35
		L ling	1.14	1.01	1.19
		L max	1.21	1.10	1.37
i inf	7 (3)	W ant	1.65	1.58	1.77
		W post	1.56	1.44	1.62
		W max	1.65	1.58	1.76
		L	2.94	2.71	3.05
		H	0.80	0.76	0.82
a1	5	L	1.17	1.15	1.18
		W	0.69	0.66	0.72
a2	4	L	0.73	0.70	0.76
		W	0.62	0.59	0.64
a3	5 (4)	L	0.21		
		W	0.35		
a4 (p4)	18	L	0.94	0.87	1.05
		W	0.67	0.57	0.73
m1	76 (19)	L	1.58	1.39	1.73
		W Tr	0.86	0.75	0.94
		W Ta	0.92	0.82	0.99
m2	84 (23)	HoM	1.49	1.18	1.74
		L	1.51	1.33	1.62
		W Tr	0.85	0.77	0.91
m3	106 (9)	W Ta	0.85	0.77	0.91
		HoM	1.48	1.08	1.71
		L	1.17	1.01	1.31
Mand	38 (4)	W Tr	0.64	0.57	0.83
		W Ta	0.50	0.39	0.80
		HoM	1.46	1.04	1.75
PCond	24 (3)*	m1-m3	3.91	3.55	4.11
		LForM	5.56	4.59	6.03
PCond	1 (3)*	CorH	5.94		
		W inf	1.31	1.33	1.42
		W sup	0.86		
		H	1.54		
		HR	1.83		

3003, 3005, 3006, 3011–3013, 3016, 3020, 3021, 3033, 3039, 3040, 3042, 3046, 3049, 3052, 3059, 3069, 3072, 3076, 3158.

Original diagnosis of *Lartetium prevostianum*: [Lartet, 1851](#)

Emended diagnosis of *L. prevostianum*: [Engesser, 2009 Description](#)

As the last good description was given by [Engesser \(2009\)](#), only the most important features are described here. No upper dentition or lower incisors were found.

The **a1** has a regular anterior curve.

The small **a2** resembles a semicircle. The small cusp is three-sided. It has a small posterobuccal ridge; a posterolingual ridge may have been present, but is worn in all specimens.

The extremely tiny **a3** is covered by the p4. It has a large root and is wider than it is long.

The **p4** has two roots. The posterior ridges are pronounced and end in either tiny cuspules or enlarged ridges. A tiny accessory ridge may be present on the posterior cingulid, connected to the flank of the cusp or buccal ridge.

The **m1** has a very narrow postentoconid valley. Its cingulids are well developed.

The **m2** has a relatively shorter and wider trigonid than the m1.

The **m3** has a small talonid with only the hypoconid as discernible cusp; both hypolophid and entocristid are present.

The **mandible** has a foramen mentale below the middle or the posterior half of the p4.

The **processus condylaris** has a small upper facet and a large buccal interarticular area.

The measurements are given in [Table 4](#).

Comparison: In the Miocene fossil record, there are some species of similar size to the one discussed here. The genus *Clapasorex* [Crochet, 1975](#) is characterised by confluent antemolar alveoli of similar size, except for the p4 posterior alveolus ([Van den Hoek Ostende, 2003](#)). In the Petersbuch 28 specimens, the alveoli are neither confluent nor of similar size, so *Clapasorex sigei* [Crochet, 1975](#), *C. bonisi* [Crochet, 1975](#) and *C. alvarezae* [Van den Hoek Ostende, 2003](#) can be excluded ([Van den Hoek Ostende, 2003](#); [Ziegler, 1989](#)).

Crocidosorex [Lavocat, 1951](#) is restricted to *C. piveteaui* [Lavocat, 1951](#), since the genus *Oligosorex* [Kretzoi, 1959](#) has been resurrected by [Van den Hoek Ostende \(2001a\)](#). *Crocidosorex* differs considerably in the p4 and might even belong to the Soricinae ([Ziegler, 1989](#)). Most “*Crocidosorex* sp.” found in older literature should therefore probably be referred to *Oligosorex*, which for a long time was considered a junior synonym of *Crocidosorex*.

Carposorex sylviae [Crochet, 1975](#) and *C. burkarti* [Hugueney, Mein and Maridet, 2012](#) are characterised by wrinkled enamel and the connection of a posterobuccal protoconid crest to the cingulid ([Hugueney et al., 2012](#)); none of these characters were found in the Petersbuch 28 species.

The genera *Viretia* [Hugueney et al., 2012](#), *Suevosorex* [Ziegler, 2009](#), and *Turiasorex* [Van Dam, Van den Hoek Ostende and Reumer, 2011](#) differ greatly in size and/or

Table 4

Measurements of the teeth and mandibles of *Lartetium cf. prevostianum* (Lartet, 1851) from Petersbuch 28 (Germany, Lower Miocene, MN 3/4).

Tableau 4

Mesures des dents et mandibules de *Lartetium cf. prevostianum* (Lartet, 1851) de Petersbuch 28 (Allemagne, Miocène inférieur, MN 3/4).

	n (ex.)	Parameter	Mean	Min	Max
i inf	1 (1)				
a1	1 (1)				
a2	2	L	0.40	0.37	
		W	0.45	0.41	
a4 (p4)	10	L	0.74	0.69	0.81
	(4)	W	0.54	0.51	0.57
m1	45	L	1.20	1.11	1.31
	(14)	W Tr	0.68	0.61	0.73
		W Ta	0.76	0.67	0.81
	45	HoM	1.09	0.87	1.25
m2	46	L	1.19	1.14	1.25
	(4)	W Tr	0.70	0.64	0.74
		W Ta	0.72	0.65	0.77
	49	HoM	1.06	0.90	1.18
m3	35	L	0.98	0.93	1.01
	(8)	W Tr	0.55	0.50	0.61
		W Ta	0.42	0.37	0.49
	48	HoM	1.05	0.87	1.18
Mand	20	m1–m3	3.11	2.97	3.23
	3	LForM	4.75	4.59	4.92
	3	CorH	3.17	2.97	3.32
PCond	5	W inf	1.03	0.88	1.11
	4	W sup	0.58	0.53	0.62
	4	H	0.95	0.92	0.97
	4	H R	1.27	1.20	1.36

premolar and molar morphology from the Petersbuch 28 sample.

A much more similar species is *Oligosorex thauensis* (Crochet, 1975). It differs from *Clapasorex alvarezae* in having a wider postentoconid valley. Given the small postentoconid valley in the Petersbuch 28 species, it cannot be determined as *O. thauensis*. The difference is also confirmed by the pictures given by Van den Hoek Ostende (2003, figures 5–7 on Plate 3 and figures 1 and 2 on Plate 4).

Oligosorex reumeri Van den Hoek Ostende, 2001 differs in having an interrupted buccal cingulid and a further anterior m1 paraconid (Van den Hoek Ostende, 2001a). *Oligosorex aff. reumeri* is nearly indistinguishable, but it has a weaker buccal cingulid and seems to have a wider postentoconid valley (Van den Hoek Ostende, 2003). *Oligosorex antiquus* (Pomel, 1853) differs in size (Huguéney et al., 2012; Van den Hoek Ostende, 2003; Ziegler, 1989).

The course of the hypolophid directly behind the entoconid is found in the genus *Lartetium* Ziegler, 1989. *L. petersbuchense* Ziegler, 1989 is larger and has an interrupted buccal cingulid (Ziegler, 1989), *L. dehmi* (Viret and Zapfe, 1951) is larger and has a wider talonid of the m1 (Viret and Zapfe, 1951), *L. zieglerei* Mein and Ginsburg, 2002 is larger (Huguéney et al., 2012; Mein and Ginsburg, 2002).

Therefore, the best candidate is *L. prevostianum* (Lartet, 1851). This shrew can only be distinguished from *Miosorex desnoyersianus* (Lartet, 1851) by its four antemolars and the narrower postentoconid valley (Baudelot, 1972; Engesser,

2009). In *M. desnoyersianus*, the hypolophid bends posteriorly before reaching the entoconid, whereas it is straight in *L. prevostianum* (Engesser, 2009). These differences are most pronounced on the m1, weak on m2 and absent on the m3 in the Petersbuch 28 material. The lower molars have, on average, stronger buccal and weaker lingual cingulids than *M. desnoyersianus*. Also, the foramen mentale is, in general, positioned more anteriorly.

The Petersbuch 28 sample differs from the measurements given by Engesser (2009), mostly in the width. These differences are also found in *M. desnoyersianus*, so a difference in the measuring technique might be responsible. Without certain identification of lower incisors or upper molars, the species discussed here can only be determined as *L. cf. prevostianum*. A remarkable difference between *L. prevostianum* from Sansan and *L. cf. prevostianum* from Petersbuch 28 is the size of the m3. In the Sansan material, the m3 is 1.03 to 1.07 mm long (Baudelot, 1972), whereas it is only 0.93 to 1.01 mm long in Petersbuch 28. A slight size increase in the m3 is unexpected, because the reduction of the m3 is a common trend within soricids (Huguéney and Maridet, 2011; Van Dam, 2004). The enlarged m3 probably provided a larger chewing surface.

The species in Petersbuch 28 is not identical to *L. cf. prevostianum* of the Austrian MN 4 site Oberdorf (Ziegler, 1998a), because of the wide postentoconid valley of the Austrian specimen.

An ancestor-descendant relationship between *L. petersbuchense* and *L. prevostianum*, as proposed by Ziegler (1999), can be excluded, because *L. petersbuchense* and *L. cf. prevostianum* were found together in Petersbuch 28. Furthermore, the processus condylaris of *L. cf. prevostianum* is more similar to *M. desnoyersianus* than to *L. petersbuchense*.

3.2.3. Genus: *Miosorex Kretzoi*, 1959

Miosorex desnoyersianus (Lartet, 1851)

Fig. 5 A–C, E–H

Material: 23 maxillary fragments with teeth (including one nearly complete skull), twelve isolated maxillary teeth, seven isolated upper incisors, 145 mandibular fragments with teeth (including a few nearly intact mandibles), four isolated lower molars, four isolated lower incisors. Collection numbers: NMA 2012–105/2058–110/2058, CMR-P/28–1781, 1796, 1822, 1824, 1825, 1828, 1829, 1831, 1834, 1837, 1838, 1892, 1905, 1917, 1919, 1924, 1935, 1950, 1972, 1976, 1988, 2114, 2166, 2649, 2668, 2676, 2684, 2703, 2734, 2757, 2800, 2809, 2858, 2870, 2877, 2878, 2880, 2881, 2883–2887, 2889–2894, 2896–2901, 2903–2906, 2908, 2909, 2911, 2912, 2914–2918, 2920, 2921, 2923, 2924, 2926, 2929, 2932, 2933, 2936–2939, 2941, 2946–2948, 2950–2953, 2955, 2957, 2958, 2960–2962, 2964–2971, 2973, 2979–2987, 2990, 2991, 2994–2998, 3001, 3002, 3004, 3007–3010, 3014, 3015, 3017–3019, 3022–3024, 3026–3030, 3032, 3034–3038, 3041, 3043–3045, 3047, 3050, 3051, 3053–3058, 3060–3065, 3067, 3068, 3070, 3071, 3074, 3077, 3078, 3081, 3082, 3085–3087, 3089–3091, 3094, 3096, 3099, 3110, 3119, 3144, 3145, 3159.

Original diagnosis: Lartet, 1851

Emended diagnosis: Klietmann et al. (2013)

Description

As the most recent description was given by Engesser (2009), only the most important features and new findings will be described here.

Two types of **I** were found associated with the dentitions of this species. The dorsal margin of **Type I** has a long, straightened part. The talon tips are small. The cingulum ends slightly anterior to the most dorsal point. **Type II** differs by the round dorsal outline.

The size sequence of the **antemolars** is $A1 > A2 > A3 > A4 > A5$. The outline is usually smooth and they are better aligned than in the larger soricids.

The **P4** is long, but narrow. It has a pronounced parastyle and protocone. The weak hypocone forms a straight ridge parallel to the hypocone of the M1.

The **M1** is almost square-shaped. Its hypoconal flange and lingual cingulum are large. The low hypocone is elongated into a straight ridge. The hypoconal flange is round.

The **M2** has a shorter hypoconal flange than the M1.

The triangular **M3** is rather short and has a small metacone connected to the protocone.

The crown of the **i** is tricuspidate; the third cuspule is faint. In one specimen, the tip and the two anterior cuspules are brownish orange.

The **a1** has a regular anterior curve.

The tiny **a2** is elliptical or semicircular, has a rather large root and is wider than long.

The **a3 (p4)** has two roots. The posterior ridges are pronounced. A tiny accessory ridge is sometimes present on the posterior flank.

The **m1** has a moderately narrow postentoconid valley.

The **m2** has a relatively shorter and wider trigonid.

The **m3** has a small talonid with only the hypoconid present. Both hypolophid and entocristid are taking their normal courses.

The foramen mentale of the **mandible** is located either below the p4 or, rarely, below the m1 paraconid.

The wide **processus condylaris** is of crocidurine shape. The buccal interarticular area is wide. The lower margin has a rather acute angle.

The measurements of *M. desnoyersianus* are given in Table 5.

Comparison: *M. desnoyersianus* (Lartet, 1851) was determined because of the three antemolars, the middle of which is tiny, and the m3 talonid with a single cusp (Baudelot, 1972; Engesser, 2009). The other genera from the Lower Miocene either have four antemolars or are larger or at least differ in molar morphology (Ziegler, 1989, 2006b). The upper molars were identified by their size, outline, the long, straight anterior part of the hypoloph, the clear cingulum and the shape of the protocone (Engesser, 2009). The number and relative size of the upper antemolars and the size and morphology of the upper and lower incisors are also consistent with *Miosorex* “pusilliformis” (Doben-Florin, 1964; Ziegler, 1989), which was shown to be a junior synonym of *M. desnoyersianus* (Klietmann et al., 2013). The second species of the genus, *Miosorex grivensis* (Depéret, 1892), is larger.

Table 5

Measurements of teeth and mandibles of *Miosorex desnoyersianus* (Lartet, 1851) from Petersbuch 28 (Germany, Lower Miocene, MN 3/4).

Tableau 5

Mesures des dents et mandibules de *Miosorex desnoyersianus* (Lartet, 1851) de Petersbuch 28 (Allemagne, Miocène inférieur, MN 3/4).

	n (ex.)	Parameter	Mean	Min	Max	
I sup	5	L	1.24	1.10	1.38	
Type I	(2)	L Ta	0.61	0.53	0.70	
		H	0.79	0.72	0.84	
		L new	1.12	1.03	1.18	
		L Ta new	0.54	0.47	0.58	
		H new	1.05	0.81	1.26	
		HTa new	0.86	0.71	0.96	
I sup	7	L	1.13	1.06	1.18	
Type II	(1)	L Ta	0.53	0.48	0.59	
		H	0.85	0.79	0.89	
		L new	1.09	1.01	1.13	
		L Ta new	0.51	0.41	0.57	
		H new	1.00	0.93	1.08	
		HTa new	0.84	0.77	0.90	
A1	7	L	0.75	0.67	0.83	
		(2)	W	0.56	0.49	0.65
A2	6	L	0.61	0.54	0.64	
		(1)	W	0.47	0.43	0.51
A3	4	L	0.51	0.47	0.53	
		(1)	W	0.44	0.42	0.46
A4	7	L	0.46	0.40	0.50	
		(1)	W	0.44	0.39	0.51
A5	11	L	0.41	0.31	0.52	
		(2)	W	0.41	0.37	0.45
P4	25	L bucc	1.28	1.21	1.37	
		(5)	L ling	0.90	0.81	0.96
		W	1.11	1.05	1.22	
		L dj	1.16	1.09	1.24	
		W dj	1.23	1.15	1.35	
		W max	1.33	1.26	1.40	
M1	23	L bucc	1.22	1.15	1.30	
		(5)	L ling	1.19	1.11	1.25
		L max	1.21	1.13	1.28	
		W ant	1.19	1.11	1.31	
		W post	1.37	1.25	1.48	
		W max	1.33	1.26	1.40	
M2	15	L bucc	1.13	1.04	1.19	
		(6)	L ling	1.10	1.00	1.18
		L max	1.14	1.04	1.18	
		W ant	1.32	1.28	1.35	
		W post	1.27	1.21	1.32	
		W max	1.33	1.28	1.37	
M3	6	L	0.56	0.55	0.57	
		(3)	W	1.07	1.04	1.09
i inf	8	L	2.57	2.42	2.73	
		(4)	H	0.68	0.66	0.69
a1	8	L	0.80	0.72	0.87	
		(2)	W	0.54	0.50	0.61
a3 (p4)	26	L	0.76	0.65	0.85	
		(4)	W	0.56	0.52	0.63
m1	99	L	1.24	1.15	1.35	
		(30)	W Tr	0.69	0.63	0.77
		W Ta	0.76	0.67	0.84	
		HoM	1.08	0.89	1.22	
m2	116	L	1.21	1.10	1.32	
		(18)	W Tr	0.70	0.63	0.80
		W Ta	0.72	0.60	0.82	
m3	124	HoM	1.03	0.82	1.22	
		90	L	0.99	0.90	1.08
		(12)	W Tr	0.56	0.49	0.62
		W Ta	0.42	0.34	0.52	
Mand	121	HoM	1.03	0.72	1.21	
		42	m1-m3	3.20	3.04	3.45
		8	LForM	4.52	4.38	4.76
12	CorH	3.35	3.25	3.54		

Table 5 (Continued)

	n (ex.)	Parameter	Mean	Min	Max
PCond	13	W inf	1.02	0.90	1.15
	8	W sup	0.56	0.40	0.67
	8	H	0.96	0.86	1.06
	8	H R	1.25	1.06	1.37

The m2 is on average slightly smaller than the m1, whereas it is larger in the samples from Sansan (France, Middle Miocene, MN 6) and southern Germany (Engesser, 2009; Ziegler, 1989). In *S. discrepans* Doben-Florin, 1964, the m1 proved to be more variable than the m2, so a shift in the relative size might be a local variation and not indicative of a general change in the whole species.

The upper incisors show two morphological types, both found in situ together with antemolars and molars. The development of two types is interpreted as a micro-evolutionary event. The elongated Type I is understood as the younger type, because Type II is morphologically similar to the specimens found in the MN 3 locality Wintershof-West (Doben-Florin, 1964). There is no correlation of the incisor types with size classes or further morphological changes in the upper dentition. The only difference is the flattened dorsal margin, so type II is interpreted as having evolved into type I in the environment of Petersbuch 28. A comparison of *M. desnoyersianus* from the Miocene localities Wintershof-West (MN 3), Stubersheim 3 (MN 3) (Ziegler, 1989), Petersbuch 28 (MN 3/4) and the type locality Sansan (MN 6) (Engesser, 2009) reveals the evolutionary trend of reducing the lower molar length. The molar widths given by Engesser (2009) differ from the widths given here or by Ziegler (1989), most probably due to the different positioning.

3.2.4. Genus: *Florinia* Ziegler, 1989

Florinia stehlini (Doben-Florin, 1964)

Fig. 6 A, B, E–H

Material: two isolated maxillary teeth, 52 mandibular fragments (including a few nearly complete mandibles), four isolated lower incisors. Collection numbers: NMA 2012-100/2058-104/2058, CMR-P/28- 2185, 2799, 2805-2808, 2810-2819, 2822, 2823, 2825, 2826, 2828-2830, 2832-2836, 2839-2848, 2851-2856, 2860, 2931, 2943, 2989, 2999, 3025, 3066, 3079.

Diagnosis: Doben-Florin, 1964

Emended diagnosis

This is a small shrew with two one-rooted antemolars situated between the incisor and the one-rooted p4. The entoconid on the m1 and m2 is small and positioned near the metaconid. The buccal and lingual cingulids are wide, the cusps massive. The metaconid of the m1 and m2 are posterolingual of the protoconid. The m3 has only one talonid cusp, the hypoconid, with only one ridge, the oblique cristid, in anterior direction. The lower incisor is tricuspidate with an extremely faint third cuspid. The tip is clearly higher than the cuspid. The foramen mentale is found below the protoconid of m1. The foramen mandibulae is located below the posterior corner of the internal temporal fossa. The condyle is low, the upper and lower

facets are not fully divided, and the buccal margin of the processus condylaris is concave.

Description

Doben-Florin (1964) gave a good description, so only the most important features and new insights are presented here.

Of the upper dentition, only the P4 and the M2 were assigned to *F. stehlini*.

The only P4 has a very weak protocone and no hypocone.

The M2 is relatively short and wide. The protocone is narrow; there is no visible metaconulus. The hypocone is rather weak; the hypoloph is short and weak.

The i is bicuspidate, but a faint third elevation is sometimes present.

The rather massive a1 has a clear cingulid.

The a2 is tear-shaped and small.

The a3 (p4) has one large root only. The shape resembles a hexagon. The posterior ridges are short; all specimens are worn.

The m1 has a large paraconid; the small metaconid is further posterior than in the other species. The entoconid is next to the metaconid, so the postentoconid valley is wide. The buccal and lingual cingulids are large.

The m2 has a less protruding paraconid and a larger metaconid.

The talonid of the m3 has just one cusp, the hypoconid. It wears only the oblique cristid, which is directed forward. In worn state, it appears to consist of two enamel ridges starting at the hypoconid and ending at the same point at the trigonid wall.

The ramus horizontalis of the mandible is thick. The symphysis reaches to below the m1 paraconid. The foramen mentale lies below the protoconid of the m1.

The processus condylaris is high and of crocidurine shape. There is a small buccal interarticular area.

The measurements of *F. stehlini* are given in Table 6.

Comparison: *F. stehlini* (Doben-Florin, 1964) is the only crocidosoricine shrew with three large single-rooted antemolars and the foramen mentale below the m1. The strong lingual cingulid, the large and rather sharp paraconid, the anterior position of the entoconid and the strong, but short entocristid are distinctive features of the m1 and m2. The single cusp of the m3 talonid is unique in having only one very wide anterior ridge.

The lower incisor does not reach the height of the incisors belonging to *M. desnoyersianus* (Lartet, 1851). The upper molars are more problematic because they differ from *L. petersbuchense* Ziegler, 1989 only by having a weaker hypocone. Based on the well-preserved material, the diagnosis for the species was emended and the morphology of the m3 talonid had to be reinterpreted. On worn teeth, the enamel cover of the flanks appears as two separated ridges ending at the same point. In samples lacking unworn teeth, the oblique cristid was therefore interpreted as two individual ridges (Doben-Florin, 1964; Ziegler, 1989). It is noteworthy that the molars of *F. stehlini* appear to be more heavily worn than the teeth of the other shrew species from Petersbuch 28.

The lower molars of *F. stehlini* from Petersbuch 28 (Germany, Middle Miocene, MN 3/4) are, on average, larger than

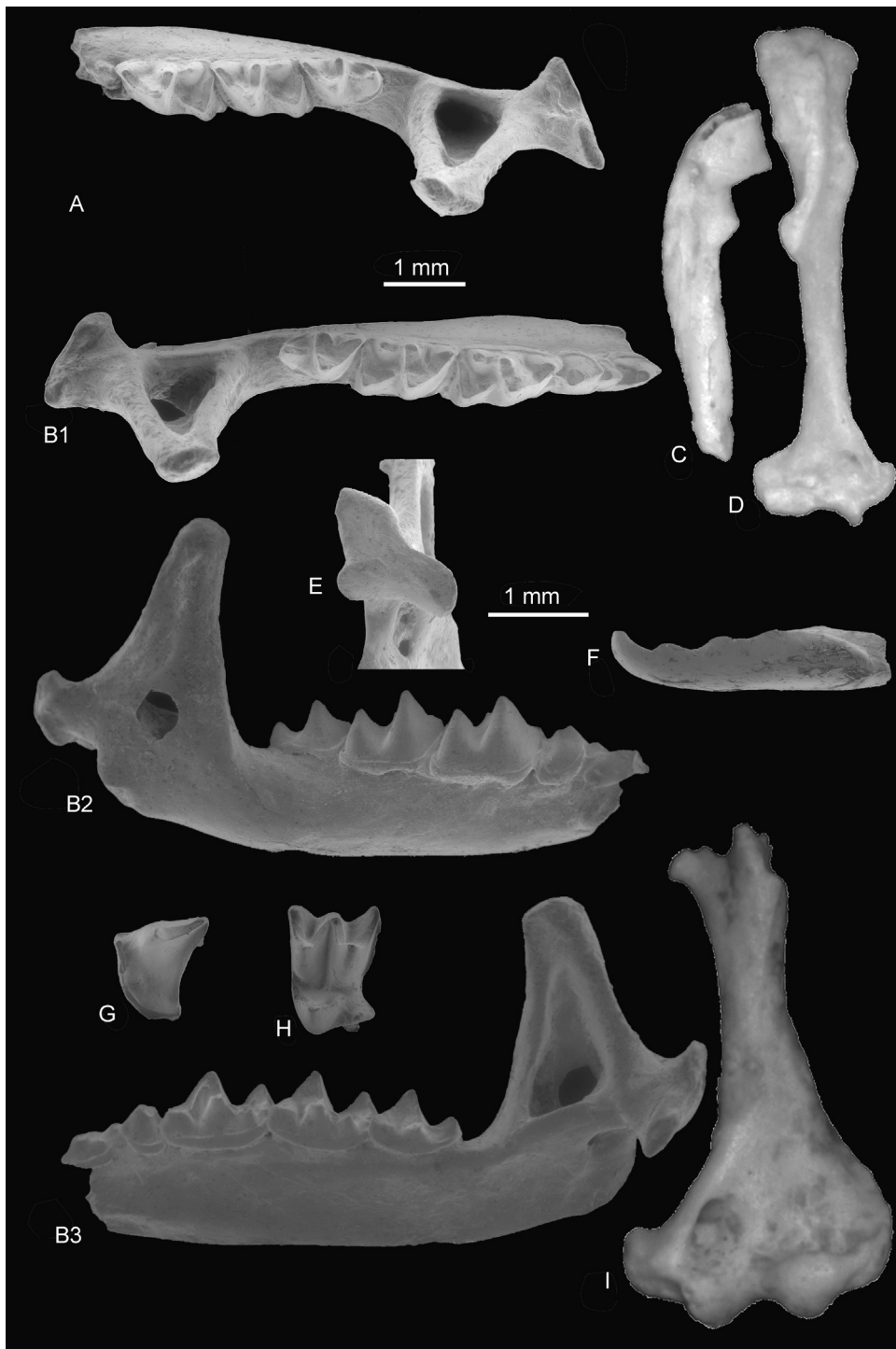


Fig. 6. *Florinia stehlini* (Doben-Florin, 1964) from Petersbuch 28 (Germany, Lower Miocene, MN 3/4). **A.** NMA 2012-102/2058: left mandible with m1–m3 (occlusal view). **B.** NMA 2012-103/2058: right mandible with a1–m3 (1–occlusal view, 2–buccal view, 3–lingual view). Soricid postcrania: **C.** NMA 2012-134/2058: right ulna (anterolateral view). **D.** NMA 2012-127/2058: right humerus, small type (anterior view). *Florinia stehlini*. **E.** NMA 2012-102/2058: left condyle (posterior view). **F.** NMA 2012-102/2058: left i (buccal view). **G.** NMA 2012-101/2058: left P4 (occlusal view). **H.** NMA 2012-100/2058: left M2 (occlusal view). Postcrania: **I.** NMA 2012-126/2058: right distal humerus, largest type (anterior view).

Fig. 6. *Florinia stehlini* (Doben-Florin, 1964) de Petersbuch 28 (Allemagne, Miocène inférieur, MN 3/4). **A.** NMA 2012-102/2058 : mandibule gauche avec m1–m3 (vue occlusale). **B.** NMA 2012-103/2058 : mandibule droite avec a1–m3 (1–vue occlusale, 2–vue labiale, 3–vue linguale). Postcrania des Soricidae : **C.** NMA 2012-134/2058 : ulna droite (vue antérolatérale). **D.** NMA 2012-127/2058 : humérus droit, petit type (vue antérieure). *Florinia stehlini*. **E.** NMA 2012-102/2058 : condyle gauche (vue postérieure). **F.** NMA 2012-102/2058 : i gauche (vue labiale). **G.** NMA 2012-101/2058 : P4 gauche (vue occlusale). **H.** NMA 2012-100/2058 : M2 gauche (vue occlusale). Postcrania : **I.** NMA 2012-126/2058 : humérus distal droit, grand type (vue antérieure).

Table 6

Measurements of teeth and mandibles of *Florinia stehlini* (Doben-Florin, 1964) from Petersbuch 28 (Germany, Lower Miocene, MN 3/4).

Tableau 6

Mesures des dents et mandibules de *Florinia stehlini* (Doben-Florin, 1964) de Petersbuch 28 (Allemagne, Miocène inférieur, MN 3/4).

	n (ex.)	Parameter	Mean	Min	Max
P4	1	L bucc	1.20		
		L ling	0.74		
		W	1.21		
		L dj	1.09		
		W dj	1.35		
M2	1	L bucc	1.16		
		L ling	1.04		
		L max	1.15		
		W ant	1.50		
		W post	1.43		
		W max	1.54		
i inf	4 (1)	L	2.60	2.53	2.41
		H	0.59	0.60	0.60
a1	2	L	0.84	0.85	
		W	0.53	0.53	
a2	2	L	0.34	0.36	
		W	0.44	0.41	
a3 (p4)	7 (1)	L	0.67	0.60	0.73
		W	0.58	0.54	0.59
m1	41 (8)	L	1.41	1.31	1.51
		W Tr	0.75	0.70	0.80
		W Ta	0.80	0.74	0.84
		HoM	1.19	1.06	1.35
m2	49 (5)	L	1.31	1.27	1.40
		W Tr	0.75	0.71	0.81
		W Ta	0.76	0.72	0.81
m3	49 (7)	HoM	1.19	1.02	1.36
		L	1.04	0.98	1.10
		W Tr	0.61	0.56	0.66
Mand	38 (7)	W Ta	0.45	0.40	0.49
		HoM	1.22	1.10	1.37
		m1-m3	3.38	3.13	3.68
		LForM	3.60	2.96	3.89
PCond	6 (4)	CorH	3.89	3.49	4.27
		W inf	1.17	1.06	1.23
		W sup	0.64	0.61	0.66
		H	1.17	1.13	1.20
		HR	1.36	1.31	1.43

the specimens from Wintershof-West (Germany, Lower Miocene, MN 3) (Ziegler, 1989) and from Sandelzhausen (Germany, Middle Miocene, MN 5) (Ziegler, 2000). The species of Sandelzhausen was determined as *F. aff. stehlini* by Ziegler (2000), but given the small size differences between Sandelzhausen and Wintershof-West, it can be comfortably included in *F. stehlini*. There is no general evolutionary trend in the size of *F. stehlini*, so its size is assumed to be a reflection of environmental differences between the habitats.

3.3. Subfamily: ALLOSORICINAE Fejfar, 1966

Genus: *Paenelimnoecus* Baudelot, 1972

Paenelimnoecus micromorphus (Doben-Florin, 1964)

Fig. 7 A–I

Material: one maxillary fragment with teeth, ten isolated upper antemolars and molars, 48 mandibular fragments with teeth (including a few nearly intact mandibles), one isolated lower incisor. Collection numbers: NMA 2012-111/2058–118/2058, CMR-P/28-1840, 2869, 3084, 3098,

3100, 3102, 3103, 3111, 2859, 3107, 3109, 3112–3118, 3120–3124, 3126–3135, 3137–3143, 3146–3157.

Original Diagnosis: Doben-Florin, 1964

Emended diagnosis: Klietmann et al. (2013)

Description

Good descriptions were given by Doben-Florin (1964) and Ziegler (1989) so only the most important or newly found features are described here.

No **upper incisors** or **antemolars** were assigned to *P. micromorphus*.

The narrow **P4** has no discernible hypocone.

The **M1** is short. The protocone is pronounced, the hypocone large. The hypoconal flange is long, but narrow.

The **M2** has weakly protruding buccal styles. The hypocone is weak, the hypoconal flange short.

No **M3** was assigned to *P. micromorphus*.

The **i** is extremely elongated and thin. It is bicuspluate or tricuspluate, depending on the interpretation of the third structure.

The **a1** is relatively short. Both posterior ridges end at about half the length.

In only one mandible the **a2** is large enough to be visible in occlusal view. In the other specimens, it is reduced to a chip between the other antemolars.

The **a3 (p4)** has one root. It is Y-shaped with a very short posterolingual ridge.

The **m1** has a very short talonid with only a faint remnant of the entoconid and entocristid. The postentoconid valley is very wide. The mesoconid is clearly visible, the metaconid posterolingual next to the protoconid. The cingulids are strong.

The **m2** is longer than the m1 on many mandibles. The paraconid is less protruding; the protoconid is a bit larger and the metaconid further anterior.

The **m3** has a very short talonid wearing only the hypoconid with oblique cristid and entocristid.

The **mandible** has a symphysis reaching below the p4. The foramen mentale is below the m1 trigonid.

The low and wide **processus condylaris** has concave curves at the lower, buccal and lingual margins. There is a large buccal interarticular area.

The measurements of *P. micromorphus* are given in Table 7.

Comparison: The small size, the two large antemolars and the extreme reduction of the entoconid suggest *Paenelimnoecus* Baudelot, 1972. Within this genus, only *P. micromorphus* (Doben-Florin, 1964) retains a weak posterolingual ridge on the p4 and a minute second antemolar. The sample from Petersbuch 28 is also similar to the descriptions and figures given by Ziegler (1989). The additional antemolar was overlooked till now and its importance is discussed elsewhere (Klietmann et al., 2013). The upper molars are longer than the single M1 from Petersbuch 2 presented by Ziegler (1989). The m1 has a bimodal width distribution, the m2 has more intermediate forms and the m3 shows no differentiation. Most specimens are similar in size to the material of Petersbuch 2 (Germany, Lower Miocene, MN 4) and narrower than the specimens from Wintershof-West (Germany, Lower Miocene, MN 3); some are similar to the specimens of Wintershof-West (Fig. 8). The large sample of Petersbuch

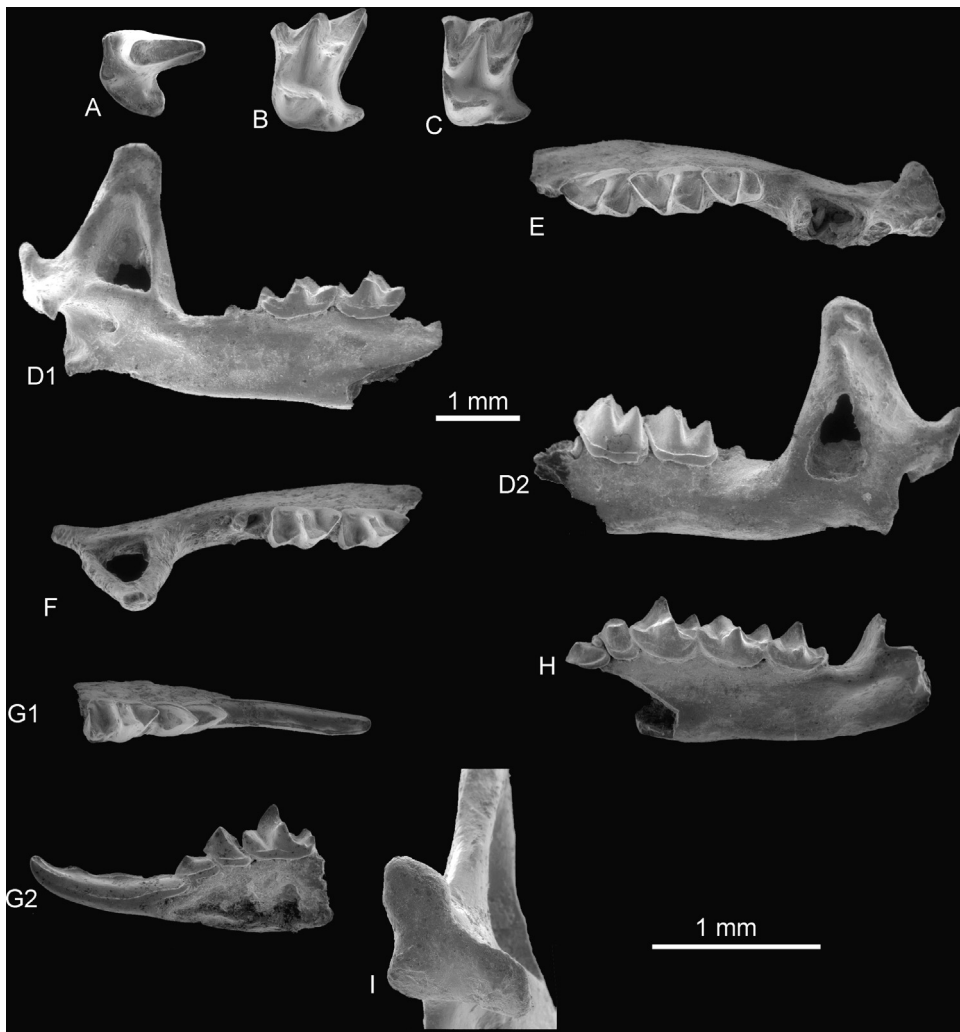


Fig. 7. *Paenelimnoecus micromorphus* (Dobson-Florin, 1964) from Petersbuch 28 (Germany, Lower Miocene, MN 3/4). **A.** NMA 2012-111/2058: left P4 (occlusal view). **B.** NMA 2012-113/2058: left M1 (occlusal view). **C.** NMA 2012-112/2058: right M2, displayed as left (occlusal view). **D.** NMA 2012-115/2058: left mandible with m1, m2 (1–lingual view, 2–buccal view). **E.** NMA 2012-116/2058: left mandible with m1–m3 (occlusal view). **F.** NMA 2012-117/2058: right mandible with m1, m2 (occlusal view). **G.** NMA 2012-118/2058: right mandible with i–m1 (1–occlusal view, 2–lingual view). **H.** NMA 2012-114/2058: right mandible with a1–m3 (lingual view). **I.** NMA 2012-115/2058: left condyle (posterior view).

Fig. 7. *Paenelimnoecus micromorphus* (Dobson-Florin, 1964) de Petersbuch 28 (Allemagne, Miocène inférieur, MN 3/4). **A.** NMA 2012-111/2058 : P4 gauche (vue occlusale). **B.** NMA 2012-113/2058 : M1 gauche (vue occlusale). **C.** NMA 2012-112/2058 : M2 droite, inverse (vue occlusale). **D.** NMA 2012-115/2058 : mandibule gauche avec m1, m2 (1–vue linguale, 2–vue labiale). **E.** NMA 2012-116/2058 : mandibule gauche avec m1–m3 (vue occlusale). **F.** NMA 2012-117/2058 : mandibule droite avec m1, m2 (vue occlusale). **G.** NMA 2012-118/2058 : mandibule droite avec i–m1 (1–vue occlusale, 2–vue linguale). **H.** NMA 2012-114/2058 : mandibule droite avec a1–m3 (vue linguale). **I.** NMA 2012-115/2058 : condyle gauche (vue postérieure).

28 bridges the gap between the two sites. A sexual dimorphism is deemed highly unlikely, because that would mean that all specimens within Wintershof-West are of the one gender and all specimens of Petersbuch 2 of the other. Other explanations of the differences invoke spatial or temporal differences between the two populations. The explanation as result of a temporal difference is preferred, suggesting the inclusion of two slightly different periods within Petersbuch 28. Intermediate specimens are very rare and might only be representative of the outer limits of the two size groups.

There has been some discussion about the taxonomic placement of the genus *Paenelimnoecus*. Engesser (1980)

included it in the Soricinae, based on the soricine p4 of most species. Reumer (1984) placed it into the soricine tribe Allosoricini, which had been proposed as a subfamily by Fejfar (1966). When Ziegler (1989) transferred “*Limnoecus*” *micromorphus* to *Paenelimnoecus*, he included the genus in the Crocidosoricinae. Reumer (1992) reallocated the genus to the resurrected Allosoricinae. Storch (1995) left the higher taxonomic position open. To keep the genus together, Ziegler (2003) argued that it would best fit within the Soricinae. Fejfar et al. (2006) erected its own subfamily, the Paenelimnoecinae. Van den Hoek Ostende et al. (2009) argued the case of the subfamily Allosoricinae. Huguency et al. (2012) retained it within the

Table 7

Measurements of teeth and mandibles of *Paenelimnoecus micromorphus* (Doben-Florin, 1964) from Petersbuch 28 (Germany, Lower Miocene, MN 3/4).

Tableau 7

Mesures des dents et mandibles de *Paenelimnoecus micromorphus* (Doben-Florin, 1964) de Petersbuch 28 (Allemagne, Miocène inférieur, MN 3/4).

	n (ex.)	Parameter	Mean	Min	Max
P4	3 (1)	L bucc	1.31	1.28	
		L ling	0.99	0.79	
		W	1.09	1.07	
		L dj	1.24	1.10	
M1	6 (4)	W dj	1.18	1.27	
		L bucc	1.24	1.20	
		L ling	1.16	1.17	
		L max	1.23	1.21	
		W ant	1.20	1.21	
M2	4 (2)	W post	1.44	1.46	
		W max	1.36	1.37	
		L bucc	1.14	1.13	
		L ling	1.11	1.09	
		L max	1.12	1.13	
i inf	6 (3)	W ant	1.29	1.36	
		W post	1.32	1.37	
		W max	1.30	1.38	
		L	2.32	2.21	2.42
a1	7 (1)	H	0.55	0.53	0.58
		L	0.63	0.56	0.69
a2	4 (3)	W	0.42	0.39	0.49
		L	0.13		
a3 (p4)	13 (4)	W	0.23		
		L	0.62	0.57	0.67
m1	30 (8)	W	0.47	0.37	0.54
		L	0.99	0.92	1.04
		W Tr	0.54	0.49	0.62
		W Ta	0.58	0.52	0.66
m2	27 (11)	HoM	0.94	0.83	1.11
		L	0.98	0.89	1.05
		W Tr	0.55	0.50	0.64
		W Ta	0.55	0.50	0.62
m3	42 (10)	HoM	0.89	0.74	1.05
		L	0.76	0.68	0.83
		W Tr	0.45	0.41	0.51
		W Ta	0.34	0.28	0.39
Mand	36 (2)	HoM	0.87	0.74	1.02
		LForM	3.13	3.22	
		CorH	2.80	2.70	
PCond	5 (4)	W inf	0.88		
		W sup	0.44		
		H	0.85		
		H R	1.02		

Paenelimnoecinae, because *Paenelimnoecus* lacks the carnassial specialisations of *Allosorex* Fejfar, 1996. This fact was acknowledged by Van den Hoek Ostende et al. (2009), but was not thought sufficient to warrant a separate subfamily for *Paenelimnoecus*. Here, we endorse this view; the carnassial specialisations are seen as an autapomorphy of the genus *Allosorex*. Apart from that *Allosorex* and *Paenelimnoecus* have sufficiently similar evolutionary trends to include them within the same subfamily.

3.4. Postcrania of the *crocidosoricines* and *Paenelimnoecus*

Fig. 6C, D, I

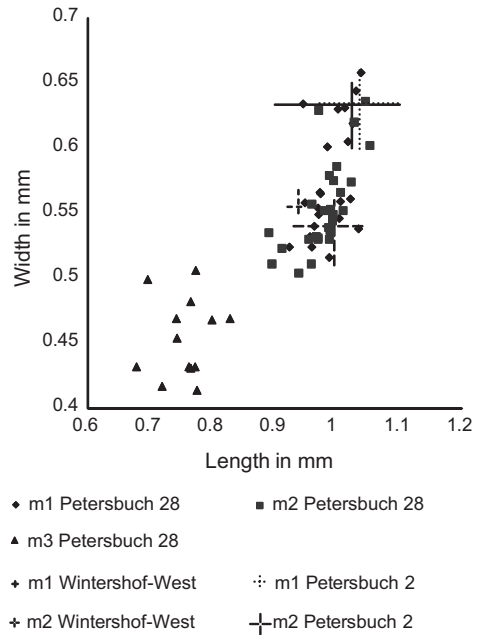


Fig. 8. Length and width of *Paenelimnoecus micromorphus* (Doben-Florin, 1964) lower molars from Petersbuch 28 (Germany, Lower Miocene, MN 3/4). Data for comparison is from Ziegler (1989).

Fig. 8. Longueur et largeur des molaires inférieures de *Paenelimnoecus micromorphus* (Doben-Florin, 1964) de Petersbuch 28 (Allemagne, Miocène inférieur, MN 3/4). Données de Ziegler (1989) pour comparaison.

Material: 15 humeri, one ulna (proximal part only).

Collection numbers: NMA 2012-126/2058, 127/2058, 134/2058, CMR-P/28- H22, H24, H30, H32, H34–H41, H43.

The **humeri** are of four different sizes, but are very similar in shape. The only complete humerus is small, slender and straight. The round caput is a little elongated alongside the shaft's axis. The tuberculum maius and tuberculum minus are small knobs. Both tubercula are connected by anterior bulges that continue in the high and narrow crista humeri, which ends in a large tubercle. In the smallest specimen, the high, strong crista humeri fades out to the surface. The trochlear area is wide and has a large fossa radialis. The trochlea is a combination of a large knob, reminiscent of the capitulum in talpids, and a more elongated part ending in a medial wall. The weak and shallow fossa olecrani has the deepest point on the medial side. The ectepicondyle is a large flange. The entepicondyle is a clear knob, connected to the shaft by a column that borders a pronounced, nearly circular foramen entepicondylaris above the trochlea's medial part.

The conserved fragment of the **ulna** shows that the complete bone would have been tiny. The incisura trochlearis is small and slender, the proximal part turned to the lateral side and protruding. A groove is present next to the incisura; it enlarges to a small proximal basin. The preserved part of the olecranon is strong, the medial area flattened. At the proximal end, a thin ridge encloses the small basin. The measurements of the humeri and the ulna are given in Table 8.

Comparison: The humeri are quite similar to *Sorex* Linnaeus, 1758 or *Crocidura* Wagler, 1832; less to

Table 8

Measurements of humerus and ulna of the Soricidae from Petersbuch 28 (Germany, Lower Miocene, MN 3/4). * = Damaged.

Tableau 8

Mesures d'humérus et d'ulna des Soricidae de Petersbuch 28 (Allemagne, Miocène inférieur, MN 3/4). * = Endommagé.

	n (ex.)	Parameter	Mean	Min	Max
Hum					
Largest	2 (2)				
	1	MDD	0.81		
	2	DiW	3.43	3.25	
	2	TroW	2.25	2.07	
	2	TroH	0.82	0.72	
Large	2 (1)				
	1	MDD	0.65		
	2 (1)	DiW	2.37	2.19*	
	2 (1)	TroW	1.65	1.37*	
	2 (1)	TroH	0.64	0.51*	
Small	10 (9)				
	1	Max L	6.16		
	2	CM L		0.97	1.06
	2	CaW		0.77	0.83
	2	ProxW		1.28	1.56
	10	MDD	0.59	0.44	0.78
	7	DiW	1.82	1.72	1.94
	6	TroW	1.26	1.05	1.42
	5	TroH	0.42	0.38	0.46
Tiny	1 (1)				
	1	MDD	0.34*		
	1	DiW	1.14*		
	1	TroW	0.82*		
	1	TroH	0.29*		
Ulna	1 (1)				
		Max L	4.46*		
		Linc	0.88		
		MDPA	1.08		
		MDD	0.42		

pronounced in Petersbuch 28, where it reaches nearly 60%, followed by Stubersheim 3, where about 57% of all shrew remains belong to *S. discrepans*. The second most common shrew in the compared localities is *M. desnoyersianus* (Lartet, 1851), although it becomes comparably rare in Petersbuch 28. *M. desnoyersianus* is nearly as common as *S. discrepans* in Stubersheim 3, reaching a frequency of

Table 9

Numbers of specimens and relative frequencies in percent of the shrew fauna from the German localities Wintershof-West, Stubersheim 3, Petersbuch 28, Petersbuch 2 and Erkertshofen 2. Data from Doben-Florin (1964); Ziegler (1989); Ziegler and Fahlbusch (1986).

Tableau 9

Nombres de spécimens et fréquences relatives des faunes de musaraignes des localités allemandes Wintershof-West, Stubersheim 3, Petersbuch 28, Petersbuch 2 et Erkertshofen 2. Données de Doben-Florin (1964); Ziegler (1989); Ziegler et Fahlbusch (1986).

Species	Wintershof-West		Stubersheim 3		Petersbuch 28		Petersbuch 2		Erkertshofen 2	
	MN 3		MN 3		MN 3/4		MN 4		MN 4	
	n	%	n	%	n	%	n	%	n	%
<i>Heterosorex neumayrianus</i>	184	35.7	14	2.1	31	2.2	40	12.3	6	15.5
<i>Dinosorex</i> aff. <i>zapfei</i>							15	4.6	2	2.4
<i>Soricella discrepans</i>	167	32.4	372	56.6	833	59.5	100	30.8	34	40.5
<i>Soricella</i> sp.							9	2.8		
<i>Lartetium petersbuchense</i>					167	11.9	51	15.7	7	8.3
<i>Lartetium</i> cf. <i>prevostianum</i>					56	4.0				
<i>Florinia stehlini</i>	7	1.36			58	4.1	7	2.2	2	2.4
<i>Miosorex desnoyersianus</i>	142	27.6	266	40.5	195	13.9	83	25.5	19	22.6
<i>Paenelimnoecus micromorphus</i>	15	2.9			60	4.3	20	6.2	7	8.3
<i>Carposorex</i> sp.			1	0.2						
Crocidosoricinae indet.			3	0.5						
<i>Hemisorex</i> (?) sp.			1	0.2						

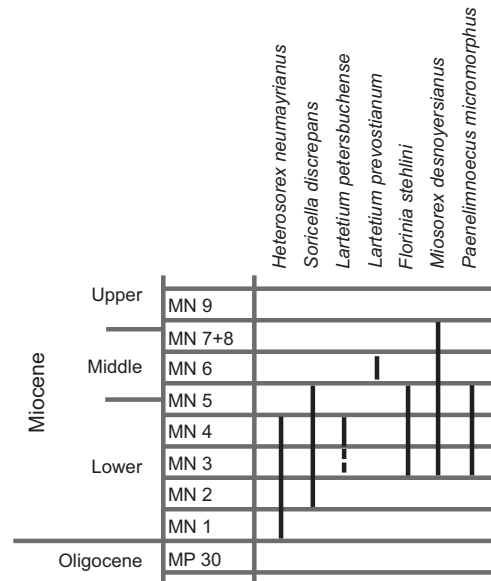


Fig. 10. Stratigraphic distribution of the shrew species present in Petersbuch 28 (Germany, Lower Miocene, MN 3/4). Data from Van den Hoek Ostende et al. (2005); Ziegler (2006b); Furió et al. (2011). *Miosorex desnoyersianus* includes the specimens determined as *M. pusilliformis*, following Klietmann et al. (2013).

Fig. 10. Distribution stratigraphique des espèces de musaraignes présentes dans Petersbuch 28 (Allemagne, Miocène inférieur, MN 3/4). Données de Van den Hoek Ostende et al. (2005); Ziegler (2006b); Furió et al. (2011). *Miosorex desnoyersianus* comprend les spécimens déterminés comme *M. pusilliformis*, en suivant Klietmann et al. (2013).

40%. Notably, *S. discrepans* and *M. desnoyersianus* comprise about 97% of all shrew specimens in Stubersheim 3. Furthermore, this is the only locality to include *Carposorex Crochet, 1975* and probably *Hemisorex Baudelot, 1967*. Therefore, the environment of Stubersheim 3 was probably harsh for most Miocene shrews, and only the most adaptable soricids could thrive there. *M. desnoyersianus* survived for a long time (Fig. 10), so it must have been able to adapt to diverse environments.

P. micromorphus (Doben-Florin, 1964) is the only shrew to become more frequent, although it remains relatively rare. Apparently, the environmental changes were favourable for *P. micromorphus*. However, being the smallest shrew, it may have suffered from interspecific competition, preventing it from establishing a higher population density. The recent *Sorex minutus* Linnaeus, 1766 is known to reach the highest population densities on habitats free of competition with the larger *S. araneus* Linnaeus, 1758 (Yalden, 1981).

Of the species present in the two localities, Wintershof-West and Petersbuch 28, *S. discrepans*, *M. desnoyersianus* and *P. micromorphus* were on average larger in size in the sample from Wintershof-West, implying that Wintershof-West had a more favourable environment for these three species.

F. stehlini (Doben-Florin, 1964) is more common in Petersbuch 28 than in the two other localities, but is still very rare. It is the only shrew that is larger, on average, in Petersbuch 28 than in Wintershof-West. Therefore, *F. stehlini* probably differed in its ecology from the other shrews of Petersbuch 28. The large cingulid, the strong cusps and the highly worn teeth indicate that *F. stehlini* might have been more durophagous than the other shrews.

On the whole, the species composition found in Petersbuch 28 is not really surprising, but the relative frequencies are interesting. The increased dominance of *S. discrepans* may indicate some sort of stress caused by the environment, which *S. discrepans* was best able to resist. Apart from *H. neumayrianus*, *S. discrepans* was the only shrew present in Petersbuch 28 that reached Spain (Fig. 9). Therefore, it was probably more euryoecious than the other shrews.

Shrews are not easily used for biostratigraphy or biochronology. Most species present in Petersbuch 28 are known from more than one Mammal Unit (Fig. 10). Except for *L. cf. prevostianum*, the shrews were found in localities of MN 3 and MN 4. *L. petersbuchense* was found in Germany only in localities belonging to MN 4 (Ziegler, 2006b), but it was reported from the Czech locality Merkur-Nord, which belongs to MN 3 (Fejfar and Sabol, 2005). The m1 and m2 from Petersbuch 2 had no buccal cingulid (Ziegler, 1989), but a faint cingulid was found on some specimens from Petersbuch 28. Therefore, the presence of *L. petersbuchense* indicates Petersbuch 28 to be younger than Wintershof-West (MN 3), but its evolutionary state indicates Petersbuch 28 to be older than Petersbuch 2 (MN 4). Both species of *Lartetium* Ziegler, 1989 may have entered Southern Germany during the time reflected in the Petersbuch 28 assemblage.

A remarkable phenomenon occurs in *S. discrepans*, *P. micromorphus* and in *M. desnoyersianus*. In *S. discrepans* and *P. micromorphus*, we find bimodal size distributions (Figs. 3 and 8). *M. desnoyersianus* has two morphological types of upper incisors with minor metrical differences.

The two populations of *S. discrepans* might have co-existed in different microhabitats and the upper incisors of *M. desnoyersianus* may be part of a sexual dimorphism. The lower molars of *P. micromorphus* tell a different story. One group has similar sizes to the specimens from Wintershof-West (MN 3), the other to the specimens from Petersbuch 2 (MN 4) (Fig. 8). Thus, the metric and

morphological differences in *S. discrepans*, *M. desnoyersianus* and *P. micromorphus* are interpreted to be micro-evolution, not sexual dimorphisms.

As Hendry and Kinnison (1999) summed up, the term micro-evolution signifies all evolutionary changes taking place within a species. These changes might be allochronic (found in a single population at two different times) or synchronic (found in two different populations of the same time). Therefore, we have to ask the question whether the microevolutionary events were allochronic or synchronic. Neither the sediment nor the chiropteran fauna of Petersbuch 28 show any traces of mixture (Rosina and Rummel, 2012). The sediment matrix is homogenous and the owl pellets are evenly distributed, so neither multiple deposition events nor a slow, ongoing deposition can be assumed based on the geologic evidence. The exceptionally good preservation precludes transportation of the material over greater distances. The owl pellets would not have remained intact during transport; nor could they withstand on the ground over a long time, so they were probably covered by sediment in short time.

On the other hand, any microevolutionary changes caused by different habitats would also be expected in Petersbuch 2, but these were not found (Ziegler, 1989). Therefore, these microevolutionary events were probably allochronic and the size differences suggest time averaging. Interestingly, there are only minor changes in the molar width of *P. micromorphus* between Wintershof-West and one size group of Petersbuch 28. Likewise, there are only small changes between the second size group of Petersbuch 28 and the entire sample from Petersbuch 2. Yet, the width changed considerably within the time of deposition of Petersbuch 28. Thus, the assemblage of Petersbuch 28 was probably deposited around the transition between MN 3 and MN 4. This conclusion agrees with previous interpretations (Rosina and Rummel, 2012).

The temporal mixing need not span considerable times on a geological time scale. Recent shrews vary considerably in size under varying ecological circumstances (White and Searle, 2007). For instance, large soricine shrews of three different sizes were found in the Late Glacial cave locality Nixloch (Austria, Upper Pleistocene, about 13 to 10 kyr) (Rabeder, 1992). They were initially determined to be three different species, but new studies revealed them to belong to the recent species *S. araneus* Linnaeus, 1758 (Prost et al., 2013). The different size groups were therefore interpreted as depositions from different time frames (Klietmann, 2008). Therefore, shrews are known to react to changing environmental conditions within comparably short time, and so an apparent hiatus in the deposition might be caused by a rapid evolutionary change in combination with comparably low deposition rates. Therefore, the best solution to the conflicting geological and palaeobiological evidences is that within the time of deposition, a considerable change in the environment caused the shrews to adapt in relatively short times. The time averaging or temporal mixing occurred without redeposition of the sediment.

P. micromorphus and *M. desnoyersianus* might have reacted to changing composition of available prey. Likewise, a population of *S. discrepans* encountering

unfavourable conditions could easily have shifted towards smaller size. The sample from Petersbuch 28 includes the smallest specimens of *S. discrepans* known from southern Germany (Ziegler, 1989). The immigration of *L. petersbuchense* may have prevented *S. discrepans* from staying small. Populations of recent *S. araneus* are known to maintain larger size in the presence of smaller species (White and Searle, 2007).

5. Conclusions

In the locality Petersbuch 28 (Germany, Lower Miocene), a diverse shrew fauna was found. In *S. discrepans*, *P. micromorphus* and *M. desnoyersianus*, microevolutionary changes are visible. *S. discrepans* has a bimodal size distribution, most pronouncedly in the m1. *P. micromorphus* has a bimodal distribution of the width of the m1 and m2. *M. desnoyersianus* has two different morphological types of upper incisors.

The wider molars of *P. micromorphus* are metrically similar to the sample of Wintershof-West (MN 3), the narrower molars resemble the specimens from Petersbuch 2 (MN 4). These resemblances back up the suggestion that Petersbuch 28 was deposited near the transition between MN 3 and MN 4, bridging the gap between Wintershof-West and Petersbuch 2.

The differences are explained as allochronic microevolutionary changes, indicating a small temporal mixing, although no sign of such a mixing was found in the sediment.

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