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Tiny teeth of consequence: Vestigial antemolars provide key to Early Miocene soricid taxonomy (Eulipotyphla: Soricidae)

Petites dents d'importance : les antémolaires vestigiales fournissent la clé de la taxonomie des soricidés (Eulipotyphla : Soricidae) du début du Miocène

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ABSTRACT

In the soricid fauna of the Early Miocene Petersbuch 28 fissure fill from Bavaria, Germany, specimens of *Miosorex desnoyersianus* (Lartet, 1851) and *Paenelimnoecus micromorphus* (Doben-Florin, 1964) retain a tiny penultimate antemolar. This antemolar was previously unknown for *P. micromorphus*, because the tiny antemolar has not been preserved until now. *Miosorex desnoyersianus* retains the rudimentary tooth; its possible function was to keep the p4 in upright position. The younger species of *Paenelimnoecus* have lost this vestigial tooth. Based on the alveoli, *Miosorex pusilliformis* is interpreted as a junior synonym of *M. desnoyersianus*, and the diagnoses of *Miosorex desnoyersianus* and *Paenelimnoecus micromorphus* are emended.

RÉSUMÉ

Dans la faune des soricidés du remplissage de fissure bavarois Petersbuch 28, Allemagne, Miocène inférieur, des spécimens de *Miosorex desnoyersianus* (Lartet, 1851) et *Paenelimnoecus micromorphus* (Doben-Florin, 1964) conservent une pénultième antémolaire (a2) minuscule. Cette antémolaire était auparavant inconnue chez *P. micromorphus*. Le nombre différent d'antémolaires n'est pas considéré comme suggérant une espèce nouvelle, mais indique plutôt que la minuscule antémolaire a été conservée pour la première fois. *Miosorex desnoyersianus* conserve la dent rudimentaire ; sa fonction était peut-être de maintenir la position verticale de la p4. Les espèces les plus récentes de *Paenelimnoecus* ont perdu cette dent vestigiale. En nous fondant sur les alvéoles, nous interprétons *Miosorex pusilliformis* comme un synonyme junior de *M. desnoyersianus*, et les diagnoses de *Miosorex desnoyersianus* et *Paenelimnoecus pusilliformis* sont émendées.

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1. Introduction

The number of antemolars is a key character in the taxonomy of shrews (e.g., Hugueney and Maridet, 2011; Ziegler, 1989, 2003). In spite of their importance, their provenance is not fully understood, hence the term "antemolars". It is unknown whether they are incisors, canines, premolars or several of the above – and how many of each kind of tooth types are represented. The most posterior lower antemolar is commonly considered the p4, and some recent authors have restricted the antemolar count to the teeth anterior to it (Hugueney et al., 2012; Rofes and Cuenca-Bescós, 2009); in older descriptions, the p4 is counted among the antemolars (Baudelot, 1972; Doben-Florin, 1964; Ziegler, 1989). In the upper dentition, the P4 is much larger and more complex morphologically than the antemolars and is therefore not counted as an antemolar, even in older descriptions (Baudelot, 1972; Doben-Florin, 1964; Hugueney et al., 2012; Rofes and Cuenca-Bescós, 2009; Ziegler, 1989). This assignment agrees with studies of living species (Choate, 1968).

For the other antemolars, the situation is less obvious. Different interpretations were given by Merriam (1895), Ärnbäck-Christie-Linde (1912), Kindahl (1960) and James (1963). Although Repenning (1967) disagreed with the previous designations, James' (1963) dental formula of I1-I2-I3-C-P2-P3 for the upper antemolars and i3–c for the lower antemolars of *Sorex* Linnaeus, 1758 and *Blarina* Gray, 1838 is widely accepted for recent soricids (Choate, 1968; Hillson, 2005). The number of antemolars can differ in living and extinct species, and no embryological studies can be conducted on the latter. Therefore, the antemolars cannot be determined as incisors, canines or premolars, except for the upper and lower P4 (Hugueney et al., 2012; Rofes and Cuenca-Bescós, 2009).

The molars of Soricidae are notoriously conservative in their morphology, and therefore have limited use in distinguishing taxa. In order to identify fossil shrews confidently, the molars, the anterior dentition and the condyle are needed. Unfortunately, complete anterior dentitions are rare. Of course, the number of antemolars can also be determined on the basis of an alveolar row. But still, complete reference material is needed for determining the sizes and numbers of roots of the antemolars.

Many specimens from the Early Miocene Petersbuch 28 fissure fill of Bavaria show excellent preservation (Rosina and Rummel, 2012). A surprising feature is the presence of a tiny lower antemolar (the a2) in *Miosorex* and *Paenelimnoecus*. This element had previously not been noted in the latter genus. In this paper, we describe the a2 and determine the consequences of this discovery for the taxonomy of the two genera. The teeth are small and featureless enough to pass as sediment grains, so we conducted a chemical analysis to make sure that they are really teeth. They are too radiant for bone or dentin and too rounded for a broken bit of enamel. The number of upper antemolars does not correspond to the number of lower antemolars (Doben-Florin, 1964; Ziegler, 1989). Furthermore, vestigial antemolars have never been found in the upper dentition. The mandibles are more commonly found than maxillary remains, so the mandibular teeth are better known and often more important for shrew taxonomy (Baudelot, 1972; Doben-Florin, 1964; Engesser, 2009; Ziegler, 1989). Therefore, we confine ourselves to the lower antemolars.

1.1. Nomenclatural history of *Miosorex* and *Paenelimnoecus*

The first description of a species now belonging to the genus *Miosorex* concerned a small shrew with three antemolars described by Lartet (1851) under the name of *Sorex desnoyersianus*; it was placed within *Miosorex* by Baudelot (1972). The next member of the genus was described by Depéret (1892), who named a quite similar but larger "*Sorex pusillus* race *grivensis*", after the French site of La Grive. The use of the generic name *Sorex* for these fossil shrews was found to be erroneous by Kretzoi (1959), who baptized the genus *Miosorex*, raising Depéret's "race" to a distinct species. Some years later, Doben-Florin (1964), in her extensive work on Miocene shrews of Wintershof-West, added another species to this group, but still used the generic assignment of *Sorex*, calling the new species "*Sorex pusilliformis*" and described it as being unique in having only two mandibular antemolars. Doben-Florin would have preferred the name "*Sorex pusillus*", but this name had already been given to another soricid by von Meyer (1846), who gave neither a sufficient description nor good drawings of the species. Kretzoi (1959) had renamed "*Sorex pusillus*" *Oligosorex meyeri*, because the name *Sorex pusillus* was preoccupied by a species named by Gmelin (1774). Von Meyer's (1846) "*Sorex pusillus*" is now considered a nomen dubium (Storch, 1988). *Oligosorex meyeri* is therefore invalid as well. The species *pusilliformis* was included in *Miosorex* by Ziegler (1989).

In *Paenelimnoecus*, a comparable situation is found. The oldest description of one of its species was given by Kormos (1934) under the name of "*Pachyura pannonica*", which was eventually included within *Paenelimnoecus* by Reumer (1984). The next of these tiny shrews to be described was *P. micromorphus*, first named "*Limnoecus micromorphus*" (Doben-Florin, 1964) for the similarities to the American genus *Limnoecus* Stirton, 1930. Bachmayer and Wilson (1970) described "*Petenyiella repenningi*", later included in *Paenelimnoecus* by Reumer (1984). The taxon *Paenelimnoecus* had been erected by Baudelot (1972), along with the new species *P. crouzeli*. Gibert Clols (1975) erected the species "*Limnoecus truyolsi*", which was reallocated to the genus *Paenelimnoecus* by Van den Hoek Ostende et al. (2009). The latest members described are *P. obtusus* Storch, 1995 and *P. chinensis* Jin and Kawamura, 1997. None of the previous studies on these taxa ever mentioned a number of lower antemolars other than two – even though Jin and Kawamura (1997) showed drawings of *P. chinensis* with only one antemolar, the p4. Table 1 gives an overview over the species discussed here.

2. Material and methods

One hundred and forty-five mandibles of *Miosorex desnoyersianus* and 48 mandibles of *Paenelimnoecus micromorphus* from the Early Miocene locality Petersbuch 28,

Table 1
List of species included in *Miosorex* Kretzoi, 1959 and *Paenelimnoecus* Baudelot, 1972, with their original names.
Tableau 1
Liste d'espèces comprises dans *Miosorex* Kretzoi, 1959 et *Paenelimnoecus* Baudelot, 1972, avec leurs noms d'origine.

Genus	Original name	Current name	Authority
Miosorex Kretzoi, 1959	*Sorex desnoyersianus* Lartet, 1851	*Miosorex desnoyersianus* (Lartet, 1851)	Baudelot (1972)
	Sorex pusillus race *grivensis* Depéret, 1892	*Miosorex grivensis* (Depéret, 1892)	Kretzoi (1959)
	Sorex pusilliformis Doben-Florin, 1964	*Miosorex desnoyersianus* (Lartet, 1851)	This paper
Unknown	*Sorex pusillus* von Meyer, 1846 = *Oligosorex meyeri* Kretzoi, 1959	[Nomen nudum, species invalid]	Storch (1988)
Paenelimnoecus Baudelot, 1972	*Pachyura pannonica* Kormos, 1934	*Paenelimnoecus pannonicus* (Kormos, 1934)	Reumer (1984)
	Limnoecus micromorphus Doben-Florin, 1964	*Paenelimnoecus micromorphus* (Doben-Florin, 1964)	Ziegler (1989)
	Petenyiella repenningi Bachmayer and Wilson, 1970	*Paenelimnoecus repenningi* (Bachmayer and Wilson, 1970)	Reumer (1984)
	Paenelimnoecus crouzeli Baudelot, 1972	*Paenelimnoecus crouzeli* Baudelot, 1972	Baudelot (1972)
	Limnoecus truyolsi Gibert Clols, 1975	*Paenelimnoecus truyolsi* (Gibert Clols, 1975)	Van den Hoek Ostende et al. (2009)
	Paenelimnoecus obtusus Storch, 1995		
	Paenelimnoecus chinensis Jin and Kawamura, 1997		

Bavaria, Germany, were examined. They will be stored at the Naturmuseum Augsburg (NMA) and the Collection Michael Rummel (CMR), Weißenburg in Bayern (Bavaria). The *Miosorex* specimens have the 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. The *Paenelimnoecus* specimens have the 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.

The nomenclature of the morphological features follows Reumer (1984). The descriptions and measurements of the teeth are given by Klietmann (2013) and are under preparation for publication. The chemical analyses of the newly found rudimentary teeth of *Miosorex* and *Paenelimnoecus* were done by Hugh Rice and Johannes Klietmann on the SEM in low vacuum, using an energy dispersive X-ray spectrometry (EDS) system, the EDAX Genesis Apex 4 X-ray Microanalysis System of Metek, which identifies the various elements through the X-rays caused by the electrons hitting the object. The machine further counts how often the signal from each searched element was found. In order to have comparable results, each probing was done for 100 s.

The MN-Units as used herein were extensively discussed in Van der Meulen et al. (2011).

3. Systematic palaeontology

Class: MAMMALIA Linnaeus, 1758
Order: EULIPOTYPHLA Waddell et al., 1999
Family: SORICIDAE Fischer, 1814

Subfamily: CROCIDOSORICINAE Reumer, 1987
Genus *Miosorex* Kretzoi, 1959
Type species: *Sorex grivensis* Depéret, 1892

Original diagnosis (Kretzoi, 1959): (..) *Miosorex* n.g. (holotype: *Sorex pusillus* race *grivensis* Depéret, 1892) which retains but two unicuspids [= antemolars] like *Myosorex*.

Three species have been assigned to the genus: *Miosorex desnoyersianus* (Lartet, 1851), *M. grivensis* (Depéret, 1892) and *M. pusilliformis* (Doben-Florin, 1964).

Miosorex desnoyersianus (Lartet, 1851)
Fig. 1A
Holotypus: none given.

Neotypus: right Mandible with p4-m3, Sa 1201, Muséum national d'Histoire naturelle, Paris.

Locus typicus: Sansan, France (Gers). Middle Miocene, MN 6.

Time range: Early Miocene (MN 3) (Ziegler, 2006a) to Middle Miocene (MN 6) (Engesser, 2009).

Emended diagnosis: small crocidosoricine with three antemolars, the second of which (a2) is extremely small. The p4 has two roots. The distal part of the first antemolar and the p4 ridges are high and resemble small accessory cuspules. On m1 and m2, the hypolophid is distinctly separated from the entoconid and forms a clear entostylid. The buccal cingulid is weak; the lingual cingulid is wide, but wears no ridge. The oblique cristid of the m1 ends about equally far from the buccal tooth border as in the m2. The m3 has a talonid with only one cusp. The foramen mentale is below the p4. The lower incisor is long and tricuspulate, the posterior border of its crown extends only a little farther backward on the buccal than on the lingual side.

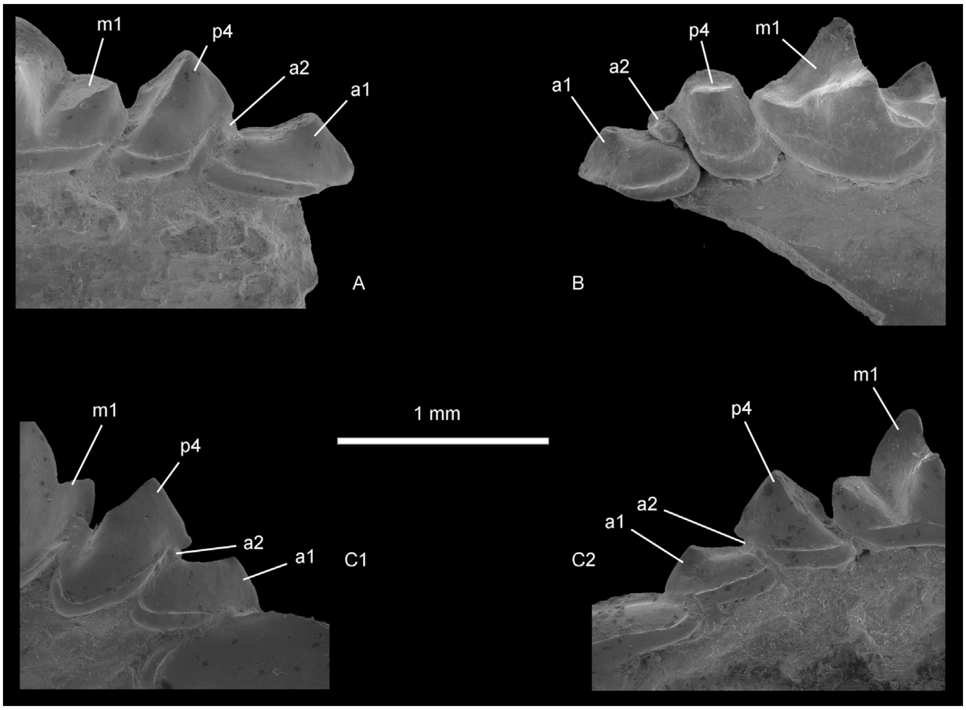

Fig. 1. SEM photographs of the vestigial teeth of *Miosorex desnoyersianus* (Lartet, 1851) and *Paenelimnoecus micromorphus* (Doben-Florin, 1964) from Petersbuch 28, Germany, Early Miocene, MN 3/4. *Miosorex desnoyersianus*. **A.** NMA 2012-110/2058: left a1, a2, p4, m1, lingual view. *Paenelimnoecus micromorphus*: **B.** NMA 2012-114/2058: right a1, a2, p4, m1; largest a2, lingual view. **C1.** NMA 2012-118/2058: right i, a1, a2, p4, m1, buccal view. **C2.** NMA 2012-118/2058: right i, a1, a2, p4, m1, lingual view.

Fig. 1. Photos MEB des dents vestigiales de *Miosorex desnoyersianus* (Lartet, 1851) et *Paenelimnoecus micromorphus* (Doben-Florin, 1964) de Petersbuch 28 (Allemagne, Miocène inférieur, MN 3/4). *Miosorex desnoyersianus*. **A.** NMA 2012-110/2058 : a1, a2, p4, m1 gauches, vue linguale. *Paenelimnoecus micromorphus* : **B.** NMA 2012-114/2058 : a1, a2, p4, m1droites; a2 plus grande, vue linguale. **C1.** NMA 2012-118/2058 : i, a1, a2, p4, m1 droites, vue buccale. **C2.** NMA 2012-118/2058 : i, a1, a2, p4, m1 droites, vue linguale.

The upper and lower facets of the condyle are not divided; the processus condylaris is emarginated on the buccal side (crocidurine shape). The hypocone of the M1 and M2 is developed as a weak cusp or a ridge, the hypoconal flange of the M1 is extensive, the anterolingual corner is rounded, and the posterior cingulum of P4, M1 and M2 is mostly uninterrupted.

Description: the single-rooted **a1** is almost triangular with a concave posterior margin. The anterior margin reaches up where the tooth covers the incisor. The cusp is in the tooth's anterior third. The cusp's ridges form a Y, having a rounded anterior ridge and two posterior ridges. Both posterior ridges end short of the cingulid. A large valley is enclosed between them. The cingulid encircles the whole tooth except the small most anterior part. It is most pronounced at the posterior corners. The tiny **a2** is completely overlain by the p4 on all specimens; it is by far wider than long and is very low and bulbous. Because the p4 covers the a2, no measurements of the a2 could be taken. The tooth seems to point in an anterobuccal direction; therefore, the highest point is at the anterior end, but it does not form a clear tip, because it is in contact with the p4 over its complete length. Two tiny ridges or bulges seem to run in lingual and buccal direction, respectively, in the larger specimens (CMR-P/28-2898, CMR-P/28-2909, CMR-P/28-2960). The buccal part of the tooth is larger and may reach further buccal than the anterior part of the p4. The root is small and reaches posteriorly below the tip of the p4.

The **p4** has two roots, the posterior being large; the small anterior root was never seen in the material described herein. The anterior margin reaches upward, where the tooth contacts the previous antemolar. The only cusp is Y-shaped and bends a bit lingually. The lower anterior margin forms a small concavity for the contact to the a2.

Subfamily: ALLOSORICINAE Fejfar, 1966
Genus *Paenelimnoecus* Baudelot, 1972
Type species: *Paenelimnoecus crouzeli* Baudelot, 1972

Diagnosis (translated from Baudelot, 1972): it is a Limnoecine and is characterized by the loss of the entoconid at the molars and its reduced size; on the m1, the buccal valley opens well above the cingulid and the metaconid is very close to the protoconid; the talonid of the m3 is reduced to a cutting crest and only a weak rest of the lingually open basin is left; the teeth were coloured.

The genus currently includes *Paenelimnoecus micromorphus* (Doben-Florin, 1964), *P. pannonicus* (Kormos, 1934), *P. repenningi* (Bachmayer and Wilson, 1970), *P. crouzeli* Baudelot, 1972, *P. truyolsi* (Gibert Clols, 1975), *P. obtusus* Storch, 1995 and *P. chinensis* Jin and Kawamura, 1997.

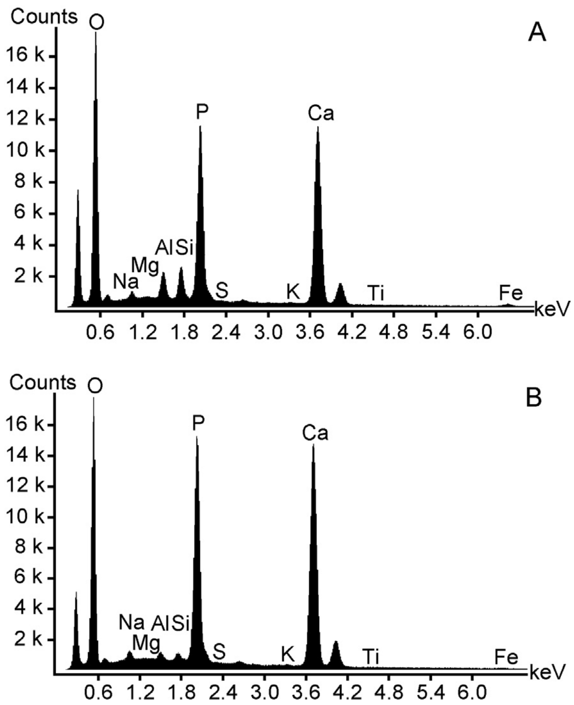

Fig. 2. Element counts of teeth of the *Paenelimnoecus micromorphus* (Doben-Florin, 1964) specimen NMA 2012-118/2058 from Petersbuch 28, Germany, Early Miocene, MN 3/4. A. Element count of the p4. B. Element count of the minute a2.

Fig. 2. Comptage des éléments des dents de *Paenelimnoecus micromorphus* (Doben-Florin, 1964) spécimen NMA 2012-118/2058 de Petersbuch 28, Allemagne, Miocène inférieur, MN 3/4. A. Comptage des éléments de la p4. B. Comptage des éléments de la minuscule a2.

Paenelimnoecus micromorphus (Doben-Florin, 1964)
Figs. 1B–C2 and 2

Holotypus: right Mandible with p4, m1, m2 and m3 in situ, posterior part broken off. Bayerische Staatssammlung für Paläontologie und historische Geologie, Munich, 1937 II 10472.

Locus typicus: Wintershof-West, Germany. Early Miocene, MN 3.

Time range: Early Miocene (MN 3–MN 4);?Middle Miocene (MN 5) (Ziegler, 2006b).

Emended diagnosis: very small shrew with two clearly visible and one vestigial lower antemolars, an elongated incisor and a much-reduced entoconid and entocristid on the m1 and m2. The m2 is usually longer than the m1. The talonid of the m3 bears one cusp. Contrary to all other species of the genus, *P. micromorphus* has a lower p4 with two posterior ridges and a minute penultimate antemolar.

Description: the single-rooted **a1** is tear-shaped with a straight posterior margin. The cusp is a large, three-sided pyramid bending slightly in a posterior direction. Its ridges form a Y consisting of the rounded anterior and two posterior ridges. Both posterior ridges end at about half the length of the tooth and border a shallow valley. The cingulid encompasses the whole tooth except for the most anterior part. It is largest in the posterobuccal corner and small on the lingual side. In only one mandible (NMA 2012-114/2058; Fig. 1B), the tiny **a2** is large enough to be visible in occlusal view; in this specimen, the a2 is almost elliptical with a concave posterior side; it is clearly wider than long and bears no ridges, only a wide, but weak bulge alongside the main axis. It is the only specimen big enough to be measured; its length is 0.13 mm and the width is 0.23 mm. Like the other antemolars, it extends anterodorsally. In the other specimens, the a2 is smaller than 0.1 mm; it cannot be measured correctly, because it is reduced to a tiny chip between the other antemolars, completely covered by the p4. It still appears to be wider than long.

The **p4** has one root and a Y-shaped wear facet. The anterior margin reaches upward where the tooth overlays the previous antemolar. In buccal view, the anterior margin follows the margin of the a2, creating a pronounced concavity, and forms a small protrusion in anterior direction above the a2.

4. Comments on the material from Petersbuch 28

Antemolars were quite rarely preserved in the mandibles. Of the 145 mandibles of *Miosorex desnoyersianus* found in Petersbuch 28, only 26 still include antemolars at all. Only eight of these 26 specimens retain other antemolars than just the p4 (Klietmann, 2013). The small additional antemolar was found in five of these eight specimens. On one of the remaining three mandibles with antemolars, all antemolars were damaged and the a2 was not found. The other two mandibles might just have lost the tiny a2 through taphonomy. None of the tiny a2 is measurable, but a considerable difference in size is visible; in one specimen, the tooth is clearly visible and projects in a buccal direction clearly out of the p4's cover. In all the other specimens, it is just a tiny bump between the antemolars. Independent of the number of antemolars, if any of them is tiny; it is the penultimate one (Klietmann, 2013). In *Paenelimnoecus micromorphus*, only thirteen out of 48 mandibles include antemolars. In the other specimens, the antemolars are missing. In seven of the thirteen specimens containing antemolars, both the a1 and p4 are preserved. The additional antemolar is preserved in four of the seven jaws; one of the three others has antemolars covered by sinter and the two remaining mandibles have damaged antemolars, so the tiny tooth is probably lost. The largest a2 (NMA 2012-114/2058; Fig. 1B) can be seen in occlusal view, because it is too large to fit low between the other teeth. The other three specimens of the a2 are extremely tiny and nearly completely featureless.

The small structure could theoretically be a sand grain; the shiny surface forbids any determination as bone or dentin. In order to test whether it was not just a grain from the matrix, a scan on the EDS System was performed and showed a quite similar chemical composition of the smallest tooth of *Paenelimnoecus micromorphus* when compared to the p4 next to it (Fig. 2). The results for *Miosorex desnoyersianus* and the unusually large a2 of *P. micromorphus* are given in the supplementary material. In comparison to the results for rodent teeth obtained by García-Alix et al. (2013), the high amount of oxygen and the extra elements like sodium, magnesium, silicium and aluminium demonstrate the specimen to be diagenetically altered. Still, the results of the structure under question and the neighbouring p4 are quite similar towards each other, apart from including more sediment. The sediment consists predominantly of aluminium, silicium and oxygen. Judging from the similarity of the chemical composition, the tiny tooth consists of hydroxyapatite that was diagenetically altered exactly like the p4. Therefore, the structure most probably belongs to the dentition. A misidentification of the small tooth as sediment grain can be excluded. Bone or dentin cannot be confused with enamel, because they are not as radiant and translucent under a light microscope; therefore, the structures cannot consist of bone or dentin. An enamel particle is a highly improbable explanation for the observed structure. First, enamel particles of comparable sizes and shapes would have been caught in exactly the same spot in multiple mandibles and nowhere else. Second, broken enamel would not be rounded and similarly smooth on all visible surfaces. Enamel particles could only be rounded under circumstances that would abrade the enamel of the neighbouring teeth considerably, but no sign of such an abrasion is visible in the material.

5. Discussion

5.1. Recognizing the a2 in other Miocene soricid material

This structure between a1 and p4 was not recognised as a tooth immediately. Rather, it was thought to be a sediment particle. This is excluded by the analysis using the X-ray Microanalysis System, as the small teeth show the same chemical composition as their respective neighbouring p4. In the element counts of the small antemolar (Fig. 2B) compared to the element counts of the neighbouring p4 (Fig. 2A), aluminium and silica are more common. This is due to problems of cleaning the tiny teeth between the larger ones, so more sediment remained on their surface; also, there are fewer surfaces to choose really clean spots for the analyses. The element counts of *Miosorex desnoyersianus* (Supplementary Figs. S1 and S2) and *Paenelimnoecus micromorphus* (Fig. 2, Supplementary Figs. S3 and S4) are also comparable, so the pattern of *P. micromorphus* corroborates the presence of an additional tooth, the a2.

Another possible explanation of the structure is that it formed part of a neighbouring tooth. In specimen NMA 2012-114/2058 of *Paenelimnoecus micromorphus*, the tooth was large enough to be recognised as a tooth of its own. Upon removing the a2, its large root became visible. Undamaged a1 and p4 do not have an enlargement that could be mistaken for the a2, so the enamel structure under discussion cannot be part of a neighbouring tooth.

Additionally, in these specimens, there is still a groove for the respective tooth between the a1 and the p4. Therefore, it can safely be concluded to be a tooth of its own, a tiny a2.

The relative size of this tooth is very small, but this is not unusual in soricids; a tiny penultimate antemolar of comparable size ratio is found in *Lartetium petersbuchense* (Ziegler, 1989) and is also present in *Miosorex grivensis* (Baudelot, 1972; Viret and Zapfe, 1951) and in the genus *Oligosorex* (Van den Hoek Ostende, 2001).

The number of lower antemolars is of great importance for the determination of soricids (e.g., Reumer, 1984; Van den Hoek Ostende, 2001; Ziegler, 1989, 1999, 2003, 2006a, b, 2009). The vestigial tooth of *Miosorex desnoyersianus* is easily lost in the taphonomic process; it is still unknown from Sansan, the locus typicus, where only the number of alveoli is known (Engesser, 2009). Doben-Florin (1964) used the number of antemolars to differentiate between *Miosorex desnoyersianus* and *M. pusilliformis*. This view was followed by Ziegler (1989), who described *M. pusilliformis* from different German sites. It is clear from his extensive discussion that recognizing *M. pusilliformis* as a separate species led to a taxonomic puzzle. Presumably, *Miosorex pusilliformis* had fewer antemolars than *M. desnoyersianus* and should therefore be considered to display a more derived dental formula. Yet, *M. pusilliformis* appeared in the older localities, with a mixed population of the two *Miosorex* species in the fissure Petersbuch 2. Thus, Ziegler (1989) had to assume the replacement of a species with a fairly derived dental formula by a virtually indistinguishable form with a more primitive dental formula.

This problem resulted from the lack of an exhaustive description of the alveoli at the time; the alveoli were not discussed in detail by Baudelot (1972). Engesser (2009) finally rectified this situation by giving a detailed and explained picture of *Miosorex desnoyersianus* alveoli from Sansan (Fig. 3C). Based on the rareness of the a2 even in the exceptionally rich material of Petersbuch 28 and the minute size of the p4's anterior root, the taxonomic situation of *Miosorex* "*pusilliformis*" had to be evaluated. The direct comparison of the pictures of *M.* "*pusilliformis*" given by Doben-Florin (1964) and Ziegler (1989) to the drawing of Engesser (2009) shows completely identical structures of the alveoli (Fig. 3). The presumed difference in the number of alveoli was the only reason for erecting a new species, so *M.* "*pusilliformis*" is according to the new data a junior synonym of *M. desnoyersianus*.

Consequently, the question arises how the antemolar could have escaped attention up to now. Doben-Florin (1964) had only one specimen of *M.* "*pusilliformis*" with both large antemolars still in place; in a photograph of this mandible, the region of the accessory antemolar appears to be covered by sinter. Also, it could have been lost without leaving a visible gap. All other specimens lacked one or both antemolars. Since it was already known that the tiny third antemolar of *Miosorex grivensis* is always represented by its alveolus (Viret and Zapfe, 1951), both large alveoli covered by the p4 were seen as belonging to this tooth (Doben-Florin, 1964). The small groove on the bony ridge below the p4 was obviously not interpreted as being an alveolus, so the specimens of Wintershof-West seemed to have only two antemolars. The two roots of the p4 were described by Doben-Florin (1964). Ziegler (1989) determined *Miosorex* "*pusilliformis*" and "*M. desnoyersianus*" based mostly on the number of alveoli, since most mandibles had already lost the antemolars. The new found synonymy of the two species indicates that the specimens determined as *Miosorex* "*pusilliformis*" belong in fact to *M. desnoyersianus*; the specimens determined as "*M. desnoyersianus*" in Petersbuch 2 by Ziegler (1989) could either belong to a different species or be specimens with an unusually large anterior alveolus of the p4. This question can only be answered by a revision of the original material.

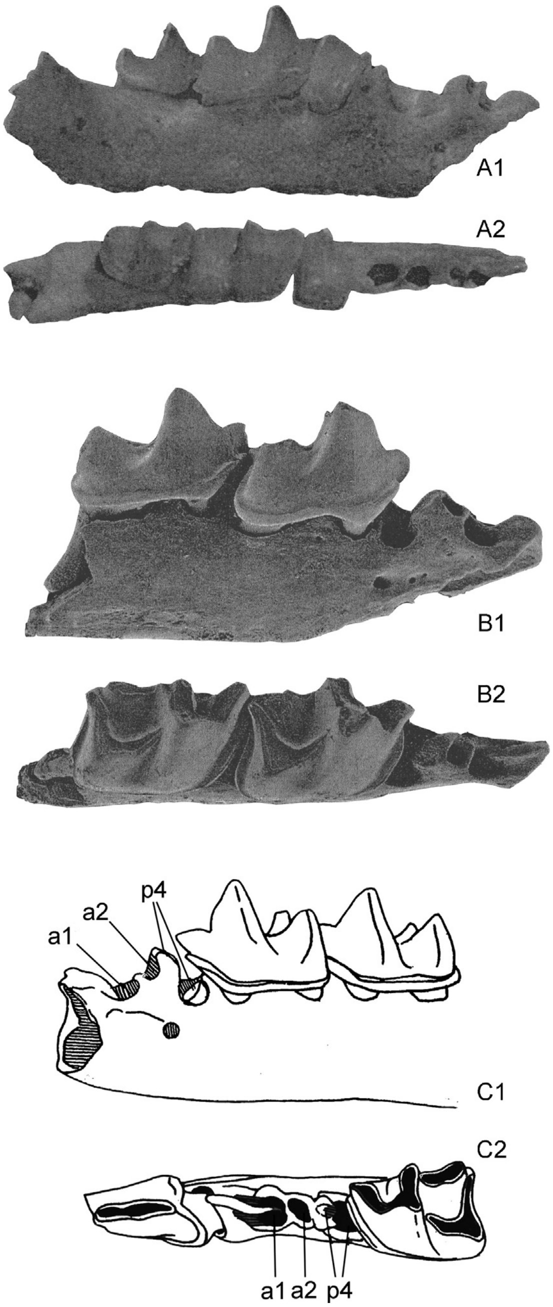

Fig. 3. Comparison of the alveoli of *Miosorex* "*pusilliformis*" from Winterhof-West (A) and Stubersheim 3 (B), both from Germany, Early Miocene, MN 3, to the alveoli of *Miosorex desnoyersianus* (Lartet, 1851) from Sansan (C), France, Middle Miocene, MN 6. Buccal (1) and occlusal (2) view. A after Doben-Florin (1964), B after Ziegler (1989), C after Engesser (2009). Not to size.

Fig. 3. Comparaison des alvéoles de *Miosorex* "*pusilliformis*" de Wintershof-West (A) et Stubersheim 3 (B), tous les deux d'Allemagne, Miocène inférieur, MN 3, avec les alvéoles de *Miosorex desnoyersianus* (Lartet, 1851) de Sansan (C), France, Miocène moyen, MN 6. Vue buccale (1) et occlusale (2). A d'après Doben-Florin (1964), B d'après Ziegler (1989), C d'après Engesser (2009). Échelle non respectée.

Even the specimens of Petersbuch 28 that have lost the a2 in course of the taphonomic process do not have a clear gap between the other teeth. Therefore, only the larger sample size provided the opportunity to actually find this tooth. Sigé et al. (1997) did not give the number of specimens or of teeth from Bouzigues 1 and 2. Stephan-Hartl (1972) worked on the entire fauna of Frankfurt-Nord Bassin; in the single shrew specimen, the anterior antemolars were lost.

In *Paenelimnoecus micromorphus*, the preservation situation is comparable. Doben-Florin (1964) had no specimens with both other antemolars in situ and described the p4 as having two roots. Ziegler (1989) also mentioned the presence of a two-rooted p4 in contrast to the one-rooted p4 in the younger species. The finding of the vestigial tooth shows that the p4 is one-rooted in *P. micromorphus*, too. The smallest shrew within the Early Miocene faunas tends to be present in relatively small numbers (Doben-Florin, 1964; Klietmann, 2013; Ziegler, 1989). Given that the tiny mandibles are usually damaged, it is nearly impossible to find a tooth of this size. In fact, except for the unusually large one, the tooth was only recognized by examining SEM photos of the specimens.

The shrew faunas of the Czech Republic's sites, as listed by Fejfar and Sabol (2005), still await description and the determinations are therefore preliminary; presence or absence of the new found tooth has still to be assessed.

Of course, following this reasoning, we must accept that within one genus, the number of antemolars is variable and the loss of an antemolar is convergent in several taxa. This is acceptable as long as it concerns teeth in a state of reduction just prior to complete loss. In *Heterosorex neumayrianus*, a heterosoricid shrew, the number of antemolars is used for determining the subspecies (Doben-Florin, 1964; Ziegler and Fahlbusch, 1986), so variability can be expected.

The last question arising from the new finds is the old question of "Why?". A tooth of this extremely small size had surely lost function in processing food, because it barely came into occlusal contact with the food or the upper dentition. Nonetheless, it was retained within *Miosorex desnoyersianus* from MN 3 in Wintershof-West to MN 6 of Sansan (Doben-Florin, 1964; Engesser, 2009; Klietmann, 2013). One possible interpretation is that the tiny tooth served somehow as an additional column, taking over the role of an additional anterior root, bearing part of the pressure exercised on the p4; this is improbable because a direct contact with the other antemolar could facilitate this better. The easiest explanation is that the small size of this tooth is part of a trend to reduce the number of antemolars, a common trend in soricids, until it did not "get in the way" anymore; after having reached this point, a further reduction would only result in a negligible saving of enamel and dentin, which was probably not important enough to cause further reduction. The tooth position could be conserved at little energetic cost – even if it did not have any function in the dentition. If we follow Furió et al. (2011) and consider *Oligosorex* to be closely related or even congeneric to *Lartetium*, this tooth position may have been retained over a long time in a single lineage, as *Oligosorex* lasted from the Upper Oligocene (MP 28) to the Early Miocene (MN 2)

(Van den Hoek Ostende, 2001); *Lartetium* is present in the Middle Miocene (MN 4 to MN 6).

The most probable function is that of a wedge, holding the p4 in its position (Van den Hoek Ostende, 2001); in contrast to the first explanation of an additional column, this does not mean it is necessary to bear the pressure, but it helps to keep the correct position of the p4. This would at least decrease the speed of the further reduction, as any reduction would have to be balanced by some change within the other antemolars to keep the p4 exactly upright. In *Paenelimnoecus* the complete reduction of the vestigial tooth happened quite early, as only the oldest species still retained this tooth position. Small changes of the adjacent teeth made the minute tooth expendable. In his figure 2, Reumer (1992) showed that the space occupied by the vestigial a2 in *P. micromorphus* is filled by an extension of the lower margin of the p4 in *P. crouzeli*. Therefore, the loss of the vestigial tooth had to be compensated by the p4 in order to keep the p4 in upright position. The minuscule tooth still played a role within the dentition of *P. micromorphus*. A similar function may be assumed in *Miosorex desnoyersianus* and other shrews still retaining minute penultimate antemolars.

5.2. Trends in soricid antemolar dentition

The earliest crocidosoricine genus known is *Srinitium* Hugueney, 1976. It had five lower antemolars anterior to the p4, more than all other known genera (Hugueney, 1976; Ziegler, 1998). In another Oligocene genus, *Ulmensia* Ziegler, 1989, the number of antemolars is reduced to three, not counting the p4 (Ziegler, 1989). Reducing the number of antemolars remained a trend within the soricids and occurred repeatedly as parallel evolution within the Crocidosoricinae and the Allosoricinae. We included *Paenelimnoecus* Baudelot, 1972 in the Allosoricinae; the taxonomic state of the genus is still debated (Hugueney et al., 2012; Prieto and Van Dam, 2012; Van den Hoek Ostende et al., 2009). Within the Crocidosoricinae, most genera retained three lower antemolars, the last being vestigial (Fig. 4). *Soricella discrepans* Doben-Florin, 1964 and *Florinia stehlini* (Doben-Florin, 1964) reached the state of having two large antemolars with no vestigial antemolar. Both species most probably reached this state as a parallelism. Given the basal position of *Soricella discrepans* in the cladogram of Hugueney and Maridet (2011), it must have evolved the reduced number of antemolars independently of most other crocidosoricines.

In *Miosorex* Kretzoi, 1959, the third antemolar was lost and the second antemolar became vestigial. Therefore, it was supposed to be the next relative to the Myosoricini/-inae by Furió et al. (2007). In the analysis of Hugueney and Maridet (2011), no species of *Miosorex* shows affinities with *Myosorex* Gray, 1838. Furthermore, the reduced number of antemolars might have evolved independently, possibly even as a parallelism within *Miosorex*.

We could demonstrate that the vestigial second antemolar was present in the oldest species of *Paenelimnoecus*, although it was lost in the younger ones. In the recent genera of soricids, there are no vestigial lower antemolars left (Dannelid, 1998), except in *Myosorex* (Dannelid, 1998; Furió et al., 2007). According to Stanley et al. (2005), vestigial lower antemolars are sometimes present in the African genus *Congosorex* Heim de Balsac and Lovett, 1956, but always absent in *C. phillipsorum* Stanley et al., 2005. Soricinae and Crocidurinae reduced their dentitions in parallel, because their respective sister clades retain a higher number of antemolars (Fig. 4).

The upper antemolars are independent of their lower counterparts in their evolutionary trends. For example, *Oligosorex* Kretzoi, 1959 and *Lartetium* Ziegler, 1989, have three lower antemolars anterior to the p4, but *Lartetium* has four upper antemolars and *Oligosorex* has five (Hugueney et al., 2012). *Soricella discrepans* has two lower antemolars anterior to the p4 and four upper antemolars (Doben-Florin, 1964), whereas *Miosorex desnoyersianus* (Lartet, 1851) has a further reduced second lower antemolar, but five upper antemolars. Likewise, the recent genus *Sorex* Linnaeus, 1758 retains five upper antemolars of slightly variable sizes, but only one lower antemolar (Moska et al., 2008). The numbers of upper and lower antemolars of more taxa are given in Fig. 4.

The evolutionary reductions of the upper and lower antemolar number are thus independent of each other and of systematic position, occurring repeatedly as parallelisms within the Soricidae. For *Blarina brevicauda*, antemolar crowding was found to be the reason for the aberrant loss of individual antemolars (Choate, 1968). The presence of vestigial antemolars should also be taken into account when considering the identification of the antemolars. Usually, the premolars are reduced from anterior to posterior direction (Hillson, 2005). If the antemolar row cannot contain four premolars, the first and then the second premolars are interpreted as being lost during evolution (James, 1963; Hillson, 2005). However, the various evolutionary states found in the Crocidosoricinae and in *Paenelimnoecus* indicate a different trend. Whenever there is a vestigial antemolar, it is the last one anterior to the p4 – independent of the actual number of antemolars. There is one antemolar anterior to the vestigial one in *Miosorex desnoyersianus*, *M. grivensis* (Depéret, 1892) and *Paenelimnoecus micromorphus* (Doben-Florin, 1964) and two in most other crocidosoricines. *Soricella discrepans* and *Florinia stehlini* do not retain any vestigial antemolars (Doben-Florin, 1964; Ziegler, 1989). The trend of reducing the premolars is therefore different in shrews than in most other mammals. The penultimate premolar – no matter which one it is – becomes tiny and is subsequently lost within the various lineages. Otherwise, we would have to assume that the vestigial premolar remained present, whereas a larger one within the antemolar row was lost completely in quite a short time. The premolars are therefore reduced in the anterior direction. The p4 is never reduced; probably its function is crucial to the mastication process.

In the upper antemolar row, the last antemolar is usually smaller than the others (Dannelid, 1998; Moska et al., 2008). The upper antemolar row itself is formed by quite uniform teeth that act as a functional unit. It is not likely that one tooth within the antemolar row would be lost completely and the others would fill the gap. The last upper antemolar is more commonly lost than most other

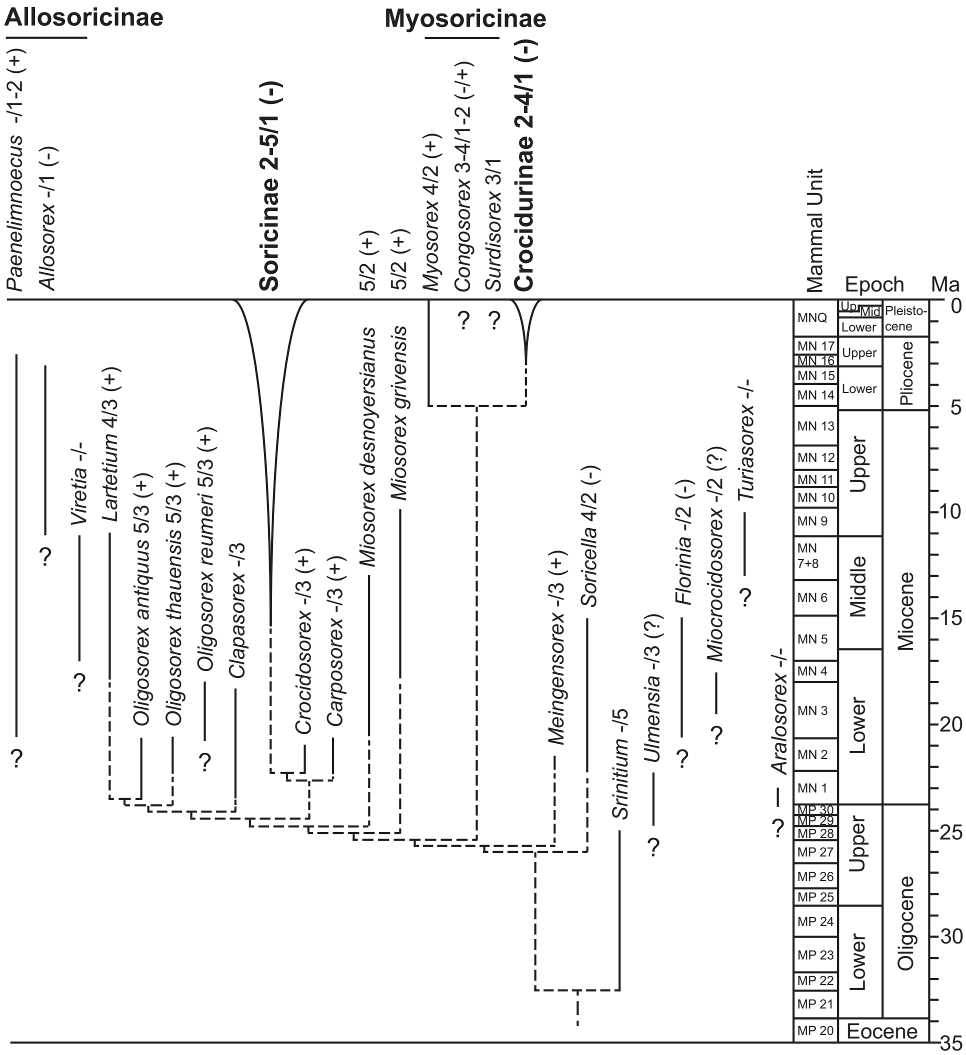

Fig. 4. Stratigraphic and systematic overview over known Crocidosoricinae and descendants of the subfamily. Solid lines indicate the stratigraphic distributions. The numbers of upper and lower antemolars (not counting the P4/p4) are given after each taxon. (+) and (–) indicate if the last antemolar is vestigial. The cladogram follows Hugueney and Maridet (2011), the stratigraphic data are based on Furió et al. (2007). If no different result was found in the cladogram of Hugueney and Maridet (2011), monophyly of higher taxa was assumed. Further information are from Doben-Florin (1964); Fejfar (1966); Hugueney (1976); Hugueney et al. (2012); Kerbis Peterhans et al. (2009); Lopatin (2004); Reumer (1992); Stanley et al. (2005); Van Dam et al. (2011); Van den Hoek Ostende (2003); Viret and Zapfe (1951); Ziegler (1989, 1998).

Fig. 4. Vue d'ensemble stratigraphique et systématique des Crocidosoricines connus et des descendants de la sous-famille. Les traits pleins indiquent les distributions stratigraphiques. Les nombres du antémolaires supérieures et inférieures (sans compter la P4/p4) sont donnés pour chaque taxon. (+) et (–) indiquent si la dernière antémolaire est vestigiale ou non. Le cladogramme suit Hugueney et Maridet (2011), les données stratigraphiques sont basées sur Furió et al. (2007). Si aucun résultat différent n'a été trouvé dans le cladogramme de Hugueney et Maridet (2011), une monophylie des taxons supérieurs a été supposée. Des informations supplémentaires proviennent de Doben-Florin (1964) ; Fejfar (1966) ; Hugueney (1976) ; Hugueney et al. (2012) ; Kerbis Peterhans et al. (2009) ; Lopatin (2004) ; Reumer (1992) ; Stanley et al. (2005) ; Van Dam et al. (2011) ; Van den Hoek Ostende (2003) ; Viret and Zapfe (1951) ; Ziegler (1989, 1998).

antemolars (Feldhaber and Stober, 1993; Jogahara et al., 2007). The antemolar interpreted as the third incisor or as the canine is lost more often in aberrant dentitions than the others (Feldhaber and Stober, 1993; Jogahara et al., 2007). Nonetheless, the state of aberrant dentition cannot be used to determine evolutionary trends, because most cases of tooth loss are postnatal and probably due to periodontal disease (Jogahara et al., 2008). More likely, the functional unit of the antemolar row is reduced at one of its ends, most probably at the posterior end, where the large P4 almost covers the small last antemolar. Like the lower antemolars, the upper antemolar row is reduced in anterior direction. Therefore, the first premolar lost is the upper or lower P3. Any hypothesis that the antemolars include the P3/p3, but not the P1/p1, can therefore be rejected on grounds of the most probable evolutionary trend.

6. Conclusions

Miosorex desnoyersianus (Lartet, 1851) and *Paenelimnoecus micromorphus* (Doben-Florin, 1964) were found in

Petersbuch 28 (Germany, Early Miocene, MN 3/4); both species exhibit a tiny penultimate antemolar that has never been described for *Paenelimnoecus micromorphus* until now. Based on the comparison of pictures of the alveoli of *Miosorex desnoyersianus* from Sansan (France, Middle Miocene, MN 6) and *M.* "*pusilliformis*" of Wintershof-West (Germany, Early Miocene, MN 3) and Petersbuch 2 (Germany, Early Miocene, MN 4), *M.* "*pusilliformis*" must be regarded as a junior synonym of *M. desnoyersianus*. The usually poor preservation of the small soricids and the extremely small size of *P. micromorphus* tooth, which is hardly visible using anything but an electron microscope, has made it very difficult to spot this feature. The younger species of *Paenelimnoecus* lack these small teeth. The function of the tooth was to keep the p4 in upright position, without adding to the length of the antemolars. In *Paenelimnoecus*, the tooth was lost in the younger species, but functionally replaced by an enlargement of the p4 covering the respective space.

A compilation of the known crocidosoricine and allosoricine genera and the recent Soricinae, Crocidurinae and Myosoricinae shows that reduction of antemolars was a common parallelism in shrews, occurring independently in multiple lineages. Based on the small sizes of the upper and lower last antemolars in most shrews, the reduction of the premolars is interpreted to start at the upper and lower P3 and commence in an anterior direction, contrary to the trends in most other mammalian taxa.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.crpv.2013.05.008.

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