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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.

Mots clés :
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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,