



Insectivore palaeoecology. A case study of a Miocene fissure filling in Germany



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ABSTRACT

Many Miocene localities yielded considerable numbers of eulipotyphlan fossils. The group as a whole is generally considered to be indicative for humid environments, but little is known about the preferences of specific taxa. We discuss the insectivores found in the German fissure filling Petersbuch 28, including an insectivorous marsupial, in an attempt to refine the knowledge of the preferred environments of insectivores. For this, we compared the assemblage in quantitative analyses with other insectivore assemblages of similar age. Our results show that, in full accordance with previous hypotheses, dimylids, most moles and shrews were shown to be indicators for humid environments, like swamps or humid forests, whereas the hedgehogs, the moles *Desmanodon* and *Theratiskos* and the shrew *Oligosorex* were more common in dryer environments.

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1. Introduction

Insectivores (Eulipotyphla), a group including the Soricidae (shrews), Heterosoricidae (a group of larger, extinct shrews), Talpidae (moles), Erinaceidae (hedgehogs) and the Dimylidae (an extinct family most closely related to the talpids), are the second largest group of micromammals in the fossils record after the rodents. In the modern fauna, and presumably also in the past, bats (Chiroptera) are the secondmost numerous group of small mammals, but their fossil record is notoriously incomplete (Teeling et al., 2005). Initially, insectivores received far less attention than rodents, leading to a taxonomic impediment which barred them from usage in, for instance, stratigraphical schemes (e.g., De Bruijn et al., 1992). Specialist papers from the 1990s and the beginning of the 21st century strongly improved this situation (Van den Hoek Ostende et al., 2005), and many taxonomic papers have appeared since then.

So far, the biostratigraphical use of insectivores appears to be limited, but they have been hailed as excellent palaeoenvironmental indicators, particularly for humidity. The rationale behind this is that insectivores feed on detritus feeders, and, therefore, particularly litter-rich forests provide a plentiful food supply (Van den Hoek Ostende, 2001d). Thus, the proportion of insectivores vs rodents (as percentage of fossils found), and the eulipotyphlan species diversity (number of species found) can be used as proxies for humidity. In addition, Van den Hoek

Ostende (2003) also calculated the Simpson's diversity index for insectivore assemblages, showing that, for instance, the German MN 3 locality Stubersheim 3 may be high in number of species ($N = 11$), but still has a low diversity as the assemblage is completely dominated by two species only. Furió et al. (2011) used insectivore diversity to demonstrate a constant humidity gradient across Europe during a large part of the Miocene.

All the papers above mainly used the insectivore order as a whole for their analyses. Obviously, different representatives of the order have a variety of ecological preferences. Most insectivore mammals prefer rather humid environments, but there are recent insectivores living in clearly arid areas, like the erinaceines *Hemiechinus auritus* and *Paraechinus aethiopicus*, which live in semi-arid and desert regions, respectively (Shkolnik and Schmidt-Nielsen, 1976) or the desert shrew *Notiosorex crawfordi* (Hoffmeister and Goodpaster, 1962). Also from the fossil record there are indications of insectivores living in dry conditions. Luis and Hernando (2000) reported *Galerix exilis* and *Miosorex cf. grivensis* from the Spanish Miocene site Somosaguas Sur, which represents a clearly dry palaeoenvironment (Domingo et al., 2008).

In view of the ecological differences within insectivores, both recent and fossil, a more detailed distinction is necessary for interpreting the palaeoecology of the various taxa and palaeoenvironment of fossil localities. Therefore, we aim to take things a step further, in attempting to reconstruct the autoecology of insectivores at or below the family level. As a basis for our analyses, we use the assemblage of the German MN3/MN4 fissure Petersbuch 28 (Table 1), which was presented in a series of publications (Klietmann et al., 2013a,b; Klietmann et al., 2014a,b,c, d). Apart from the insectivores, our analyses include the last marsupial *Amphiperatherium frequens* von Meyer, 1846, because it was a

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Table 1

Presence data of the species in the compared sites Petersbuch 28, Wintershof-West, Stubersheim 3 and Petersbuch 2. Data from Klietmann (2013), Klietmann et al. (2014a,b,c,d), Ziegler (1989), Ziegler and Fahlbusch (1986).

	Petersbuch 28	Wintershof-West	Stubersheim 3	Petersbuch 2
<i>Amphiperatherium frequens</i>	X	X	X	X
<i>Amphechinus</i>				2 species
<i>Lantanotherium</i> spp.	cf.			
<i>Galerix aurelianensis</i>	X	X	X	X
<i>Galerix symeonidisi</i>		X?		X
<i>Chainodus intercedens</i>	X	X	X	X
<i>Plesiodimylus</i>	aff. <i>chantrei</i>	<i>huerzeleri</i>		<i>chantrei</i>
Dimylidae indet			X	
<i>Desmanella engesseri</i>	X	X	aff.	X
<i>Myxomygale hutchisoni</i>	X	X	X	X
<i>Talpa</i> spp.	Only Postcrania	X		2 species
Talpini indet				X
<i>Proscapanus intercedens</i>	X			X
<i>Hugueneya primitiva</i>				cf.; only Postcrania
<i>Geotrypus</i> spp.		X	X	
<i>Desmanodon antiquus</i>			X	
cf. " <i>Scaptonyx</i> " <i>edwardsi</i>	X			
<i>Heterosorex neumayrianus</i>	X	X	X	X
<i>Dinosorex zapfei</i>				aff.
<i>Soricella discrepans</i>	X	X	X	X
<i>Soricella</i> sp.				X
<i>Lartetium petersbuchense</i>	X			X
<i>Lartetium</i> cf. <i>prevostianum</i>	X			
<i>Florinia stehlini</i>	X	X		X
<i>Miosorex desnoyersianus</i>	X	X	X	X
<i>Miosorex</i> "cf. <i>desnoyersianus</i> "				X
<i>Paenelimnoecus micromorphus</i>	X	X		X
<i>Hemisorex</i> sp.			X	
<i>Carposorex</i> sp.			X	
Crocidosoricinae indet			X	
<i>Plesiosorex</i> sp.				X?

ground-dwelling insectivorous to omnivorous animal (Kurz, 2005) and therefore of comparable ecology as the larger eulipotyphlan species.

The discussion of the autecology of extinct species is usually based on four principles. First, the actualistic approach, which means assuming comparable ecology to the species' living relatives. Second, the morphology of the teeth may indicate the feeding habits, as some skeletal adaptations may be related to behaviour, like the humerus in burrowing moles. Third, the facies of a locality also gives vital clues to the palaeoenvironment, lignites, for instance, indicating relatively humid conditions. The fourth method is comparing the abundance of species in different localities, so a correlation may be found. These correlations may help reconstructing the unknown ecology of an extinct species by comparing it to the known ecology of other species from the same time and place, as was done by Van der Meulen and Daams (1992).

Before analyzing the composition of the various insectivore assemblages, we will discuss which assumptions were made in literature on the various insectivores from Petersbuch 28. As noted above, Eulipotyphla are mostly considered valuable humidity indicators. Van Dam (2006) used them as part of a proxy for Mean Annual Precipitation (MAP) in the later part of the Neogene. No such calculations based on insectivores were made for the earlier Neogene, and the ecology of taxa is usually indicated as preferring either humid or relatively dry environments. Other proxies, however, have yielded estimates for this time period. Based on the co-existence approach (Mosbrugger and Utescher, 1997), the average MAP for the late Burdigalian of Central Europe lies between 1300mm and 1600mm (Utescher et al., 2012; fig. 8). These values would correspond to the more humid forested environments in which most the early Neogene insectivores lived. In the same figure, Utescher et al. (2012) also show results of another proxy, based on the composition of the lower vertebrates fauna (Böhme et al., 2006). These estimates (200mm–1400mm) are clearly lower and more varying than those from the botanical record. Nevertheless,

they are important because they allow a direct comparison with the insectivore record, mostly originating from the same samples. The lower vertebrate record shows clearly that the precipitation in the Early Miocene of Spain was considerably lower than in Central Europe (Böhme et al., 2006, 2011), with values of 300mm–400mm. These values, corresponding to more open environments, represent the environments of the dry tolerant insectivores discussed in this article. The proxy using lower vertebrates is of particular interest for us, as Gardner and Böhme (2008) made an estimate for Petersbuch 28 using this locality, leading to a MAP of around 300 mm.

1.1. Dimylidae

Dimylids are generally considered as indicative for wet environments. The exoedaenodont and amblyodont teeth have been interpreted as indicator of malacophagy, and thus as trait of animals living in humid environments (Hürzeler, 1944; Müller, 1967). *Plesiodimylus*, the most numerous genus in Petersbuch 28, is very common or dominant in numbers amongst the insectivores in localities of fluvial origins or lignitic sites, like Oberdorf (Austria, MN 4) or Hambach 6C (Germany, MN 5) (Ziegler, 1998; Ziegler and Mörs, 2000; Ziegler, 2005), which originated from a very wet, swampy environment (Daxner-Höck, 1998; Ziegler and Mörs, 2000). Dimylids are also very common in the fissure Devínska Nová Ves (Fejfar and Sabol, 2009). The Anatolian dimylid *Turkodimylus* was also found in lignites together with faunas indicating a humid environment (Van den Hoek Ostende, 1995b).

Ziegler (2005) pointed out that snails may also thrive in dry surroundings, so malacophagy in itself does not prove any preference for wet environments. *Plesiodimylus* does not have extremely enlarged teeth; therefore, it was probably more insectivorous than the more specialized dimylids (Engesser, 1980; Ziegler and Mörs, 2000; Kálin and Engesser, 2001). Its wider ecological habits are also apparent from its

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