

Reappearance of *Galerix* (Erinaceomorpha, Mammalia) at the Middle to Late Miocene transition in South Germany: biostratigraphic and palaeoecologic implications

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Abstract

The presence of *Galerix* molars in the South German fossil locality Hammerschmiede 3 is interpreted as evidence for a re-immigration of West European origin into the North Alpine Foreland Basin at the transition of the Middle to Late Miocene. The brief re-appearance of *Galerix* in southern Germany can be used as a biostratigraphic marker that allows promising correlations between local biostratigraphic subdivisions from Spain and Germany, suggesting that, contrary to previous thought, the Hammerschmiede locality may antedate the hipparionine horses' appearance event. Based on the supposed climatic adaptation of galericine taxa and lower vertebrate record, it is hypothesized that short term climatic fluctuations occurred in South Germany around the time of the first appearance of the hipparionine horses in Europe.

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Introduction

The Middle Miocene is characterized by major global climate changes, including the end of the Miocene climatic optimum (Böhme, 2003) due to global cooling (Shevenell *et al.*, 2004). In Europe, the end of the Middle Miocene is subjected to an aridity peak, followed by warm conditions and considerably more precipitation than present during the Tortonian ('washhouse' climatic phases, Böhme *et al.*, 2008). Coincident with these climatic events, a major reorganization in the European mammal faunas takes place (Casanovas-Vilar *et al.*, 2010). For instance, a new wave of hominoids entered Europe (Casanovas-Vilar *et al.*, 2008a).

From a biostratigraphical perspective, the most important immigrants at the boundary between Middle and Late Miocene are the hipparionine horses. The transition from Middle to Late Miocene is well documented in Spain, in sections with both large and small mammals in the Daroca-Calamocha area of the Teruel Basin (Álvarez Sierra *et al.*, 2003), and the Vallés-Penedés Basin (Casanovas-Vilar *et al.*, 2006; Casanovas-Vilar, 2007). Unfortunately, the entrance of these perissodactyls is not accompanied with major changes in the small mammal faunas (Casanovas-Vilar *et al.*, 2010).

In sharp contrast to the Spanish record, the transition from Middle to Late Miocene is poorly documented in Germany and in Central Europe in general. This hampers correlations through Europe and thus the understanding of large scale patterns in faunal distribution. The German locality Hammerschmiede is one of the few small mammal localities of North Alpine

Foreland Basin (NAFB) that represents this time interval. Traditionally, it is placed in MN 9 (earliest Late Miocene), but as no *Hipparion* s.l. was found in the locality, there is no direct evidence for this designation. In the NAFB, the period is marked by the end of the molasse sedimentation (Frisch *et al.*, 1999), the uplift of the southern part of the Bohemian massive (Ziegler and Dèzes, 2007), the uplift of the eastern Alps (Kuhleman, 2007) and change in the fluvial direction in the basin from originally east-west to west-east. Hammerschmiede sediments (Fig. 1, 6 km NNW of Kaufbeuren, Germany, see Mayr and Fahlbusch (1975) for details) derive from the youngest deposits of the Upper Freshwater Molasse (UFM) of the NAFB. These deposits are referred to as the Obere Serie (Doppler, 1989; Doppler *et al.*, 2005), which is biostratigraphically defined by the presence of the large-sized *Deinotherium giganteum* Kaup, 1829 (Dehm, 1955). The UFM deposits of Hammerschmiede are known for their rich fossil content, dominated by small mammals, ectothermic tetrapods and fishes (fossil layer 1, Mayr and Fahlbusch, 1975; Fahlbusch and Mayr, 1975; Prieto and Rummel, 2009b). The layer of Hammerschmiede 3 corresponds to an erosional channel rich in lignitic pebbles near the top of the sequence.

In the absence of a link with the entrance of the hipparionine horses, mammal palaeontologists had to come up with another marker for MN 9 (Mammal Neogene, De Bruijn *et al.*, 1992; Mein, 1999), the first mammal unit of the Late Miocene. The presence of the highly specialized cricetid rodent *Microtocricetus*

molassicus Fahlbusch and Mayr, 1975 in Hammerschmiede (Fahlbusch and Mayr, 1975; Mayr and Fahlbusch, 1975) is the usual argument to place the locality in MN 9 as the species is traditionally considered as to be typical for this faunal unit in Central and Eastern Europe (De Bruijn *et al.*, 1992: 70; Mein, 1999).

The discovery of *Galerix* molars in Hammerschmiede 3 is remarkable. The genus was believed to have become extirpated in the region halfway the Middle Miocene (Ziegler, 2006a), while surviving up to the Late Miocene in Spain (Van den Hoek Ostende, 2001; Van den Hoek Ostende and Furió, 2005). Given the good record of the latter part of the Middle Miocene in Germany, we have to assume that *Galerix* re-migrated into the region. In this paper we explore the stratigraphical and environmental conclusions that can be drawn from this unexpected re-occurrence of the gymnure.

Material and methods

The descriptive terminology for Erinaceidae molars follows Engesser (1980). The orientation of the elements for measuring is after Prieto *et al.* (2010a).

The systematics of the Galericinae follows Van den Hoek Ostende (2001) and Doukas and Van den Hoek Ostende (2006), except that *Tetracus* is considered a separate genus (Hugueney and Adrover, 2003; Van den Hoek Ostende, 2003). All teeth sizes are given in mm and all figured teeth are shown in left orientation. The

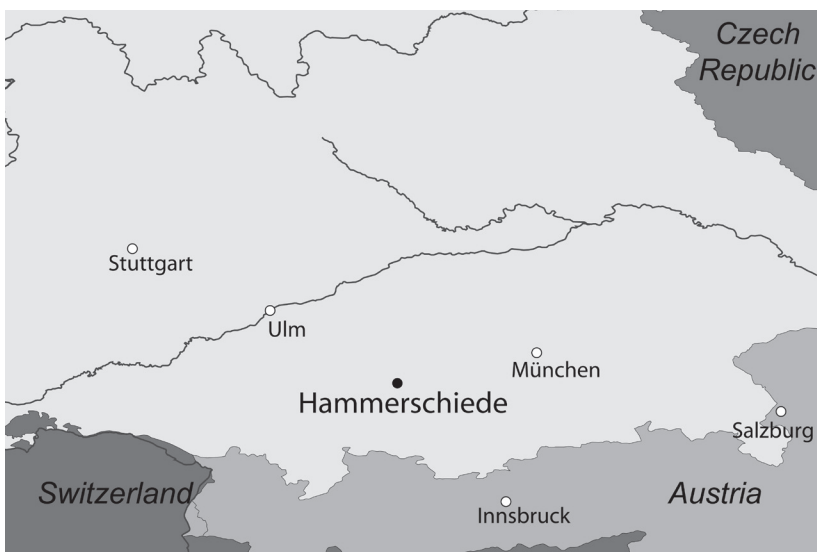


Fig. 1. Geographical map of southern Germany demonstrating the position of the studied locality.

material comprises of 50 isolated teeth (2 D3, 3 P3, 5 P4, 7 M1, 10 M2, 3 M3, 2 p2, 1 p3, 3 p4, 8 m1 (all damaged or corroded), 3 m2, 3 m3) and is stored in the Bayerische Staatssammlung für Paläontologie und Geologie in Munich (BSPG) under the reference numbers 1980 XXVIII 59 to 108.

The separation of the mammal ‘zones’ MN 7 and MN 8 follows the concept of Kálin *et al.* (2001).

Results

A short overview of the Galericini of Central and Western Europe

Before discussing the *Galerix* fossils from Hammer-smiede and their biogeographical and stratigraphical consequences, we first present the current state of knowledge of the Galericini record in Central Europe and Spain. Before we can go into that, however, we need to note that there still is an important taxonomic problem that needs to be resolved.

Taxonomic comments on the genera Parasorex and Schizogalerix

The evolutionary history of *Schizogalerix*, as well as the systematic attribution of the oldest species either to *Schizogalerix*, *Parasorex* or *Galerix*, are still under debate (Van den Hoek Ostende, 2001; Ziegler, 2003, 2005; Doukas and Van den Hoek Ostende, 2006). In contemporary taxonomic interpretations, *Schizogalerix* is not recorded in the late Middle/earliest Late Miocene (MN 7/8, MN 9) deposits from Western Europe (Spain, France). It is, however, important to note that the Spanish *Parasorex* material shares some similarities with *Schizogalerix*, as recorded in Central Europe (Engesser, 1980; Kálin and Engesser, 2001), especially the configuration of the mesostyle of the M1 and M2 (cf. De Jong, 1988: pl. 1, figs 4, 6; Engesser, 1980: fig. 4b). This suggests possible differences in the taxonomical interpretation between western European and central/eastern European scholars, at least concerning the species *Parasorex socialis* and *S. voesendorfenensis*. In the following, if not specified, *P. socialis* will be understood as proposed in Van den Hoek Ostende (2001).

We include the specimens from Jamm (Austria), originally described as *Galerix exilis* (Thenius, 1949) and later interpreted as *Parasorex socialis* (Ziegler and Daxner-Höck, 2005; Ziegler, 2006a), into *Schizo-*

galerix, based on the strong posterior cingulum that directly joins the entoconid on the m1 and m2, and the morphology of the mesostyle. Rzebik-Kowalska and Lungu (2009) record the presence of *Parasorex socialis* in the Moldavian MN 10 locality of Kejnár. No M1 or M2 was found, so the identification was based on the absence of a connection between the posterior cingulum and the entoconid on m1 and m2. However, their illustrations (o.c., figs 4e-f) show that this connection was indeed present, thus refuting the identification as *P. socialis*. The Kejnár assemblage is very interesting, as its galericine is more primitive than the *Schizogalerix* of Buzor 1, a locality that the authors correlate to MN 9.

Although *Parasorex socialis* is reported in literature from the upper part of the Middle Miocene in Romania (Feru *et al.*, 1979, 1980) and Serbia (Markovic, 2003), the specimens are not described in detail, so their identity cannot be checked. Thus, the presence of *P. socialis* east from the NAFB has not been convincingly demonstrated.

Regardless of the generic attribution of the Spanish *Parasorex* material, the immigration of *Schizogalerix* into the NAFB must have come from the eastern part of Europe/Anatolia, as is evident from the good fossil record in the larger part of Middle Miocene from the Turkey (Engesser, 1980; Selänne, 2003). In the Middle Miocene, *Schizogalerix anatolica* is known from Mátraszölös (Hungary, Gál *et al.*, 1999). Some specimens are also recorded in the Middle Miocene from Greece (Doukas, 2005), MN 9 from Slovakia (Sabol *et al.*, 2004, and see references in Fejfar and Sabol, 2005), and MN 9 from Moldova (Rzebik-Kowalska and Lungu, 2009). The genus is also present in the early Sarmatian of Rumania in Tășad (Mészáros, written communication in Hír *et al.*, 2001).

Galerix, Parasorex and Schizogalerix: current state of knowledge in Germany

The first representatives of Galericini are recorded in Germany in the MN 3 fissure fillings of the Swabian and Franconian Alb and in Frankfurt/Nordbasin (Ziegler *et al.*, 2005). Most of this material is identified as *Galerix aurelianensis*, but some smaller specimens have been questionably attributed to *G. symeonidisi*. In MN 4 fissure fillings, *G. aurelianensis* certainly coexists with *G. symeonidisi*, whereas in contemporaneous stratified localities of the NAFB only the latter species is found (e.g., locality Raucheröd, Ziegler and Fahlbusch, 1986). In MN 5 localities, all from fluviatil

deposits, one Galericipini species is recorded, which is incorporated by Ziegler and Fahlbusch (1986) into the *G. symeonidisi*-*G. exilis* lineage. Van den Hoek Ostende and Doukas (2003) do not recognize this lineage in Spain and proposed that *G. exilis* gradually replaced the *G. symeonidisi* (comments in Ziegler, 2005: 138). Scarce evidence of *G. aurelianensis*-like forms is recorded from the late Karpatian of Sandelzhausen (Ziegler, 2000) and possibly Maßendorf (*Galerix* sp. in Schötz, 1988). In MN 6 localities (stratified and fissures; e.g. locality Goldberg, Ziegler 1983) *G. exilis* is mostly the only Galericipini. A larger *Galerix* species was recently described in the fissure filling Petersbuch 68 (probably latest MN 6, Prieto and Rummel, 2009a).

Parasorex socialis is recorded from both fissure fillings (Ziegler, 2005) and stratified localities in MN 7 and 8, such as Steinheim, Anwil, Kleineisenbach and Giggenhausen (Engesser, 1972; Prieto, 2007).

At the base of the MN 9, *Schizogalerix voesendorffensis* (Rabeder, 1973) co-occurs with *Schizogalerix* sp. in the Swiss locality Nebelbergweg (Kälin and Engesser, 2001). Ziegler et al. (2005) and Ziegler (2006a) listed *P. socialis* in the MN 9 faunas from Aumeister and Grosslappen near Munich. Much of the original material from these localities, published by Stromer (1940), was lost during the World War II. On the basis of the remaining fossils stored in the BSPG, we find no evidence for the presence of *P. socialis* in MN 9 localities. The material from Grosslappen is too poorly

preserved (BSPG 1927 VIII 20, 1933 IV 44) to be confidently identified. According to us, the well-preserved mandible from Aumeister belongs to the genus *Schizogalerix*, as is indicated by the strong posterior cingulum that directly joins the entoconid on the m1 and m2. The sizes of the teeth (p3: L: 1.86 × W: 0.98; p4: L: 2.03 × W: 1.55; m1: L: 3.00 × W1: 1.79 × W2: 2.01; m2: L: 2.30 × W1: 1.79 × W2: 1.84) agree with those of *Schizogalerix* sp. from Nebelbergweg (Kälin and Engesser, 2001).

Galerix exilis and *Parasorex socialis* in Spain

The first occurrence of *Parasorex socialis* in Spain is in the Vallès-Penedès Basin in San Quirze, a locality that is correlated to the *Megacricetodon ibericus* - *Democricetodon crusafonti* Zone (corresponding to the MN 8 sensu Mein and Ginsburg 2002, Casanovas-Vilar et al., 2008a). This zone extends from 11.9-11.5 to 10.9 Ma (Casanovas-Vilar et al., 2008b) and may correspond to the upper part of the zone G3 of the Calatayud-Daroca and Teruel Basins (Casanovas-Vilar, 2007). *Galerix exilis* is not recorded in the Vallès-Penedès. *Parasorex socialis* is also documented in the Teruel basin with its first occurrence in Nombrevilla 2 (11.5 Ma in Daams et al., 1999; 11.69 Ma in Van Dam et al., 2006).

The presence of *Galerix exilis* in the Daroca-Calatayud area of the Teruel Basin was noted by De Jong (1988), who described material from the late

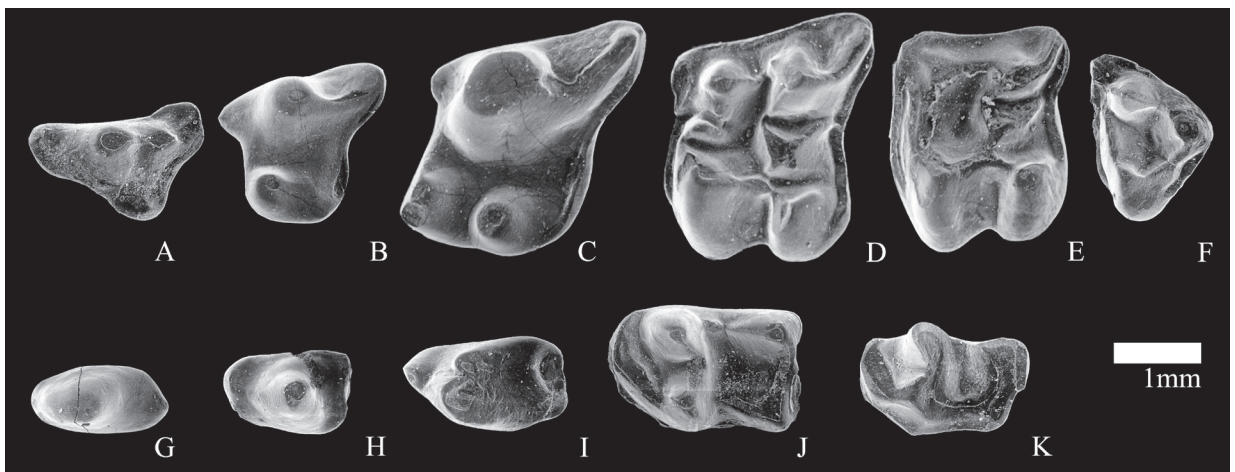


Fig. 2. *Galerix* cf. *exilis* (de Blainville, 1839) from Hammerschmiede 3. A: right D3 (inversed, BSPG 1980 XXVIII 59); B: right P3 (inversed, BSPG 1980 XXVIII 60); C: right P4 (inversed, BSPG 1980 XXVIII 61); D: left M1 (BSPG 1980 XXVIII 61); E: right M2 (inversed, BSPG 1980 XXVIII 63); F: right M3 (inversed, BSPG 1980 XXVIII 64); G: left p2 (BSPG 1980 XXVIII 65); H: left p3 (BSPG 1980 XXVIII 66); I: left p4 (BSPG 1980 XXVIII 67); J: left m2 (BSPG 1980 XXVIII 68); K: right m3 (inversed, BSPG 1980 XXVIII 69).

Middle Miocene. The species was present earlier, and, according to Van den Hoek Ostende and Doukas (2003), gradually replaced *G. symeonidisi*. The older material of *G. exilis* has not yet been described in detail, and the entire sequence is currently under study. According to Van den Hoek Ostende and Doukas (2003: Figs 1-2), the species is certainly present from zone D upwards (MN 5). The last occurrence of *G. exilis* depends on the dating of Carrilanga 1 (10.5 Ma according to Daams *et al.*, 1999, 11.57 Ma according to Van Dam *et al.*, 2006). As the biostratigraphic correlation of Carrilanga proves to be so difficult we place the last occurrence of *G. exilis* in Spain at 11.5 Ma, based on its occurrence in Nombrevilla 2, pending ongoing research of the Museo Nacional de Ciencias Naturales (Madrid) on the Aragonian/Vallesian sections in the area.

The Hammerschmiede galericine

Figure 2 shows a selection of the molars from the Hammerschmiede gymnure. The upper molars, which are clearly wider than long and possess a distinct, crescent-shaped metaconule, identify the Hammerschmiede gymnure as a member of the Galericipini. Because most of the M1 (five out of eight) and M2 (one out of two) have a short posterior arm of the metaconule, the P3 have one lingual cusp, and there is no division of the mesostyle in the M1 and M2, the material must be attributed to *Galerix* (Van den Hoek Ostende, 2001).

Since a substantial fraction of the molars are worn in our sample, the relative abundance of specimens having a protocone-metaconule connection on M1/M2 is difficult to establish. Most of the specimens do not have this ridge complete, but it is often incipiently present. On one considerably damaged M2, the protocone-metaconule connection is present and the hypocone is isolated. The connection of the posterior arm of the metaconule with the posterior cingulum, if present, is weak. The metaconid of the single unworn p4 is about half the height of the protoconid. On the two other specimens, the metaconid seems to be relatively high due to the abrasion of the teeth. The cuspids are worn on their posterior side.

One M1 from Hammerschmiede (Fig. 2D) has a curved anterior arm of the protocone, so that the anterior part of the molar seems to be compressed in comparison with the other specimens. Given the limited number of molars, this tooth is here interpreted as an aberrant specimen.

Compared to *Galerix exilis* from older localities in southern Germany (Ziegler, 1983), and from the type locality Sansan (Engesser, 2009), the Hammerschmiede 3 assemblage differs in having a long posterior arm of the metaconule on several M1 and M2 (three out of eight M1, one out of two M2). It also differs in the morphology of the P3, as the three preserved premolars from Hammerschmiede 3 have a better-developed lingual part of the tooth. Furthermore, the parastyle and the posterior arm of the para-

Table 1. Measurements of *Galerix* cf. *exilis* from Hammerschmiede 3.

	L or L1	L2	W or W1	W2
D3	2.06		1.09	
D3	2.01		1.23	
P3	1.98		1.74	1.66
P3	1.76		1.54	1.64
P4	2.40		2.33	2.74
P4	2.38		2.30	2.40
P4	2.61		2.48	2.63
P4	2.19		2.38	2.45
M1	2.70		2.80	3.05
M1	2.35		2.53	2.81
M1	2.51		2.68	3.05
M1	2.54		2.80	3.18
M1	2.63		2.73	3.16
M1	2.41		2.65	3.00
M1	2.66		2.95	3.18
M1	2.48		2.73	3.09
M2	2.01		2.64	2.53
M2	2.06		2.78	2.48
M3	1.65	1.39	2.06	
M3	1.38	1.15	1.84	
M3	1.51	1.39	1.94	
p2	1.45		0.73	
p2	1.68		0.85	
p3	1.61		1.08	
p4	2.05		1.21	
p4	2.08		1.18	
m2	2.31		1.40	1.45
m2	2.39		1.63	1.54
m2	2.35		1.68	1.63
m3	1.90		1.20	
m3	1.80		1.30	

cone are smaller on P3 and P4. The p2 and p3 are about the same length as the teeth from Goldberg and Steinberg, but are somewhat wider. The specimens from Hammerschmiede agree in overall size and morphology with *G. exilis* from Solera, a locality representing the latest Middle Miocene in east Central Spain (De Jong, 1988), and are thus assigned to *G. cf. exilis*. The measurements for the Hammerschmiede *Galerix* are given in Table 1.

Discussion

Implication for the Middle/Upper Miocene biostratigraphy in the NAFB

The first occurrence of hipparionine horses in Europe defines the beginning of MN 9 (*e.g.*, Mein, 1999). In the Vallès-Penedès Basin (Catalonia, Spain) the oldest occurrence of Hipparionine horses is in the locality of Creu Conill 22 in the Can Guitar 1 section, and is correlated to the base of the chron C5r.1n, about 11.1 Ma (Garcés *et al.*, 1996, 2003; Casanovas-Vilar *et al.*, 2006). This is somewhat older than the estimate for the first occurrence of hipparionine horses in the Daroca-Calatayud area in Central Spain (10.7–10.8 Ma in Garcés *et al.*, 2003) and slightly younger than the estimated age of this event in Austria (11.2 Ma in Daxner-Höck, 1996; Rögl and Daxner-Höck, 1996). In the NAFB *Hippotherium primigenium* is rare, reported only from the large mammals localities Charmoille (Kälin, 1993), Lugnez (Erzinger, 1943), Hausruck (Thenius, 1952) and Höwenegg (*e.g.*, Tobien, 1938, 1982). The latter fossil locality is dated 10.3 Ma (Steinger *et al.*, 1996: 14) to 10.8 ± 0.4 Ma (Baranyi *et al.*, 1976; Becker-Platen *et al.*, 1977).

Thus, the presence of *Galerix cf. exilis* challenges the validity of the earliest Late Miocene correlation of Hammerschmiede 3. We propose that *Galerix* must have entered the NAFB before its extinction in Spain, *i.e.*, before or at least at 11.5 Ma (the age of Nombrevilla 2). The alternative scenario, in which *Galerix* survived in France in between its extirpation in Spain and entrance into the NAFB is deemed highly unlikely, but cannot be precluded given the current knowledge of the French fossil record.

Following this interpretation, there is no strong argumentation against Hammerschmiede being older than the first appearance of *Hippotherium* in the NAFB. However, this inference challenges the biostratigraphic value of *Microtocricetus* and the relative

dating of some fossil faunas (see complementary discussion in Prieto *et al.*, 2010b).

Correlating Hammerschmiede to the late Middle Miocene may also have consequences for the correlation of other localities in the NAFB. Based on the evolutionary stage of the cricetid rodent *Collimys*, Prieto and Rummel (2009b) proposed that Hammerschmiede is older than the Swiss locality of Nebelbergweg, which has also been considered an MN 9 locality (Kälin and Engesser 2001). This correlation is mainly based on the presence of *Schizogalerix voesendorfensis* in the Swiss locality, because until now the oldest occurrence of *Schizogalerix voesendorfensis* in Austria was in its type locality (Vösendorf/Inzersdorf), dated between 10.3 and 10.6 Ma (Daxner-Höck, 2004; Ziegler and Daxner-Höck, 2005). Recent discoveries, however, indicate that this species is already present in the late Sarmatian s. str. (late Middle Miocene) of the Styrian Basin (around 12.2 Ma, Prieto *et al.*, 2010a). Thus, the locality of Nebelbergweg cannot unambiguously be correlated to the early Late Miocene. Similarly, the German locality Aumeister cannot be confidently correlated based on *Schizogalerix*. However, a single *Collimys* m1 was found in Aumeister (Fig. 3). This tooth agrees morphologically with *C. longidens* from Nebelbergweg and its size (1.86 × 1.21) is intermediate between *C. hiri* from Hammerschmiede and *C. longidens*. This suggests that the locality Aumeister is probably slightly younger than Hammerschmiede. Excluding ecological and/or taphonomical bias, it could signify that between the last occurrence of *Parasorex socialis* (MN

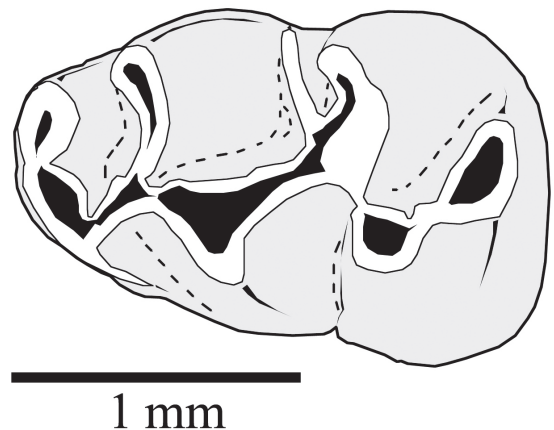


Fig. 3. *Collimys cf. longidens* Kälin and Engesser, 2001 from Aumeister. Left m1 (BSPG 1926 V 21).

8; Engesser, 1972; Kälin, 1993; Prieto, 2007) and the first appearance of *Schizogalerix* in Nebelbergweg, the faunas of the NAFB could have been characterized by *Galerix cf. exilis*.

Ecological implications

Assuming that the ecology of the fossil galericines was similar to that of the extant representatives of this subfamily as found in Southeast Asia, they should have been adapted to forest environments close to water (Ziegler, 2005, 2006b). This certainly seems to be true for *Lantanotherium*, the only member of the subfamily in the European Miocene that is not included in the tribe Galericini (Furió *et al.*, 2011). *Lantanotherium* often co-occurs with the presumably water-adapted Dimylidae (*Plesiodimylus*), *e.g.* in the German locality of Hambach 6C (Ziegler and Mörs, 2000; mean annual precipitation (MAP) > 1100 mm, M. Böhme unpublished data estimated after the method of Böhme *et al.*, 2006) and of Maßendorf (Schötz, 1988; mean MAP: 887mm, M. Böhme unpublished data), in Devínska Nová Ves – Bonanza (Slovakia, Sabol, 2005), in Tobel Hombrechtikon (Switzerland, Bolliger, 1992), in Götzendorf (Austria, Ziegler, 2006b, MAP: 1.303mm (Böhme *et al.*, 2006)) and in Bełchatów B (Poland, Rzebik-Kowalska, 1993, 1996, 2005). Its distribution is mostly restricted to Central Europe. In Spain, the genus is present in the more humid Vallès-Penedès Basin (Casanovas-Vilar and Agusti, 2007; Furió *et al.*, 2011), but absent in the inner basins (Van den Hoek Ostende and Furió, 2005). All indications are that *Lantanotherium* preferred humid environments.

In contrast, the Galericini seemed to have been more generalists (Furió *et al.*, 2011), as is already indicated by their almost ubiquitous presence in Miocene faunas. Based on functional morphological observations and faunal associations, Van den Hoek Ostende (2001) proposed that *Parasorex*, *Schizogalerix* and probably *Galerix symeonidisi* were adapted to a more herbivorous diet than the other members of the tribe. The preferred habitat of the various species of *Galerix* has been debated (Van den Hoek Ostende and Doukas, 2003; Van den Hoek Ostende, 2003; Van den Hoek Ostende and Fejfar, 2006). Certainly, *Galerix exilis* must have been able to cope with dry environments, such as the semiarid climate of the Middle Miocene German localities of Goldberg and Steinberg (Bolten *et al.*, 1976; Ballmann,

1979; Ziegler, 1983) and, *e.g.* Somosaguas Sur in Spain (Luis and Hernando, 2000). It is one of the few insectivores which remains present in the sections of the Aragonian type-area in Spain following a dramatic decrease in humidity near the boundary of local zones C and D at approximately 15.9 Ma (Van der Meulen and Daams, 1992, fig. 7, with age corrected according to Daams *et al.*, 1999).

Based on comparisons of faunal associations of the late Middle Miocene fissure fillings and stratified fossil localities of Germany, Prieto (2007) proposed that *Parasorex socialis* was not necessarily dependent on humid or forest-covered habitat. The occurrence of *P. socialis* in the NAFB in Steinheim, between 14 to 13.5 Ma, is almost contemporaneous with the local disappearance of *Galerix exilis*. This could suggest different ecological preferences for the two genera. Nevertheless, *Galerix* and *Parasorex* can co-occur in a single locality as shown in La Grive (Mein and Ginsburg, 2002; Maridet, 2003), Petersbuch 68 (Prieto and Rummel, 2009a) and Carrilanga (De Jong, 1988).

Notably, the migration of *Parasorex* in the NAFB coincides with a global cooling event around 14 to 13.5 Ma (Shevenell *et al.*, 2004; Böhme, 2003). This climatic deterioration resulted in a stronger latitudinal temperature gradient in Europe and marks the beginning of a more distinct climatic zonation on the continent. The thermophilic ectotherms survived only in southern regions (south of 37° N palaeolatitude, Böhme, 2003). The cooling event has also been observed in the Teruel Basin (Van der Meulen and Daams, 1992: fig. 7, absolute ages corrected according to Daams *et al.*, 1999). As we noted, *Galerix exilis* survived here during the late part of the Middle Miocene. It becomes extinct near the boundary between local zones G3 and H, *i.e.*, the Aragonian/Vallesian boundary. This time frame coincides with a minor cooling, at a time that humidity increases again (Van der Meulen and Daams, 1992). Therefore, we postulate that *Parasorex socialis* (*sensu* Engesser, 1972) was a cooler temperature adapted faunal element, whereas *Galerix exilis* probably preferred higher temperatures.

Consequences for Hammerschmiede

Galerix cf. exilis is a rare element of the fauna from Hammerschmiede 3 and is missing in the two other fossil layers of the locality. Putting aside the possible effects of taphonomic processes, we can hypothesize:

1] that during the sedimentation of the Hammerschmiede section the climate was somewhat warmer

and/or dryer and *Galerix* cf. *exilis* represents a new immigrant, which was not well established in the faunas. This scenario is in conflict with the high precipitation estimates from the herpetological community of Hammerschmiede (Böhme et al., 2006).

2] that the environment of Hammerschmiede 3 was not optimal for the *Galerix* cf. *exilis*, but the (re-) immigration of *Galerix* in the NAFB occurred somewhat earlier during an episode in which the environment differed from that found at Hammerschmiede. Such an episode presented unfavourable conditions for *Parasorex socialis* (sensu Engesser, 1972), which led to its disappearance.

The second hypothesis implies a brief but distinct temperature increase and/or decrease in precipitation between Anwil and Hammerschmiede. Such decrease in precipitation is recorded in the NAFB. Böhme et al. (2008) demonstrate that the mean annual precipitation in the region decreased significantly between 12.7 and 11.5 Ma (Sarmatian). The rare presence of crocodiles in Anwil (Böhme, 2003) shows that there were indeed episodes with increased temperature during the later part of the Middle Miocene.

Conclusion

Galerix cf. *exilis* is a short-duration Spanish (re-) immigrant in the NAFB (transient sensu Van der Meulen et al., 2005) and *Parasorex socialis* a central/eastern European immigrant into Spain. In this hypothesis Hammerschmiede should be older than the last occurrence of *G. exilis* in Spain (11.5 My), and thus should be older than traditionally accepted, probably antedating the Middle to Late Miocene transition. The re-appearance of *Galerix* in the NAFB suggests climatic fluctuations at the end of the Middle Miocene, leading to temporary warmer and/or dryer conditions. At the actual stage of knowledge 1) we conclude that *Schizogalerix* appears in the NAFB following the re-entrance of *G. exilis*, and 2) *Microtocricetus* can no longer be maintained as marker for MN 9.

Although a revision of the genera *Galerix*, *Parasorex* and *Schizogalerix* is necessary at the European scale, the re-appearance of *Galerix* cf. *exilis* in the NAFB is a very promising event in local and large-scaled biostratigraphical terms. Indeed, this migration can be correlated with major climatic global events and thus allows us to follow the consecutive faunal interchanges near the limit Middle to Late Miocene.

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References

- Álvarez Sierra MA, Calvo JP, Morales J, Alonsa-Zarza A, Azanza B, García Paredes I, Hernandez Fernandez M, Meulen AJ van der, Peláez-Campomanes P, Quirralte V, Salesa MJ, Sánchez IMY, Soria D. 2003. El tránsito Aragoniense-Vallesiense en el área de Daroca-Nombrevilla (Zaragoza, España). Pp. 171-178 in: López-Martínez N, Peláez-Campomanes P, Hernández Fernández M, eds, En torno a fósiles de mamíferos: datación, evolución y paleoambiente. *Coloquios de Paleontología, Volumen Extraordinario 1*.
- Ballmann P. 1979. Fossile Glareolidae aus dem Miozän des Nördlinger Rieses (Aves: Charadriiformes). *Bonner Zoologische Beiträge* 30: 52-102.
- Baranyi I, Lippolt HJ, Todt W. 1976. Kalium-Argon-Alterbestimmungen an tertiären Vulkaniten des Oberrheingraben-Gebietes: II. Die Altertraverse vom Hegau nach Lothringen. *Oberrhein geologische Abhandlungen* 25: 41-62.
- Becker-Platen JD, Benda L, Steffens P. 1977. Litho- und biostratigraphische Deutung radiometrischer Altersbestimmungen aus dem Jungtertiär der Türkei. *Geologische Jahrbuch Reihe B* 25: 139-167.
- Böhme M. 2003. Miocene Climatic Optimum: evidence from Lower Vertebrates of Central Europe. *Palaeogeography, Palaeoclimatology, Palaeoecology* 195: 389-401.
- Böhme M, Ilg A, Ossig A, Küchenhoff H. 2006. New method to estimate paleoprecipitation using fossil amphibians and reptiles and the middle and late Miocene amphibians and reptiles and the middle and late Miocene. *Geology* 34: 425-428.
- Böhme M, Ilg A, Winkelhofer M. 2008. Late Miocene 'wash-house' climate in Europe. *Earth and Planetary Science Letters* 275: 393-401. doi: 10.1016/j.epsl.2008.09.011
- Bolliger T. 1992. Kleinsäugerstratigraphie in der miozänen Hörschüttung (Ostschweiz). *Documenta Naturae* 75: 1-296.
- Bolten R, Gall H, Jung W. 1976. Die obermiozäne (sarmatische) Fossil-Lagerstätte Wendung im Nördlinger Ries (Bayern). Ein Beitrag zur Charakterisierung des Riessee-Biotop. *Geologische Blätter für Nordost-Bayern* 26: 75-94.
- Casanovas-Vilar I. 2007. The rodent assemblages from the Late Aragonian and the Vallesian (Middle to Late Miocene) of the Vallès-Penedès Basin (Catalonia, Spain). PhD thesis, Universitat Autònoma de Barcelona.

- Casanovas-Vilar I, Furió M, Agustí J. 2006. Rodents, Insectivores and paleoenvironment Associated to the First-Appearing Hipparione Horses in the Vallès-Penedès Basin (North-eastern Spain). *Beiträge zur Paläontologie* 30: 89-107.
- Casanovas-Vilar I, Agustí G. 2007. Ecogeographical stability and climate forcing in the Late Miocene (Vallesian) rodent record in Spain. *Paleogeography, Paleoclimatology, Paleogeology* 248: 169-189.
- Casanovas-Vilar I, Alba DM, Moyà-Sola S, Galindo J, Cabrera L, Garcés M, Furió M, Robles JM, Köhler M, Angelone M. 2008a. Biochronological, taphonomical and paleoenvironmental background of the fossil great ape *Pierolapithecus catalaunicus* (Primates, Homiidae). *Journal of Human Evolution* 55: 589-603.
- Casanovas-Vilar I, Garcés M, Galindo J, Cabrera L, Robles JM, Alba DM, Moyà-Sola S, Galindo J, Rotgers C, Carmora R, Almécija S, Bertó Mengual JV, Beamud E. 2008b. Chronology of the recently discovered Middle Miocene primate-bearing sites of the Vallès-Penedès Basin (Catalonia, Spain). Abstracts Workshop European fossil primates, Grosseto: 122-123.
- Casanovas-Vilar I, García-Paredes I, Alba DM, van den Hoek Ostende LW, Moyà-Solà S. 2010. The European Far West: Miocene mammal isolation, diversity and turnover in the Iberian peninsula. *Journal of Biogeography* 37: 1079-1093.
- Daams R, Meulen AJ van der, Álvarez Sierra MA, Peláez-Campomanes P, Calvo JP, Alonzo Zarza MA, Krijgsman W. 1999. Stratigraphy and sedimentology of the Aragonian (Early to Middle Miocene) in its type area North-Central Spain). *Newsletters on Stratigraphy* 37: 103-139.
- Daxner-Höck G. 1996. Faunenwandel im Obermiozän und Korrelation der MN-'Zonen' mit den Biozonen des Pannons der Zentralen Paratethys. *Beiträge zur Paläontologie* 21: 1-9.
- Daxner-Höck G. 2004. Flying Squirrels (Pteromyiinae, Mammalia) from the Upper Miocene of Austria. *Annalen des Naturhistorischen Museums in Wien* 106 A: 387-423.
- De Bruijn H, Daams R, Daxner-Höck G, Fahlbusch V, Ginsburg L, Mein P, Morales J. 1992. Report on the RCMNS working group on fossil mammals, Reischensburg 1990. *Newsletter on Stratigraphy* 26: 65-118.
- De Jong F. 1988. Insectivora from the Upper Aragonian and Lower Vallesian of the Daroca-Villafeliche area in the Calatayud-Teruel Basin (Spain). *Scripta Geologica, Special Issue* 1: 253-285.
- Dehm R. 1955. Die Säugetier-Faunen in der Oberen Süßwassermolasse und ihre Bedeutung für die Gliederung. Pp. 81-88 in: *Bayerisches Geologisches Landesamt, ed., Erläuterungen zur Geologischen Übersichtskarte der Süddeutschen Molasse*. München: Bayerisches Geologisches Landesamt.
- Doppler G. 1989. Zur Stratigraphie der nördlichen Vorlandmolasse in Bayerisch-Schwaben. *Geologica Bavarica* 94: 83-113.
- Doppler G, Heissig K, Reichenbacher B. 2005. Zur Gliederung des Tertiärs im süddeutschen Molassebecken. *Newsletters on Stratigraphy* 41: 359-375.
- Doukas CS. 2005. Greece. Pp. 99-112 in: van den Hoek Ostende LW, Doukas CS, Reumer JWF, eds, The Fossil Record of the Eurasian Neogene Insectivores (Erinaceomorpha, Soricomorpha, Mammalia), Part I. *Scripta Geologica, Special Issue* 5.
- Doukas CS, van den Hoek Ostende LW. 2006. Insectivores (Ericeomorpha, Soricomorpha; Mammalia) from Karydia and Komotini (Thrace, Greece; MN 4/5). *Beiträge zur Paläontologie* 30: 109-131.
- Engesser B. 1972. Die obermiozäne Säugertierfauna von Anwil (Baselland). *Tätigkeitsberichte der Naturforschenden Gesellschaft Basel* 28: 37-363.
- Engesser B. 1980. Insectivora and Chiroptera (Mammalia) aus dem Neogen der Türkei. *Schweizerische Paläontologische Abhandlungen* 102: 45-149.
- Engesser B. 2009. The Insectivores (Mammalia) from Sansan (Middle Miocene, south-western France). *Schweizerische Paläontologische Abhandlungen* 128: 1-91.
- Erzinger E. 1943. Die Oberflächenformen der Ajoie (Berne Jura). *Mitteilungen Geographisch Ethnologischen Gesellschaft Basel* 5: 1-138.
- Fahlbusch V, Mayr H. 1975. Microtoide Cricetiden (Mammalia, Rodentia) aus der Oberen Süßwasser-Molasse Bayerns. *Paläontologische Zeitschrift* 49: 78-93.
- Fejfar O, Sabol M. 2005. Czech Republic and Slovak Republic. Pp. 51-60 in: Van den Hoek Ostende LW, Doukas CS, Reumer JWF, eds, The Fossil Record of the Eurasian Neogene Insectivores (Erinaceomorpha, Soricomorpha, Mammalia), Part I. *Scripta Geologica, Special Issue* 5.
- Feru M, Radulesco C, Samson P. 1979. La faune de Micromammifères du Miocène de Tauț (dép. d'Arad). *Travaux de l'Institut de Spéologie 'Emile Racovitza'* XIX: 185-190.
- Feru M, Radulesco C, Samson P. 1980. La faune de Micromammifères du Miocène de Comănești (dép. d'Arad). *Travaux de l'Institut de Spéologie 'Emile Racovitza'* XIX: 171-190.
- Frisch W, Brügel AJ, Dunkl I, Kuhlemann J, Satir M. 1999. Post-collisional large-scale extension and mountain uplift in the Eastern Alps. *Memorie di Scienze Geologiche (Padova)* 51: 3-23.
- Furió M, Casanovas-Vilar I, van den Hoek Ostende LW. 2011. Predictable structure of Miocene insectivore (Lipotyphla) faunas in Western Europe along a latitudinal gradient. *Paleogeography, Paleoclimatology, Paleogeology* 304: 219-229. doi: 10.1016/j.palaeo.2010.01.039
- Gál E, Hír J, Kessler E, Kókay J. 1999. Középső-miocén ősmaradványok, a Mátraszőlős, Rákóczi-kápolna alatti útbévágásból. I. A Mátraszölős 1. lelőhely [Middle Miocene fossils from the sections at the Rákóczi chapel at Mátraszölős. Locality Mátraszölős I.] *Folia Historico Naturalia Musei Matraensis* 23: 33-78.
- Garcés M, Agustí J, Cabrera L, Parès JM. 1996. Magnetostratigraphy of the Vallesian (late Miocene) in the Vallès-Penedès Basin (Northeast Spain). *Earth and Planetary science letters* 142: 381-396.
- Garcés M, Krijgsman W, Peláez-Campomanes P, Álvarez Sierra A, Daams R. 2003. Hipparion dispersal in Europe: magnetostratigraphic constraints from the Daroca area (Spain). Pp. 171-178 in: López-Martínez N, Peláez-Campomanes P, Hernández Fernández M, eds, En torno a fósiles de mamíferos: datación, evolución y paleoambiente. *Coloquios de Paleontología, Volumen Extraordinario* 1.
- Hír J, Kókay J, Venczel M. 2001. Middle Miocene molluscs and microvertebrata from Tășad (Bihor County, Romania). *Acta Paleontologica Romaniaae* 3: 161-172.
- Hugueney M, Adrover R. 2003. *Tetracus daamsi*, une nouvelle espèce de Galericiinae (Erinaceidae, Mammalia) dans l'Oligocène de Majorque (Espagne). Pp. 311-324 in: López-Martínez N, Peláez-Campomanes P, Hernández Fernández

- M, eds, En torno a fósiles de mamíferos: datación, evolución y paleoambiente. Coloquios de Paleontología, *Volumen Extraordinario 1*.
- Kälin D. 1993. *Stratigraphie und Säugetierfaunen der oberen Süßwassermolasse der Nordwestschweiz*. Dissertation, Eidgenössischen Technischen Hochschule Zürich.
- Kälin D, Engesser B. 2001. Die jungmiozäne Säugetierfauna vom Nebelbergweg bei Nunningen (Kanton Solothurn, Schweiz). *Schweizerische Paläontologische Abhandlungen* 121: 1-61.
- Kälin D, Weidmann M, Engesser B, Berger JP. 2001. Paléontologie et âge de la Molasse d'eau douce supérieure (OSM) du Jura Neuchâtelois. *Schweizerische Paläontologische Abhandlungen* 121: 63-101.
- Kuhlemann J. 2007. Paleogeographic and paleotopographic of the Swiss and Eastern Alps since the Oligocene. *Global Planetary Change* 58: 224-236.
- Luis A, Hernando JM. 2000. Los microvertebrados del Miocene Medio de Somosaguas Sur (Pozuel de Alarcón, Madrid, Spain). *Colloquios de Paleontología* 51: 87-136.
- Maridet O. 2003. *Révision du genre Democricetodon (Mammalia, Rodentia, Cricetinae) et dynamique des faunes de rongeurs du Néogène d'Europe occidentale: évolution, paléodiversité et paléogéographie*. PhD Thesis, l'Université Claude-Bernard Lyon 1.
- Markovic Z. 2003. The Miocene small mammals of Serbia, a review. Pp. 287-303 in: Reumer JWF, Wessels W, eds, Distribution and migration of Tertiary mammals in Eurasia. A volume in honour of Hans de Bruijn. *Deinsea* 10.
- Mayr H, Fahlbusch V. 1975. Eine unterpliozäne Kleinsäugerfauna aus der Oberen Süßwasser-Molasse Bayerns. *Mitteilungen der Bayerischen Staatssammlung für Paläontologie und historische Geologie* 15: 91-111.
- Mein P. 1999. European Miocene Mammal Biochronology. Pp. 25-38 in: Rössner G, Heissig K, eds, *The Miocene Land Mammals of Europe*. Munich: Dr. Friedrich Pfeil.
- Mein P, Ginsburg L. 2002. Sur l'âge relatif des différents dépôts karstiques miocènes de la Grive-Saint-Alban (Isère). *Cahiers scientifiques Muséum d'Histoire naturelle Lyon* 2: 7-47.
- Prieto J. 2007. *Kleinsäuger-Biostratigraphie und Paläoökologie des höheren Mittelmiozäns (MN 8) Bayerns: Spaltenfüllungen der Fränkischen Alb und Lokalitäten der Oberen Süßwassermolasse im Vergleich*. PhD thesis, LMU München.
- Prieto J, Rummel M. 2009a. Erinaceidae (Mammalia, Erinaceomorpha) from the Middle Miocene fissure filling Petersbuch 68 (South Germany). *Zitteliana* 48/49: 103-111.
- Prieto J, Rummel M. 2009b. Evolution of the genus *Collimys* Daxner-Höck, 1972. (Rodentia, Cricetidae). A key to Middle to Late Miocene biostratigraphy in Central Europe. *Neues Jahrbuch für Geologie und Paläontologie* 252: 237-247.
- Prieto J, Gross M, Böhmer C, Böhme M. 2010a. Insectivores and bat (Mammalia) from the late Middle Miocene of Gratkorn (Austria): biostratigraphic and ecologic implications. *Neues Jahrbuch für Geologie und Paläontologie* 258: 107-119.
- Prieto J, Böhme M, Gross M. 2010b. The cricetid rodents from Gratkorn (Austria, Styria) – A benchmark locality for the continental Sarmatian s.str. (late Middle Miocene) in the central Paratethys. *Geologica Carpathica* 61: 419-436.
- Rabeder R. 1973. *Galerix* und *Lantanoherium* (Erinaceidae, Insectivora) aus dem Pannon des Wiener Beckens. *Neues Jahrbuch für Geologie und Paläontologie Monatshefte* 7: 429-446.
- Rögl F, Daxner-Höck G. 1996. Late Miocene Paratethys correlations. Pp 47-55 in: Bernor RL, Fahlbusch V, Mittmann W, eds, *The Evolution of Western Eurasian Neogene Mammal Faunas*. Columbia Press 16.
- Rzebik-Kowalska B. 1993. Insectivora (Mammalia) from the Miocene of Bełchatów, Poland. I. Metacodontidae: *Plesioorex* Pomel, 1854. *Acta Zoologica Cracoviensia* 36: 267-274.
- Rzebik-Kowalska B. 1996. Insectivora (Mammalia) from the Miocene of Bełchatów, Poland. III. Dimylidae Schlosser, 1887. *Acta Zoologica Cracoviensia* 39: 447-468.
- Rzebik-Kowalska B. 2005. Erinaceomorpha and Soricomorpha (Mammalia) from the Miocene of Bełchatów, Poland. IV. Erinaceidae Fischer von Waldheim, 1817 and Talpidae Fischer von Waldheim, 1817. *Acta Zoologica Cracoviensia* A 48: 71-91.
- Rzebik-Kowalska B, Lungu A. 2009. Insectivore mammals from the Late Miocene of the Republic of Moldova. *Acta Zoologica Cracoviensia* 52 A: 11-60.
- Sabol M. 2005. Middle Miocene assemblage of insectivores from Bonanza site near Devínska Nová Ves (Slovakia). *Geologica Carpathica* 56: 433-445.
- Sabol M, Joniak P, Holec P. 2004. Succession(-s) of mammalian assemblages during the Neogene – a case study from the Slovak part of the Western Carpathians. *Scripta Facultatis Scientiarum Naturalis Universitatis Masaryk, Brunensis* 31-32: 65-84.
- Schötz M. 1988. Die Erinaceiden (Mammalia, Insectivora) aus Niederaichbach und Maßendorf (Obere Süßwassermolasse Niederbayerns). *Mitteilungen der bayerischen Staatssammlung für Paläontologie und historische Geologie* 28: 65-87.
- Selänne L. 2003. Genus *Schizogalerix* (Insectivora). Pp. 69-89 in: Fortelius M, Kappelman J, Sen S, Bernor RL, eds, *Geology and Paleontology of the Miocene Sinap Formation, Turkey*. New York: Columbia University Press.
- Shevenell AE, Kennet JP, Lea DW. 2004. Middle Miocene Southern Ocean Cooling and Antarctic Cryosphere Expansion. *Science* 305: 1766-1770.
- Steininger FF, Bergreen WB, Kent DV, Bernor RL, Sen S, Agustí J. 1996. Circum Mediterranean Neogene (Miocene and Pliocene) marine continental chronologic correlations of European mammal units and zones. Pp 7-46 in: Bernor RL, Fahlbusch V, Rietschel S, eds, *Later Neogene European Biotic Evolution and Stratigraphic Correlation*. Columbia University press.
- Stromer E. 1940. Die jungtertiäre Fauna des Flinkzes und des Schweiß-Sandes von München. *Abhandlungen der Bayerischen Akademie der Wissenschaften, mathematisch-naturwissenschaftliche Abteilung, Neue Folge* 48: 1-102.
- Thenius E. 1949. Zur Revision der Insektivoren des steirischen Tertiärs. *Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften in Wien* 158: 671-693.
- Thenius E. 1952. Die Säugetierreste aus dem Jungtertiär des Hausruck und Kobernauberwaldes (O.Österr.) und die Altersstellung der Fundschichten. *Jahrbuch der Geologischen Bundesanstalt Wien* 95: 119-144.
- Tobien H. 1938. Über *Hipparion*-Reste aus der obermiozänen Süßwassermolasse Südwestdeutschlands. *Zeitschrift der Deutschen Gesellschaft für Geowissenschaften* 90: 177-192.

- Tobien H. 1982. Osteologische Bemerkungen zum Fußbau von *Hipparion* (Equidae, mammalia) aus der jungtertiären Wirbeltier-Fundstätte Höwenegg/Hegau (Baden-Württemberg, BRD). *Zeitschrift für geologische Wissenschaften* 10: 1043-1057.
- Van Dam JA, Abdul Aziz H, Álvarez Sierra MÁ, Hilgen FJ, van den Hoek Ostende LW, Lourens LJ, Mein P, Meulen AJ van der, Peláez-Campomanes P. 2006. Long-period astronomical forcing of mammal turnover. *Nature* 443: 687-691.
- Van den Hoek Ostende LW. 2001. A revised generic classification of the Galericipini (Insectivora, Mammalia) with some remarks on their palaeogeography and phylogeny. *Geobios* 34: 681-695.
- Van den Hoek Ostende LW. 2003. Insectivores (Erinaceomorpha, Soricomorpha, Mammalia) from the Ramblian of the Daroca-Calamocha area. Pp. 281-310 in: López-Martínez N, Peláez-Campomanes P, Hernández Fernández M, eds, En torno a fósiles de mamíferos: datación, evolución y paleoambiente. *Coloquios de Paleontología, Volumen Extraordinario* 1.
- Van den Hoek Ostende LW, Doukas CS. 2003. Distribution and evolutionary history of the Early Miocene erinaceid *Galerix symeonidisi* Doukas, 1986. Pp. 287-303 in: Reumer JWF, Wessels W, eds, Distribution and Migration of the tertiary mammals in Eurasia. A volume in honour of Hans de Bruijn. *Deinsea* 10.
- Van den Hoek Ostende LW, Furió M. 2005. Spain. Pp. 149-284 in: Van den Hoek Ostende LW, Doukas CS, Reumer JWF, eds, The Fossil Record of the Eurasian Neogene Insectivores (Erinaceomorpha, Soricomorpha, Mammalia), Part I. *Scripta Geologica, Special Issue* 5.
- Van den Hoek Ostende LW, Fejfar O. 2006. Erinaceidae and Talpidae (Erinaceomorpha, Soricomorpha, Mammalia) from the Lower Miocene of Merkur-Nord (Czech Republic, MN 3). *Beiträge zur Paläontologie* 30: 175-203.
- Van der Meulen AJ, Daams R. 1992. Evolution of Early-Middle Miocene rodent faunas in relation to long-term paleoenvironmental changes. *Palaeogeography, Palaeoclimatology, Palaeoecology* 93: 227-253.
- Van der Meulen AJ, Peláez-Campomanes P, Levin SA. 2005. Age structure, residents and transients of Miocene rodent communities. *The American Naturalist* 165: 108-125.
- Ziegler PA, Dèzes P. 2007. Neogene uplift of Variscan Massifs in the Alpine foreland: Timing and controlling mechanisms. *Global and Planetary Change* 58: 237-269. doi: [10.1016/j.gloplacha.2006.12.004](https://doi.org/10.1016/j.gloplacha.2006.12.004)
- Ziegler R. 1983. *Odontologische und osteologische Untersuchungen an Galerix exilis (BLAINVILLE) (Mammalia, Erinaceidae) aus den miozänen Ablagerungen von Steinberg und Goldberg im Nördlinger Ries (Süddeutschland)*. PhD Thesis, Ludwig-Maximilians-Universität München.
- Ziegler R. 2000. The Miocene Fossil-Lagerstätte Sandelzhausen: 17. Marsupialia, Lipotyphla and Chiroptera (Mammalia). *Senckenbergiana Lethaea* 80: 81-127.
- Ziegler R. 2003. Insektenfresser (Lipotyphla) aus dem Mittel-Miozän von Mühlbach am Manhartsberg und Grund, Niederösterreich. *Annalen des Naturhistorischen Museums in Wien* 104 A: 251-265.
- Ziegler R. 2005. Erinaceidae and Dimylidae (Lipotyphla) from the Upper Middle Miocene of South Germany. *Senckenbergiana Lethaea* 85: 131-152.
- Ziegler R. 2006a. Miocene Insectivores from Austria and Germany – An Overview. *Beiträge zur Paläontologie* 30: 481-494.
- Ziegler R. 2006b. Insectivores (Lipotyphla) and Bats (Chiroptera) from the Late Miocene of Austria. *Annalen des Naturhistorischen Museums in Wien* 107 A: 93-106.
- Ziegler R, Fahlbusch V. 1986. Kleinsäuger-faunen aus der basalen Oberen Süßwasser-Molasse Niederbayerns. *Zitteliana* 14: 3-58.
- Ziegler R, Dahlmann T, Reumer JWF, Storch G. 2005. Germany. Pp. 61-98 in: van den Hoek Ostende LW, Doukas CS, Reumer JWF, eds, The Fossil Record of the Eurasian Neogene Insectivores (Erinaceomorpha, Soricomorpha, Mammalia) Part I. *Scripta Geologica, Special Issue* 5.
- Ziegler R, Daxner-Höck, G. 2005. Austria. Pp. 11-29 in: van den Hoek Ostende LW, Doukas CS, Reumer JWF, eds, The Fossil Record of the Eurasian Neogene Insectivores (Erinaceomorpha, Soricomorpha, Mammalia) Part I. *Scripta Geologica, Special Issue* 5.
- Ziegler R, Mörs T. 2000. Marsupialia, Lipotyphla und Chiroptera (Mammalia) aus dem Miozän des Braunkohlentagebaus Hambach (Niederrheinische Bucht, NW-Deutschland). *Palaeontographica A* 257: 1-26.

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