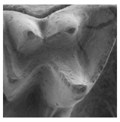
Amphiperatherium and Erinaceidae of Petersbuch 28

JOHANNES KLIETMANN, DORIS NAGEL, MICHAEL RUMMEL & LARS W. VAN DEN HOEK OSTENDE



The only marsupial and the Erinaceidae from the Bavarian fissure filling Petersbuch 28 are described. The marsupial is *Amphiperatherium frequens erkertshofense*, the Erinaceidae are represented by *Galerix aurelianensis* and an unknown large galericine, which is present only by four isolated teeth. The three species are mostly present by single teeth; distal ends of humeri of *Amphiperatherium* and *Galerix*, astragali of *Galerix* as well as calcanei of *Amphiperatherium* are also described; the calcaneus for the first time from material which was not *in situ*. • Key words: *Amphiperatherium*, Erinaceidae, Miocene, Germany, Petersbuch.

KLIETMANN, J., NAGEL, D., RUMMEL, M. & HOEK OSTENDE, L.W. VAN DEN 2014. *Amphiperatherium* and Erinaceidae of Petersbuch 28. *Bulletin of Geosciences 89(1)*, 1–20 (9 figures, 3 tables). Czech Geological Survey, Prague. ISSN 1214-1119. Manuscript received May 30, 2013; accepted in revised form August 28, 2013; published online December 2, 2013; issued January 21, 2014.

Johannes Klietmann (corresponding author) & Doris Nagel, University Vienna, Department of Palaeontology, Althanstraße 14, A-1090 Vienna, Austria; johannes.klietmann@yahoo.de, doris.nagel@univie.ac.at • Lars W. van den Hoek Ostende, Naturalis, PO Box 9517, 2300 RA Leiden, The Netherlands; Lars.vandenHoekOstende@Naturalis.nl • Michael Rummel, Naturmuseum, Augusta Arcaden, Ludwigstraße 2, D-86152 Augsburg, Germany; michael.rummel@augsburg.de

Southern Germany is well known for its rich fossil mammal faunas. A long tradition in mammal palaeontology has made the Bavarian record one of the best for the Early and Middle Miocene, both for large and small mammals (Abdul Aziz *et al*. 2008, 2010; Böhme 2003; Böhme *et al*. 2002; Eronen & Rößner 2007; Heissig 1997). The Miocene faunas come from two entirely different geological settings. On the one hand, there are the terrestrial deposits in the North Alpine Foreland Basin, which allow us to place the faunal sequence in a chronostratigraphic framework for detailed palaeoecological analyses (Abdul Aziz *et al*. 2008, 2010; Kuhlemann & Kempf 2002; Prieto *et al*. 2009). Directly adjacent to the basin is the Franconian Alb, the fissure fillings from which have yielded various extremely rich faunas (Bolliger & Rummel 1994; Rummel 1993; Herán *et al*. 2010; Ziegler 2003a, b, c, 2005, 2007). The systematic study of the micromammal faunas from the area started with Richard Dehm, followed by the work of Volker Fahlbusch, Wighart von Koenigswald and co-workers. Micromammal studies show a strong bias towards the study of rodents. But not so in the Bavarian and Suebian record. After the initial work of Dehm's students, such as Doben-Florin (1964) and Müller (1967), it is particularly through the work of Ziegler (1989, 1990a, b, 2003b, c, 2005; Ziegler & Fahlbusch 1986) that the Southern German fossil insectivore record is one of the best studied in the world.

Arguably, one of the most interesting periods preserved in the fossil record of the area is the so-called cricetid vacuum, which correlates to MN 3 (Agustí *et al*. 2001, Daams & Freudenthal 1990). It is the only period in the Neogene in which the small mammal faunas were not dominated by muroid rodents. Instead, it is the heyday of eomyids and glirids. The cricetid vacuum encompasses a substantial time span, with estimates running up to 2.5 my (Steininger 1999). Yet, in Bavaria this period is only represented to date by two fissure fillings, Stubersheim 3 and Wintershof-West. The latter is the reference locality to MN 3 (Bruijn *et al*. 1992). In the wider surroundings, the period is also known from the Czech locality of Merkur-Nord (Fejfar *et al*. 2003).

The discovery of the fissure filling Petersbuch 28 is thus a welcome addition. The rodents of this locality can also be correlated to MN 3/4 (Rummel, pers. obs.). This paper is the first in a series that deals with the insectivores from Petersbuch 28, which were studied as the subject of the PhD thesis of the first author (Klietmann 2013). In addition to the fossil Erinaceidae, the only marsupial from the site is described here. Forthcoming papers will deal with the Dimylidae, Talpidae and Soricidae, as well as with some of the more spectacular findings from the locality.

The finding situation of Petersbuch

Bolliger & Rummel (1994) have presented the only detailed work about the Petersbuch geology and the fissure

DOI 10.3140/bull.geosci.1454

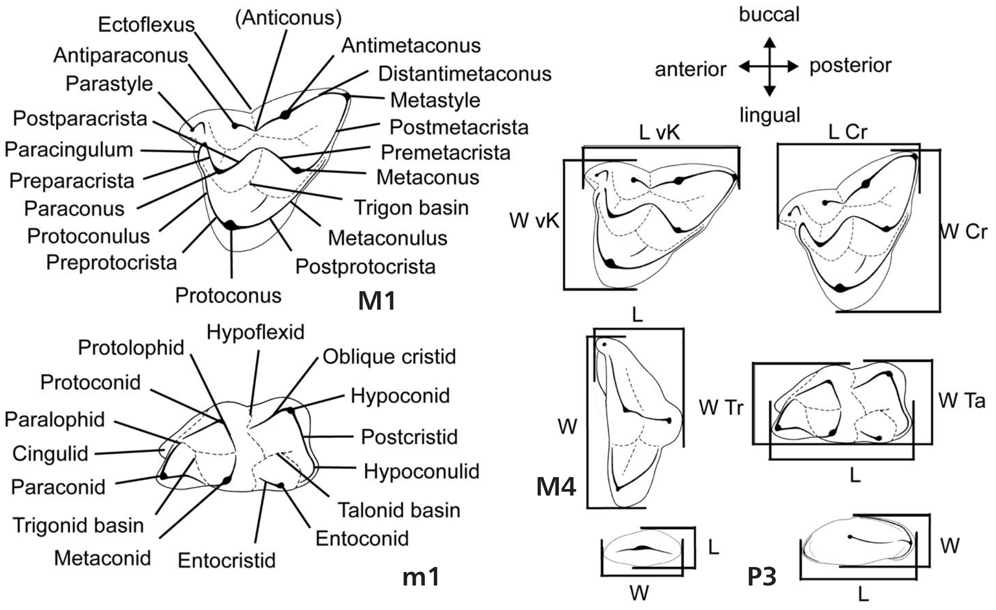


Figure 1. Terminology and measurements of the teeth of *Amphiperatherium frequens* after von Koenigswald (1970).

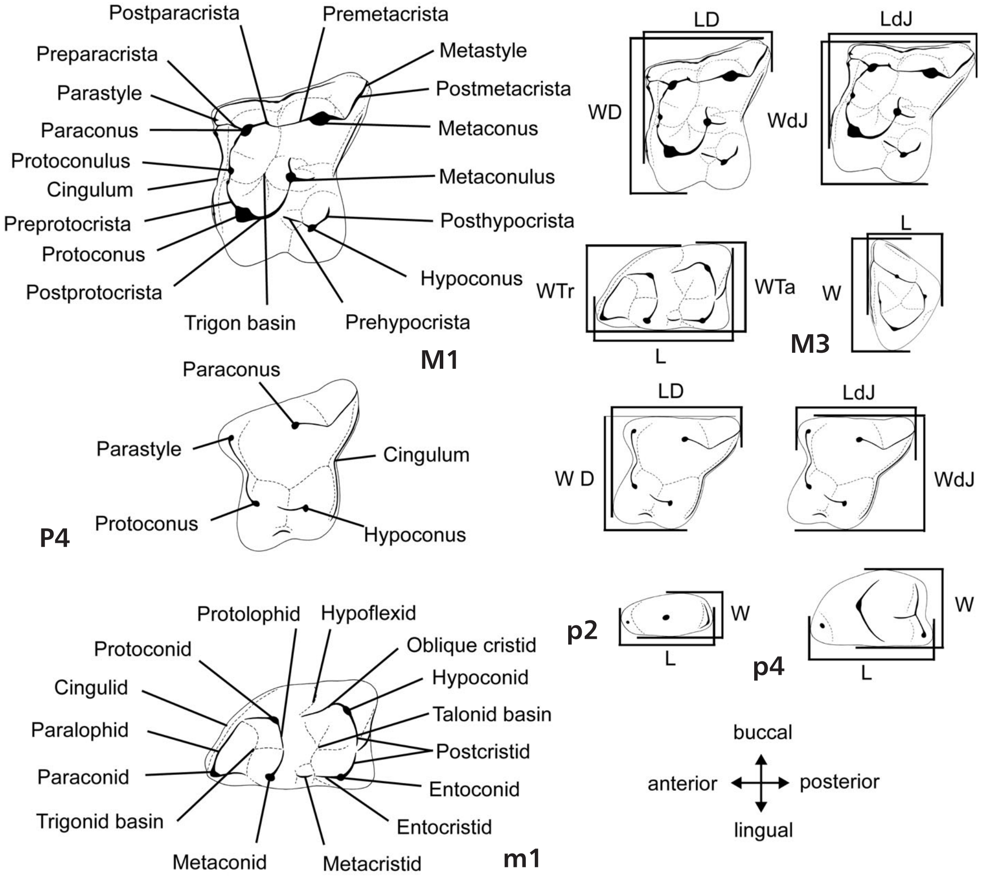


Figure 2. Terminology and measurements of the teeth of the Erinaceidae after Ziegler (1990a).

fillings so far. The fissure fillings are situated in Upper Jurassic limestone, in the Schöpfel quarry near Eichstätt, northwest of Munich. Most important for understanding micromammalian fossil assemblages is the interpretation that the remains were brought to the vicinity of the fissure by predators. The concentration of small mammal findings is usually seen as being due to the predation by owls, especially owls with less acid digestive fluids, resulting in undamaged bones, whole jaws and crania (for details see Andrews 1990).

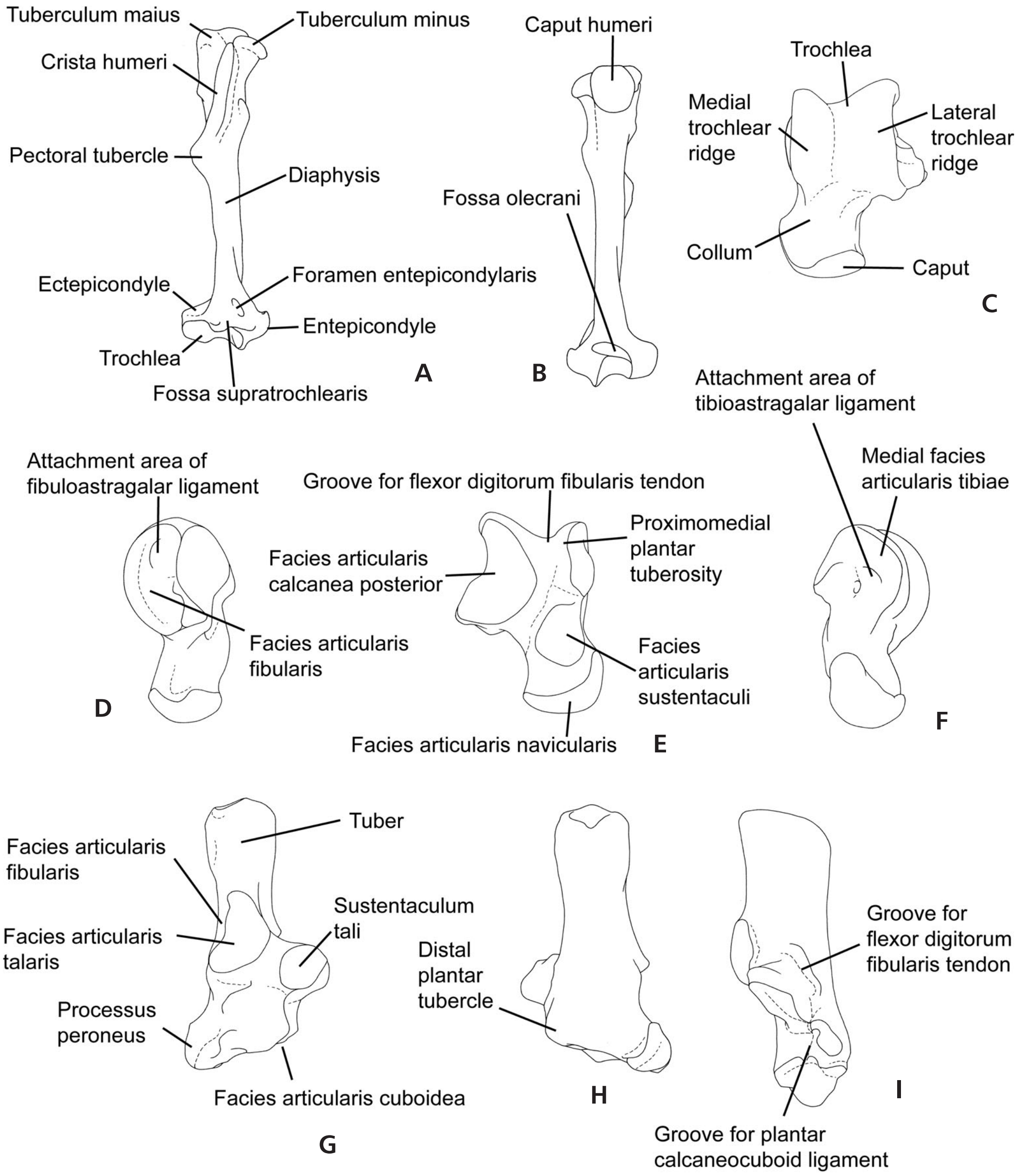


Figure 3. Terminology of the humerus, astragalus and calcaneus of *Amphiperatherium frequens* and the Erinaceidae. • A – right humerus, anterior view. • B – right humerus, posterior view. • C – left astragalus, anterior view. • D – left astragalus, lateral view. • E – left astragalus, posterior view. • F – left astragalus, medial view. • G – right calcaneus, anterior view. • H – right calcaneus, lateral view. • I – right calcaneus, posterior view.

The exact process of fissure forming in the area is not fully understood. Heissig (1978) correlated this with the transgression of the Molasse Sea, but Bolliger & Rummel (1994) contradicted this view, because this does not hold true for the MN 8–9 fissures. Another factor is the regional climate, like increases in humidity, for example the warm and moist climate of the times of deposition of the MN 3–4 faunas. Overall, there seems to have been a large and complex karstification over a long period of time, and in different regions.

The sediment of the fissure filling Petersbuch 28 consists of reddish to brown clayey loam. The preservation of the fine elements contradicts any possibility of transport; most likely the material was accumulated via bird pellets (Rosina & Rummel 2012).

Material and methods

The terminology of *Amphiperatherium* tooth morphology follows von Koenigswald (1970) (Fig. 1). New studies found the Herpetotheriidae to be the sister group of all crown group Marsupialia (Horovitz *et al.* 2009), but we

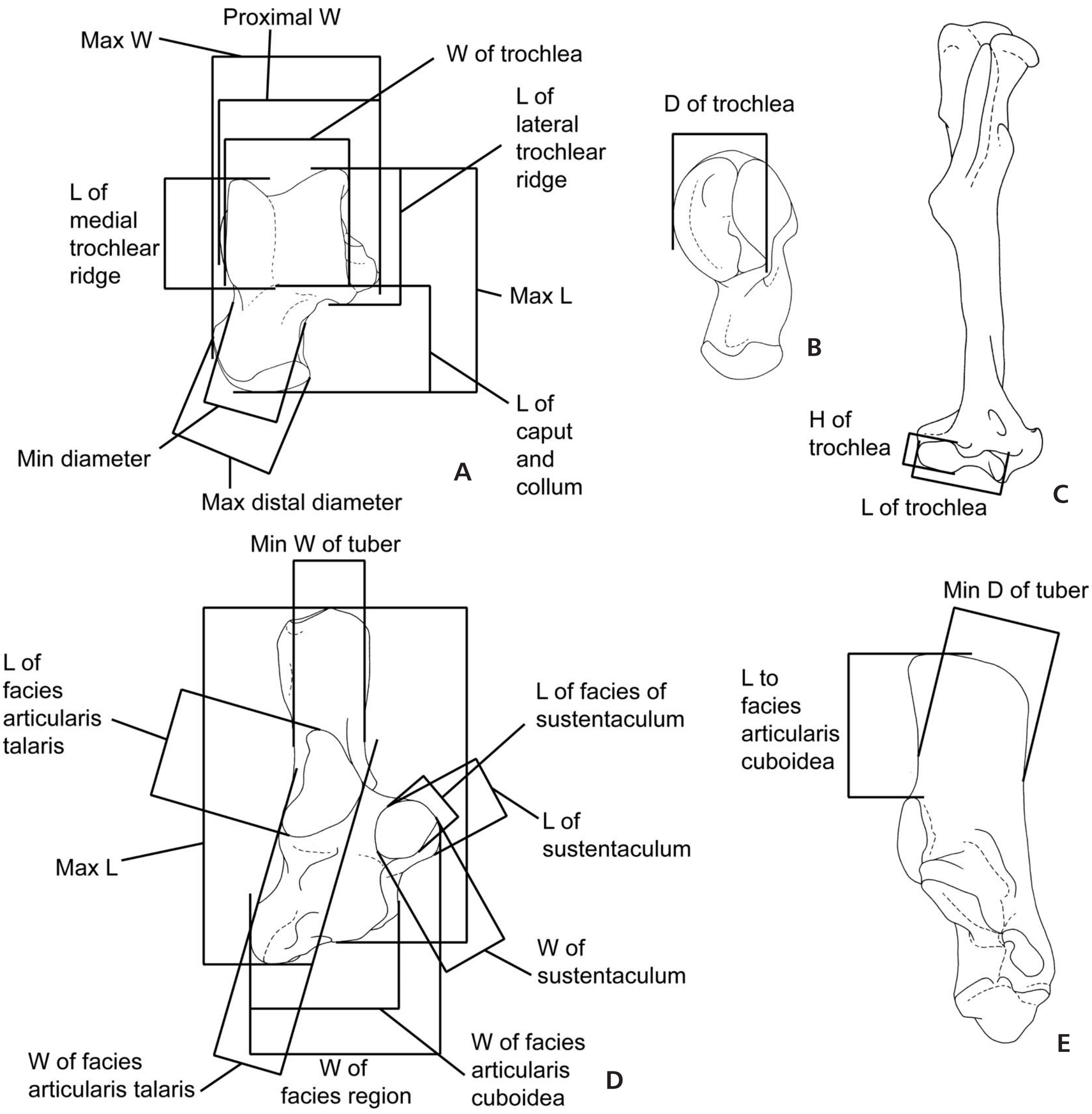


Figure 4. Measurements of humerus, astragalus and calcaneus of *Amphiperatherium frequens* and the Erinaceidae. • A – left astragalus, anterior view. • B – left astragalus, lateral view. • C – right humerus, anterior view. • D – right calcaneus, anterior view. • E – right calcaneus, lateral view.

follow Ladevèze *et al*. (2012), who wrote that "the vernacular denomination marsupial is however convenient and used here to refer to any metatherian taxa, herpetotheriids and others". The terminology of the Erinaceidae follows Ziegler (1990a) (Fig. 2). Morphological features of the astragalus and the humerus are indicated with the usual Latin names; some features of the astragalus and calcaneus are named after Hooker (2001), but in Latinized version (Fig. 3). The method for measuring postcranial bones is given in Fig. 4.

To assign the postcranial bones, they were compared to micromammal bones in the Natural History Museum Vienna. All teeth and bones were measured using a Leica M420 Microscope and a Mitutoyo measuring clock. Repeated measuring of some teeth gave a maximum error of 0.03 mm for the teeth and 0.05 mm for the bones.

The lower molars were measured with the entoconid exactly vertical, following the methods of Jong (1988), Doukas (1986), von Koenigswald (1970), and Ziegler (1990a) (Figs 1 and 2).

The upper molars and the single dP3 of *Amphiperatherium* were measured using the methods of Crochet (1980) and von Koenigswald (1970). The M4 was measured using the anterior margin as reference line (Fig. 1). On the whole, the method of von Koenigswald (1970) is preferred, because it is easier to reproduce. Crochet's (1980) argument that it would not consider the true length of the molar is rejected, because a three-dimensional object in a complex outline like a maxilla can hardly have a single "true" length, especially considering teeth like the M1, where the buccal and the lingual parts of the tooth row diverge, causing the tooth to have different "true lengths". Also, the easier any measurement can be reproduced, the better it can be used for comparison.

The upper molars and P4 of the Erinaceidae were measured using the methods of Jong (1988) and Doukas (1986); the method of Jong (1988) is preferable. Both are similarly easy to reproduce, but the anterior margin is less variable than the buccal margin (Fig. 2).

The p4 were measured alongside the lingual margin, because this is also parallel to their main axis (Fig. 2). All other teeth were measured alongside their main axis, giving the greatest length, and the width in right angle to the length. In the incisors, the length was taken parallel to their ridge (Figs 1 and 2). The length of the complete molar row (m1–m4) was taken in buccal view. The drawings were done by Norbert Frotzler in Vienna. The SEM photos were made using an FEI Inspect S electron microscope in low vacuum at a voltage of 10 kV. Because the SEM could not photograph entire jaws, multiple photos were taken and merged afterwards using Adobe Photoshop 7 and CS 5.

The calculations and diagrams were made using Microsoft Excel 2007. Mean value, minimum and maximum values are given in mm. In the tables, n is the total number of specimens present; the number in brackets, "(excl.)" stands for the number of specimens that are damaged or covered by sinter; they were excluded from the calculations. In cases of less than three usable specimens, the individual values are given; mean, minimum and maximum were not calculated in those cases. Length and width are indicated with the name of the author they were taken according to.

The material will be stored at the Naturmuseum Augsburg, Germany and the Collection of Michael Rummel, Weißenburg, Germany.

Abbreviations. – NMA – Naturmuseum Augsburg; CMR – Collection Michael Rummel; L – length; W – width; H – height; W Tr – trigonid width; W Ta – talonid width; HoM – height of mandible below the respective molar; MDD – minimum diameter of the diaphysis; D – Doukas; dJ – de Jong; vK – von Koenigswald; Cr – Crochet.

Systematic palaeontology

Infraclass Metatheria Huxley, 1880
Family Herpetotheriidae Trouessart, 1879

Genus *Amphiperatherium* Filhol, 1879

Type species. – *Oxygomphius frequens* von Meyer, 1846.

Amphiperatherium frequens (von Meyer, 1846)

Figures 5, 6, Table 1

Material. – Dental material: 96 specimens: 22 isolated lower molars, six mandible fragments with only one molar, nine mandible fragments with molars, seven maxillary fragments with more than one molar and sometimes premolars, 27 isolated upper molars, two isolated lower premolars, one mandible fragment with three premolars, eight isolated upper premolars, one maxillary fragment with two premolars and a damaged canine, one maxillary fragment with three incisors, one fragment with one incisor and eleven isolated canines, consisting of five lower and six upper canines. Postcranial material: three distal ends of the humerus, four calcanei. Collection numbers: NMA 2012-2/2058–2012-13/2058, 119/2058, 138/2058; CMR-P/28-1–5; 7, 8, 10–12, 15, 17, 19–58, 60–63, 65–69, 71–75, 118, 136, 145, 147, 148, 152, 154, 566, 2359, 1260, 1262, 1521, 3177; H54, H160, C383, C446, C1471.

Diagnosis. – (Translated from von Koenigswald 1970.) Length of the molars in the lower jaw nearly equal. On the m4, the tips of the talonid are connected to a cutting edge, which is, however, very shortly interrupted between hypoconulid and entoconid. Posterior cingulum variably present. Large upper and lower canines. The anticonus of the stylar row is often reduced. M1 usually without anticonus; M2 antimetaconus often double-tipped; M3 often with small anticonus. Lower jaw slender and bending at the lower margin.

Description. – The upper incisors each have one large root. All incisors are positioned with the main axis of their crown parallel to the premaxillary. Of the I1, only the alveolus is preserved. The outline of the I2 is a long ellipse with sharp anterior and posterior curves and a wider buccal curve. The single ridge covers the entire surface, making a slight curve, ending in lingual direction. The most buccal point is also the highest. For the large I3, like for the other incisors, the alveolus is considerably larger than the root, so it appears to be too wide. The overall shape is an ellipse with a small semicircle added low at the posterolingual side, as the lingual side has a clear enlargement of the crown base in the posterior part. The single ridge covers the complete crown except for the posterolingual enlargement. A small posterior conule is present. The I4 is elliptical, but a bit enlarged on the posterobuccal side. The lingual side is nearly straight, the enlargement present at a very low level. At the anterior and posterior ends, the ridge forms small cusplets; it runs more lingually and is less steep here. The **C** sup. is simple; the crown continues the shape of the large root. All of the canini are broken and isolated, except for one damaged tooth, which is still in situ in a mandible fragment lacking all other teeth. The elliptical P1 has two roots.

Table 1. Measurements of the *Amphiperatherium frequens* (von Meyer, 1846) teeth and postcranial material from Petersbuch 28 (Germany, Early Miocene). * = damaged.

	n (excl.)	Measured parameter	mean	min	max
I2 sin	1	L	0.57		
		W	0.28		
I3 sin	2 (1)	L	0.98		
		W	0.48		
I4	1	L	0.50		
		W	0.29		
C sup.	6	Greatest diameter	1.78	0.99	2.33
P1	1	L	1.08		
		W	0.50		
P2	5 (1)	L	1.53	1.40	1.62
		W	0.77	0.73	0.85
P3	6	L	1.72	1.66	1.80
		W	0.90	0.71	1.08
dP3	1	L Cr	1.75		
		W Cr	1.49		
		L vK	1.85		
		W vK	1.24		
M1	12 (1)	L Cr	2.12	1.98	2.26
		W Cr	2.11	2.04	2.24
		L vK	2.19	2.08	2.32
		W vK	1.85	1.73	1.90
M2	8 (1)	L Cr	2.07	1.99	2.16
		W Cr	2.40	2.26	2.47
		L vK	2.11	2.04	2.18
		W vK	2.18	2.07	2.27
M3	13 (4)	L Cr	2.02	1.93	2.09
		W Cr	2.52	2.41	2.73
		L vK	2.03	1.98	2.09
		W vK	2.39	2.26	2.51
M4	5	L	1.20	1.05	1.34
		W	2.35	2.27	2.44
c inf.	5	Maximum diameter	1.38	0.99	1.71
p1	1	L	0.91		
		W	0.43		
p2	4	L	1.55	1.51	1.61
		W	0.67	0.64	0.70
p3	5 (2)	L	1.68	1.70	1.69
		W	0.81	0.90	0.88
m1	9 (1)	L	2.01	1.87	2.12
		W Tr	1.06	0.96	1.22
		W Ta	1.12	1.03	1.23
	10	HoM	2.87	2.30	3.52
m2	13 (3)	L	2.16	2.04	2.26
		W Tr	1.18	1.02	1.27
		W Ta	1.26	1.12	1.35
	14	HoM	3.00	2.38	3.85
m3	21 (2)	L	2.19	2.04	2.49
		W Tr	1.22	1.01	1.31
		W Ta	1.19	1.10	1.34
	10	HoM	3.17	2.39	4.07
m4	10 (3)	L	2.15	2.07	2.21
		W Tr	1.13	1.08	1.17
		W Ta	0.78	0.66	0.84
	8	HoM	3.34	2.88	4.16
Mandible	2	m1–m4	8.12	7.51	
Humerus	1	MDD	1.87		
	1	Distal W	5.43		
	2	Trochlear W	3.61	3.97	
	3	Trochlear H	1.64	1.56	1.00*
Calcaneus	3	Maximum L	4.42	4.23	4.72
	4	Min W of Tuber	1.05	1.01	1.13
	3	Max W of Facies Region	2.47	2.32	2.67
	3	Max W of Facies articularis cuboidea	1.63	1.52	1.71
	4	L of Tuber above facies articularis talaris	1.66	1.54	1.77
	4	Min D of Tuber	1.46	1.40	1.54
	4	W of Sustentaculum	0.84	0.73	0.98
	2	L of Sustentaculum	1.66	1.81	
	4	Max L of Facies articularis talaris	1.35	1.21	1.47
	3	W of Facies articularis talaris	1.16	0.98	1.33

The large paracone is high and elongated anterior-posteriorly. It has a small anterior and a larger posterior ridge. At the posterobuccal side, there is a small accessory cuspule, with two bulges alongside the posterior margin. The P2 differs in its greater size, the lack of a clear anterior ridge and a larger cingulum around the anterior and posterior ends. The P3 is even larger and has a larger cingulum forming a small anterior cuspule. The dP3 resembles an M1. It has three roots. There is no cingulum, antiparaconus or metaconulus; the large antimetaconus has a tiny anterior part that may represent an anticonus. All molars prior to the M4 have three roots. The M1 is triangular in outline. The buccal outline is curved around antiparaconus and antimetaconus. The stylar cusps are large; there is no anticonus and only some specimens have a tiny distantimetaconus. The accessory ridges connecting the arms of the protocone to the bases of paracone and metacone are clearly visible. The M2 is quite similar to the M1, but, apart from being larger, has a deeper ectoflexus with the parastyle and metastyle protruding. The whole tooth is more slender than the

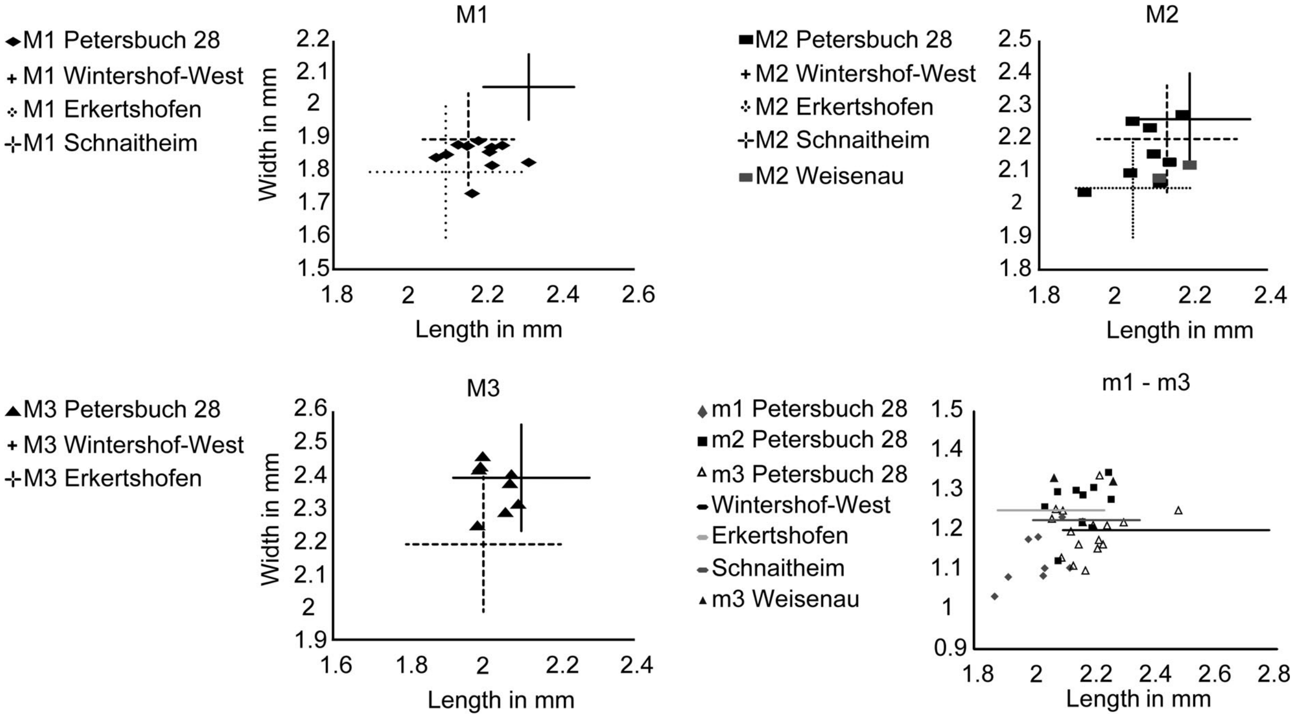


Figure 5. *Amphiperatherium frequens* (von Meyer, 1846) from Petersbuch 28 (Germany, Early Miocene). Comparison of M1–M3 and m1–m3. Data for comparison are from von Koenigswald (1970); the widths of the lower molars were not given in his work.

M1, the protocone base not enlarged. There is no anticonus nor distantimetaconus. The M3 has parastyle and metastyle protruding further buccally, resulting in the largest ectoflexus among the upper molars; the stylar cusps are weaker and the whole tooth appears more slender than the M2. The accessory ridges are weak. The M4 has two roots. It has a very distinct shape; the outline is basically triangular, but extremely slender. The weak parastyle and antiparaconus are the only stylar cusps. The only accessory ridge connects the preprotocrista to the base of the paraconus.

No lower incisors or their alveoli could be identified in the material.

The **c** inf. resembles the upper canine, but its tip is bent more distinctly and it has a small groove from contact with the C sup. In all lower premolars, the protoconid is in the anterior part and it is slightly curved backwards. The elliptical p1 has two roots. The protoconid is elongated. The anterior ridge is faint; the posterior ridge runs along the buccal side. There is a slight posterobuccal cuspule continued by two blunt ridges, one in lingual direction and one to the protoconid. There is no cingulid. The p2 differs from the p1 in its larger size and the larger posterior cingulid. The p3 is even larger than the p2 and relatively wider. A blunt ridge is present at the lingual side of the protoconid, reaching in posterior direction alongside the tooth margin. All molars have two roots. They have a deep trench in the paralophid between its cusps. The trigonid basin is narrow and open. The talonid basin is large and closed with the exception of the gap between hypoconulid and entoconid. In the **m1**, the hypoflexid is weak and the talonid wider than the trigonid; protoconid and metaconid are closely together. The anterior cingulid, next to the paralophid, is the only cingulid. The m2 is a bit longer and it has a larger protoconid and metaconid further apart and a cingulid reaching the hypoconid in two of the four specimens. The m3 is similar to the m2, but its talonid is narrower than the trigonid. The hypoflexid is wider than on the m2. In one specimen, a small postcingulid is present between hypoconulid and hypoconid. The m4 has the talonid strongly reduced in size and its cusps are very low and only weakly differentiated against their ridges. The hypoflexid is quite wide. The ramus horizontalis of the mandible is quite high with flat sides. It is most convex below the m2. The foramen mentale is doubled, one being situated below p1, the other below the talonid of m1. The ramus ascendens starts going upwards behind the m4 in a blunt angle, but is damaged on all specimens. The fossa temporalis on the buccal side is quite deep. The processus condylaris is situated on the buccal side, slightly below the tooth row. The processus angularis is bent to the lingual side. The large foramen mandibulae is situated in the anterior corner of the fossa formed by the processus angularis.

Only the distal parts of the humeri are preserved. The humerus is strong, the distal area wide. The trochlea has two rounded, protruding parts. Above the trochlea, a large fossa is formed. The posterior side of the fossa is saddle-shaped, the fossa olecrani shallow. The small entepicondyle is a bulge clearly protruding next to the trochlea, the entepicondylar foramen is a bit tear-shaped. The ectepicondyle is a long flange reaching very far in posterior and proximal directions. The smallest specimen represents a juvenile, as proven by the still clearly visible sutures between the diaphysis and the epiphysis. The calcaneus has a very short and strong tuber with a weakly pronounced tip. A clear ridge or bulge leads from the tip to the facies articularis talaris. This facet is large and nearly circular. The sustentaculum tali is almost as long as the tuber above the facies articularis talaris; its medial margin is nearly straight. The facies articularis sustentaculi is much elongated alongside the outer margin of the sustentaculum. The processus peroneus is small, situated at the distolateral end of the bone. The groove for the flexor digitorum fibularis tendon is weak. The facies articularis cuboidea is large; it is on the medial side of the bone; it reaches from the main axis to the end of the sustentaculum in a concave curve. The distal plantar tubercle is just a faint enlargement of the bone; the groove for the plantar calcaneocuboid ligament is very weak.

Remarks. – The distinct stylar cusps as well as the clear hypoconulid of the lower molars, but most importantly the presence of four molars identify this animal as a marsupial.

The species *Amphiperatherium frequens* (von Meyer, 1846) is the last species of marsupials present in Europe (Ziegler 1990a); it can be distinguished by having lower molars of nearly equal length, the cutting blade of the talonid cusps of the m4, which is only interrupted by the small groove between entoconid and hypoconulid, the large canines and the slender, bent ramus horizontalis of the mandible (von Koenigswald 1970). Further typical traits are the reduction of the cingula and the stylar cusps. The measurements fit well to data of the species given by von Koenigswald (1970), Ziegler (1990a) and Ziegler & Mörs (2000).

Recently, Ladevèze *et al.* (2012) questioned the validity of the genus *Amphiperatherium* Filhol, 1879 because the features to distinguish it from *Peratherium* Aymard, 1850 might be too variable and therefore not diagnostic, as von Koenigswald (1970) already pointed out. Unlike von Koenigswald (1970), Ladevèze *et al*. (2012) did not judge *Amphiperatherium* to be invalid, because a thorough revision of *Peratherium* and *Amphiperatherium* would be needed in order to decide the question. Therefore, the genus name *Amphiperatherium* is retained in here.

Von Koenigswald (1970) described different subspecies of *Amphiperatherium frequens*, not accepted by Crochet (1980), but seen as valid by Ziegler & Fahlbusch (1986) and Ziegler (1990a). The upper molars from Petersbuch 28 lack the anticonus like *Amphiperatherium frequens wintershofense* (von Koenigswald, 1970), but no M1 from Petersbuch 28 has an enlarged base of the protocone like many specimens from Wintershof-West, the type locality of that subspecies (von Koenigswald 1970). *Amphiperatherium frequens erkertshofense* (von Koenigswald, 1970) is similar to the upper molars from Petersbuch 28 in morphology, except for the presence of an anticonus in many specimens from its type locality Erkertshofen 1 (von Koenigswald 1970). *Amphiperatherium frequens frequens* (von Meyer, 1846), the oldest subspecies, always has posterior cingulids on the lower molars; in Wintershof-West (MN 3), the postcingulid is present on 30% of the lower molars, in the younger locality Erkertshofen (MN 4), it is present on 10% of the molars (von Koenigswald 1970), and it is completely absent in younger assemblages (Ziegler 1990a). In Petersbuch 28, the posterior cingulid is present only once. The rather modern lower molars and the relatively narrow M1 allow determining the subspecies from Petersbuch 28 as *A. frequens erkertshofense*. The upper molar sizes fit best with the material from Schnaitheim (MN 3) (Fig. 5), of which the subspecies was not determined (von Koenigswald 1970); apparently, the assemblage from Schnaitheim represents an intermediate stage between *A. frequens wintershofense* and *A. frequens erkertshofense*. The lack of an anticonus in the upper molars and the molar size therefore indicate the specimens from Petersbuch 28 to be a rather archaic form of *A. frequens erkertshofense*.

The assignment of the fragmentary premaxillary to *A. frequens* was done because it has more than three incisors. The relative sizes and positions of the alveoli are similar to the premaxillary shown by von Koenigswald (1970); the upper incisors themselves are here recorded for the first time.

The humerus is quite similar to large Rodentia humeri, but its trochlea is more rounded and elongated and the ectepicondylar flange is unusually curved in posterior

Figure 6. *Amphiperatherium frequens* (von Meyer, 1846) from Petersbuch 28 (Germany, Early Miocene). • A – NMA 2012-9/2058: C sup. • B – NMA 2012-10/2058: C inf. • C – NMA 2012-6/2058: maxillary sin, rest of C, P1, P2. • D – NMA 2012-5/2058: P3 dext, reversed. • E – NMA 2012-119/2058: humerus dext, distal end. • F – NMA 2012-8/2058: premaxillary with I2, I3 sin. • G – NMA 2012-7/2058: premaxillary with I3 sin. • H – NMA 2012-8/2058: detail of the I2. • I – NMA 2012-7/2058: detail of the I3. • J – NMA 2012-138/2058: calcaneus dext. • K – NMA 2012-11/2058: mandible with p1, p2, p3 sin. • L – NMA 2012-12/2058: m4 sin. • M – NMA 2012-4/2058: dP3, M1 sin. • N – NMA 2012-3/2058: M1, M2 dext, reversed. • O – NMA 2012-2/2058: M3, M4 sin. • P – NMA 2012-13/2058: mandible with p2, p3, m1, m2, m3, m4 dext, reversed.

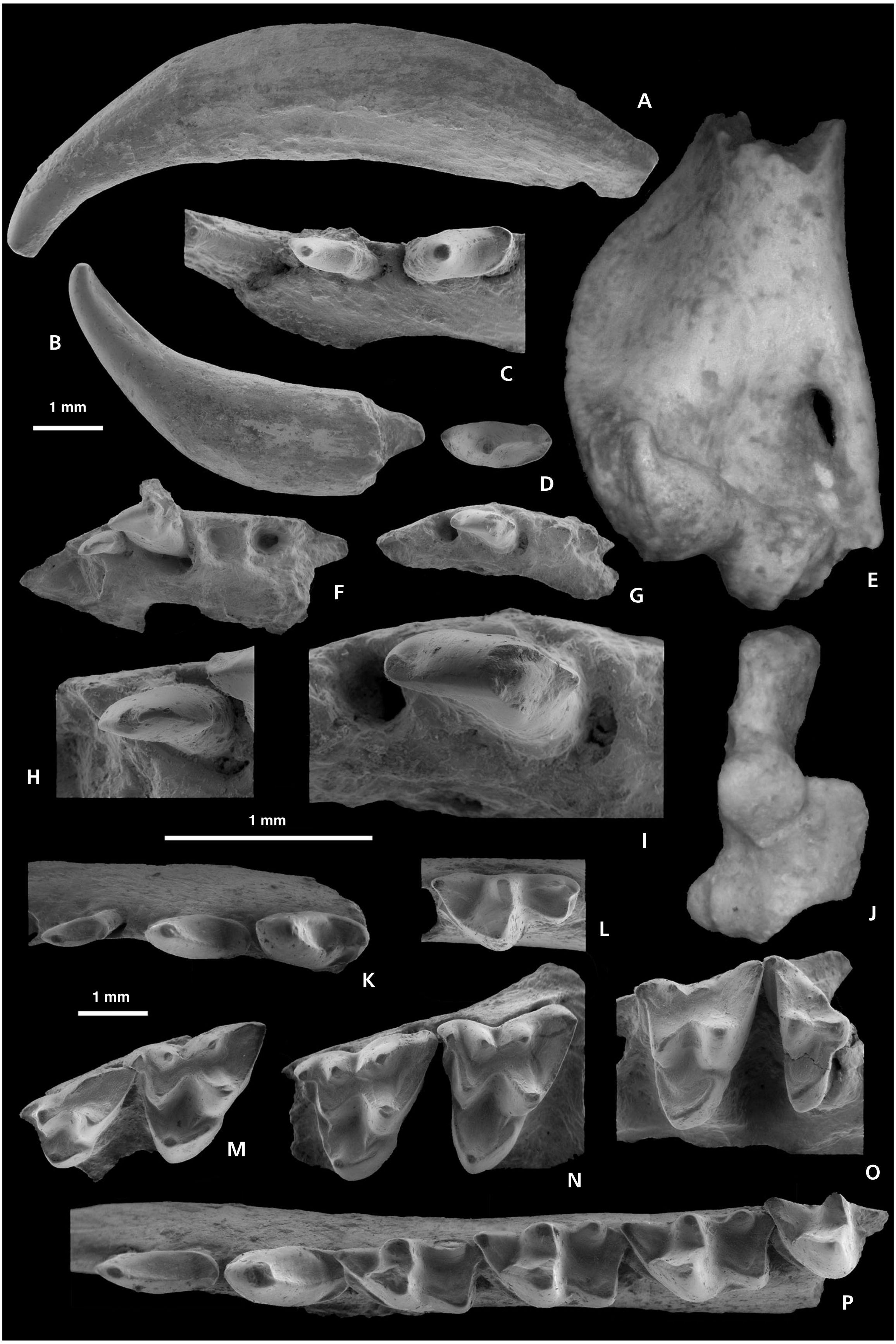

A
B
C
D
E
F
G
H
I
J
K
L
M
N
O
P
1 mm
1 mm
1 mm

Table 2. Measurements of the teeth of Galericinae gen. et sp. indet. from Petersbuch 28 (Germany, Early Miocene). * – measurements are only a minimum, because the tooth's damaged buccal side; they are only presented to give an idea of the specimen's size.

	n (excl.)	Measured parameter	
P4	1	L dJ	3.57
		L D	3.12
		W dJ	3.34
		W D	3.12
M2	1 (1)*	L dJ	3.65
		L D	3.49
		W dJ	3.75
		W D	3.80
M3	1	L	2.11
		W	2.71
m3	1	L	3.25
		W Tr	1.98
		W Ta	1.84

direction. The overall shape of the trochlea and the ectepicondyle is similar to recent *Didelphis aurita* zu Wied-Neuwied, 1826. Apart from the much smaller size of the fossil species, the only difference is its more rounded and a bit shorter entepicondylar foramen.

The easily recognizable calcaneus differs from the respective bone of *Didelphis aurita* in its much smaller size, the relatively larger facies articularis talaris and tuber, the facies articularis cuboidea a bit more to the medial side, the longer sustentacular facet and, especially, by having the processus peroneus at the distal end, not opposite of the sustentaculum. It is similar to the one described by Kurz (2001) from a complete skeleton of *Amphiperatherium* cf. *maximum* Crochet, 1979 from the Eocene locality Messel. It is much more similar to *Herpetotherium fugax* Cope, 1873 than to *Didelphis aurita*. The calcaneus of *Amphiperatherium frequens* differs from that of *Herpetotherium fugax* by its less sculptured plantar surface and the slightly wider distal area, formed especially by the further protruding sustentacular facet, and the slightly less distal processus peronealis (Sánchez-Villagra *et al.* 2007).

Infraclass Eutheria Huxley, 1880
Order Eulipotyphla Waddell, Okada, Hasegawa, 1999
Family Erinaceidae Fischer, 1814
Subfamily Galericinae Pomel, 1848

Galericinae gen. et sp. indet.
Figure 8R–U, Table 2

Material. – Four isolated teeth; P4, M2, M3 and m3. Collection numbers: NMA 2012-14/2058–17/2058.

Description. – The P4 has three roots. The outline resembles a trapezium with concave anterolingual and posterolingual sides. The large paracone is bent posteriorly. Its ridge makes an abrupt angle halfway before running to the posterobuccal style. The large protocone is anterolingual to the paracone. Its small anterior ridge forms the parastyle anterior to the paracone. The small posterior ridge of the protocone ends near the hypocone. The hypocone is the smallest cone, wearing a faint ridge in anterobuccal direction, ending at the protocone base. The only cingulum runs between the base of the hypocone and the style. The M2 is somewhat trapezoidal in outline; the posterior part is narrower. The large paracone and metacone are of the same size. The parastyle, metastyle and the buccal part of the cusps are broken off. The protocone is by far the largest cusp, protruding strongly in lingual direction. The protoconule is an enlargement of the preprotocrista, close to the paracone. The postprotocrista runs nearly straight in posterior direction to the low, but large hypocone. The conical metaconule is the smallest cusp of the tooth. It only has a faint ridge connecting low to the postprotocrista. The anterior cingulum reaches buccally from the anterolingual margin of the protocone; the posterior cingulum starts at the posterior margin of the hypocone. The M3 has three roots. The outline is triangular with the metacone protruding a bit posteriorly. The paracone is slightly smaller than the metacone. The ridges of the large protocone meet at nearly a right angle. The preprotocrista connects to the elongated parastyle, which is a small ridge separated from the paracone. The postprotocrista reaches the metaconule, a slight enlargement at the metacone base. The trigon basin is wide and deep. There are no cingula. The paraconid of the m3 is just an elevation of the paracristid; all ridges are rather blunt. The trigonid basin is open, the talonid basin closed; the hypoflexid is barely present. The hypoconid is the second largest cusp after the protoconid, but lower than the trigonid cusps. The entoconid is elongated anteriorly. The mesoconid at the end of the oblique cristid is weak. Metacristid and entocristid are short, but strong. The only cingulid reaches from the paraconid to the hypoconid.

Remarks. – The determination of isolated and partly damaged erinaceid teeth is impossible to the species level; it is even problematic to determine the genus. All four teeth belong to the same species, judging from their size. It is very improbable to find two or more erinaceid species of exactly similar size, each represented by one or two teeth only. Furthermore, all four teeth might even belong to a single individual, because all of them are unworn.

The triangular M3 with three large cusps cannot belong to Erinaceinae, since this subfamily has M3 with only two distinct cusps (Butler 1948, Frost *et al.* 1991, Ziegler 1990a). Judging from the size, it corresponds to the large

M2. However, they do not represent the same maxilla, because they are a left and a right tooth, respectively.

The small, conical metaconule is reminiscent of the galericine *Lantanotherium*. Although the genus is not yet known from Germany from sites older than MN 4 (Ziegler 2006), it was found in Beaulieu, a French site correlated to MN 3 (Aguilar *et al.* 2003). As finds of *Lantanotherium* are known from MN 3 and MN 4 of Europe (Fig. 9), this genus could be expected. This galericine is similar in size to *Lantanotherium*, but there are morphological differences between them. The metacone of the M3 is large, but not as dominant or set off as usual in *Lantanotherium* Filhol, 1888, the galericine genus most similar in size; the distinct accessory posterior cusp (Baudelot 1972, Butler 1948, Rzebik-Kowalska 2005, Ziegler & Mörs 2000) is missing.

The M2 is also very large, but more slender in shape than the *Lantanotherium* molar. Furthermore, *Lantanotherium* usually has a larger metaconule and narrower and squarer teeth with a stronger developed hypocone (Rabeder 1973, Ziegler & Mörs 2000). The M2 is more similar to a member of the tribe Galericini, but lacks the distinct semilunar metaconulus (Van den Hoek Ostende 2001).

The size of the lower molar indicates that it belongs to the large upper molars; it is quite similar to a specimen Engesser (1980, p. 88, fig. 26) described and pictured as an m2 possibly belonging to *Mioechinus* Butler, 1948. Since the erinaceine m3 lacks the talonid (Frost *et al.* 1991), the m3 from Petersbuch 28 also belongs to a galericine. Nevertheless, it is not helpful in a further determination of the large-sized erinaceid material.

The finds from Petersbuch 28 might represent an early form possibly related to *Lantanotherium*, retaining a simple galericine M3, but already indicating the trends of setting off the metacone and introducing a metaconule or hypocone. Including these finds in *Lantanotherium* would, however, imply that the definition of that genus needs to be widened. Given the uncertainties in the identification, we believe that would be premature. Therefore, the assemblage has been classified as Galericinae gen. et sp. indet.

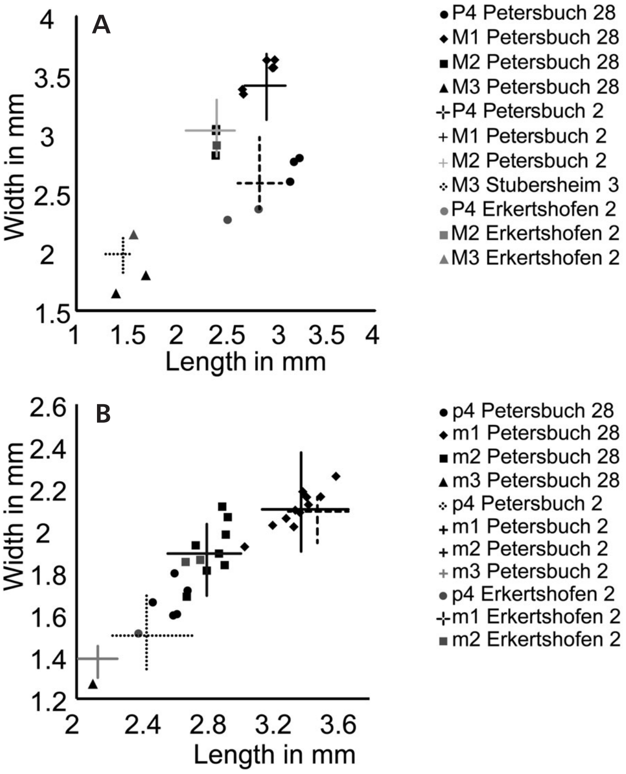


Figure 7. *Galerix aurelianensis* Ziegler, 1990 from Petersbuch 28 (Germany, Early Miocene). • A – measurements of P4–M3. • B – measurements of p4–m3. Data for comparison from Ziegler (1990a).

Tribus Galericini Pomel, 1848

Genus *Galerix* Pomel, 1848

Type species. – *Viverra exilis* de Blainville, 1839.

Galerix aurelianensis Ziegler, 1990

Figures 7, 8A–Q, V–W, Table 3

Material. – 17 isolated upper molars, 14 isolated upper non-molars, 31 isolated lower teeth, three mandibles with some teeth still in position, one edentulous mandible, one distal end of a humerus, three astragali. Collection numbers: NMA 2012-18/2058–35/2058; 120/2058, 136/2058; CMR-P/28-78–83, 86–89, 91, 92, 95–104, 106–112, 114, 121, 123, 124, 127, 130–132, 134, 137–140, 142, 596, 1411, 3174, A5, A56.

Diagnosis. – (Translated from Ziegler 1990a.) Large *Galerix* species; p2 larger than p3, p4 with metaconid bud of two thirds height, somewhat lower paraconid. P3 with one inner conus. M1+2 predominantly two modi: Ridge protoconus posterior arm-hypoconus anterior arm-lingual arm of metaconule equal, weak or ridge protoconus posterior arm-metaconulus strong, hypoconus anterior arm suppressed, hypoconus isolated.

Description. – The C sup. has two large roots. It is elliptical and rather narrow. The small posterior bulge of the paracone ends in a small, conical cuspule. There are no cingula. The elliptical P1 has two roots. There is a weak posterobuccal bulge, ending in a small, conical cuspule. There are no clear cingula. The P2 is larger and has a clear bulge in anterior direction and one or two blunt posterior ridges. The posterior cingulum is small. Since only the enamel crowns of the dP3 are preserved, the number of roots cannot be judged. The general outline of the tooth is triangular, the lingual side forming a rounded, wide angle. The buccal margin is slightly concave. The paracone is low, but very large. The posterocrista runs in a large curve to the posterobuccal corner. A curved bulge on the lingual side creates the small lingual part of the tooth. Buccally of the ridge, there is a groove, ending in a shallow basin. There are three cingula around the tooth, at the anterior, posterobuccal and posterior sides; the first bears a small cuspule. The P4 has three roots. The large paracone ridge and style superficially resemble the postmetacrista of the molars. The protocone is anterolingual to the paracone. A small anterior ridge curves around the paracone margin, forming a small parastyle; its posterior ridge ends short of the smallest cone, the hypocone. The only cingulum starts at the hypocone base and ends next to the paracone ridge. The four-rooted M1 is sub-rectangular, being slightly wider than long; the lingual roots are fused. The protoconule and metaconule are large. The metaconule is crescent-shaped with short anterior and posterior arms in most specimens; the posterior arm is missing in some specimens. The prehypocrista is always weaker than the postprotocrista, but invariably present. A posthypocrista is present in most specimens. The cingulum runs around the anterior, buccal and posterior sides, being interrupted by the parastyle and the metastyle. In one specimen, a small lingual cingulum is present. The M2 is nearly trapezoidal; the posterior side is narrower than the anterior one. The protocone is protruding further lingual than in the M1, the metastyle is less pronounced; the complete outline is less curved. Some specimens miss the short posterior metaconule arm. The posthypocrista is always present. The three-rooted M3 is triangular in outline. The U-shaped protocone is the largest cusp; the metacone is smaller than the paracone. In the larger specimen, the parastyle is an anterior area where the preparacrista divides into a buccal and a lingual ridge; this part is slightly damaged. In the smaller specimen, the parastyle is situated further buccally and is a rather large cone. The protoconule is a slight enlargement of the preprotocrista. There is no metaconule. Three cingula are present between metacone and protocone, protocone margin and parastyle and parastyle to the tooth margin posterobuccal of the paracone, respectively.

The c inf. has one large, posterior root. The crown is elliptical and curves a bit in lingual direction. The protoconid has a rounded tip in the anterior part and a posterior ridge ending in a tiny cuspule. The p1 has one large root. The overall outline resembles a bent ellipse with a lesser anterior than posterior curve. Small anterior and posterior cuspules are present, but no cingula. The p2 and all teeth posterior to it have two roots. It is similar to the p1, but the anterior and posterior cuspules are much weaker and formed by small cingulids; they are positioned further lingually. The occlusal outline of the dp4 forms more or less a parallelogram. It resembles the p4, but its cusps are lower, the paraconid is larger and the protoconid and metaconid are nearly of equal size. A blunt posterior ridge starts at the protoconid. The posterolingual faint entoconid is created by the cingulid. The shape of the p4 is sub-rectangular to sub-triangular. The conical protoconid is the dominating cusp. Its posterior flank is flattened and wears a buccal bulge. The lingual side carries a bulge or a tiny conical metaconid; in one specimen, it is a simple wall. The paraconid is a small anterolingual cuspule. The only cingulid is the postcingulid, which reaches up as a small anterior ridge ending at the protoconid flank. At the lingual end, it connects to a tiny entoconid. The m1 has a small but clearly defined, conical paraconid. The metaconid is only a bit smaller than the protoconid. The trigonid basin is an open valley. The talonid is a bit shorter and wider than the trigonid. The entoconid is the second largest cusp. The entocristid connects to a small and low metacristid. The hypoflexid is small; the talonid basin is large and closed. The postcingulid reaches upward from the base of the hypoconid; it connects to the postcristid or ends slightly short of it. In one specimen, it connects to the entoconid part of the postcristid, creating a small gap in the postcristid. The m2 resembles the m1, but is relatively shorter. The paraconid is just a small enlargement at the end of the paralophid; it lies less lingual than in the m1. The only available m3 is still in crypt. The general outline resembles the m2, but the talonid is narrower. There are no cingulids visible.

The mandible is high and robust, the lingual and buccal sides flattened. The aboral margin is convex, but straightened below the molars. The foramen mentale lies below the anterior root of the p4. The only part of a mandible anterior to the molars is a fractured mandible carrying a canine, which is large and also broken. There are three alveoli

Figure 8. A–R, U – *Galerix aurelianensis* Ziegler, 1990 from Petersbuch 28 (Germany, Early Miocene). • A – NMA 2012-25/2058: C sin; B – NMA 2012-24/2058: P1 sin; C – NMA 2012-24/2058: P2 sin; D – NMA 2012-26/2058: dP3 sin; E – NMA 2012-23/2058: P4 dext, reversed; F – NMA 2012-18/2058: M1 sin; G – NMA 2012-19/2058: M2 dext, reversed; H – NMA 2012-21/2058: M3 sin; I – NMA 2012-22/2058: M3 sin; J – NMA 2012-34/2058: c dext, reversed; K – NMA 2012-35/2058: p1 dext, reversed; L –NMA 2012-31/2058: p2 dext, reversed; M – NMA 2012-30/2058: dp4 sin; N – NMA 2012-32/2058: p4 sin; O – NMA 2012-28/2058: m1 dext, reversed; P – NMA 2012-27/2058: m2 dext, reversed; Q – NMA 2012-29/2058: m3 sin; R– NMA 2012-120/2058: humerus sin, distal part; U – NMA 2012-136/2058: astragalus sin. • S, T, V, W – Galericinae gen. et sp. indet. from Petersbuch 28. S – NMA 2012-16/2058: P4 sin; T – NMA 2012-15/2058: M2 dext, reversed; V – NMA 2012-14/2058: M3 sin; W – NMA 2012/17/2058: m3 dext, reversed.

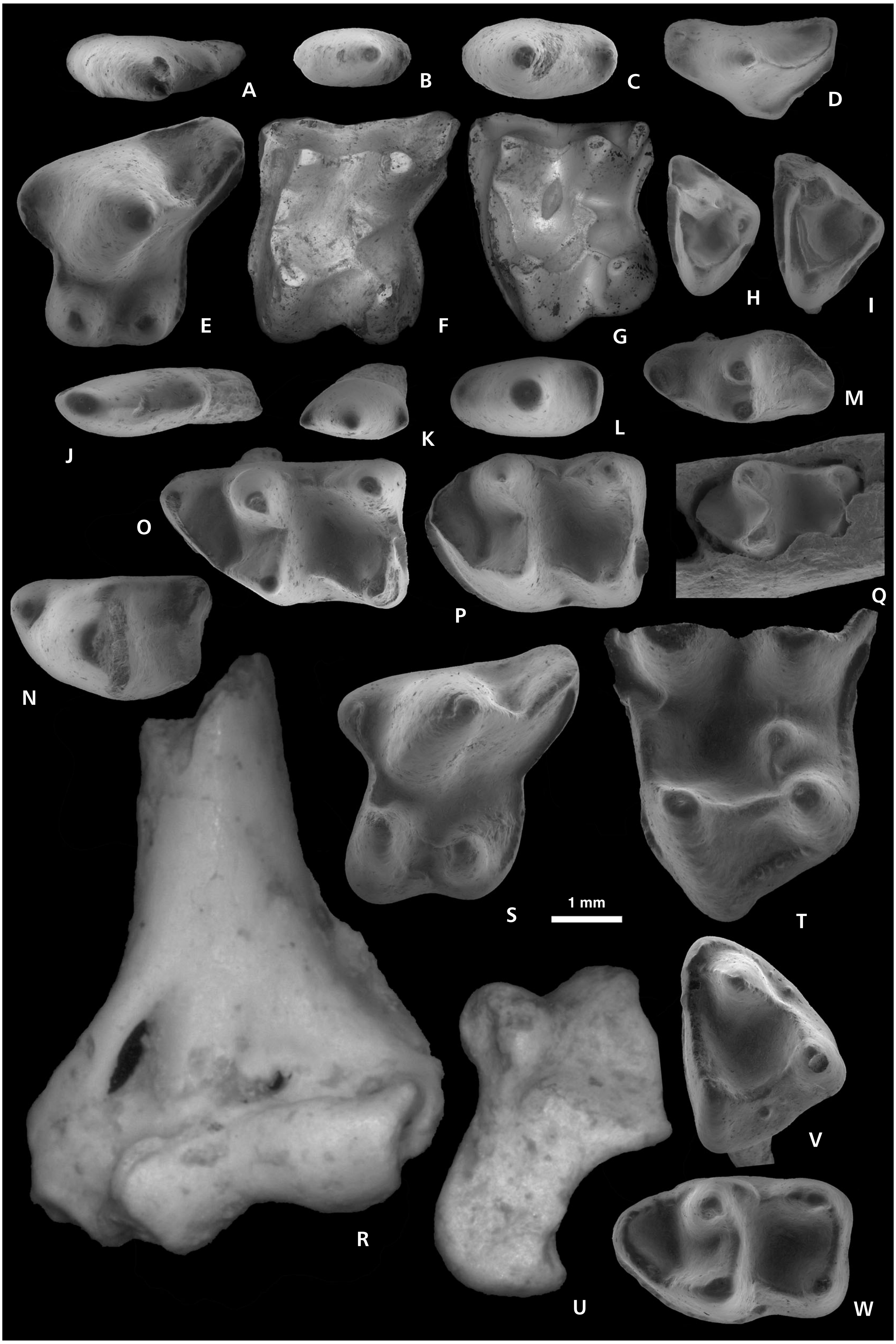

A
B
C
D
E
F
G
H
I
J
K
L
M
N
O
P
Q
R
S
1 mm
T
U
V
W

Table 3. Measurements of the teeth and bones of *Galerix aurelianensis* Ziegler, 1990 from Petersbuch 28 (Germany, Early Miocene). * – the lower mandible is juvenile with the only m3 still in crypt; measurements of this m3 are therefore estimated. ** – the measurements of the damaged specimen are still given because of the rareness.

	n (excl.)	Measured parameter	mean	min	max
C sup.	1	L	1.98		
		W	0.85		
P1	1	L	1.59		
		W	0.79		
P2	4 (1)	L	2.07	1.92	1.94
		W	1.07	1.08	0.99
dP3	3	L	2.27	2.12	2.42
		W	1.32	1.24	1.39
P4	5 (1)	L dJ	3.28	3.15	3.57
		L D	3.13	2.99	3.34
		W dJ	2.82	2.60	3.12
		W D	2.82	2.57	3.12
M1	9 (3)	L dJ	2.87	2.67	2.99
		L D	3.15	2.67	3.45
		W dJ	3.52	3.34	3.63
		W D	3.24	3.06	3.37
M2	6 (3)	L dJ	2.40	2.40	2.40
		L D	2.44	2.43	2.39
		W dJ	3.04	3.03	2.82
		W D	2.96	2.92	2.77
M3	2	L	1.24	1.45	
		W	1.92	1.99	
c inf.	2	L	2.17	1.95	
		W	0.93	0.94	
p1	1	L	1.47		
		W	0.77		
p2	3	L	1.98	1.93	2.01
		W	1.07	1.04	1.09
dp4	1	L	2.52		
		W	1.34		
p4	5	L	2.59	2.47	2.68
		L max	2.67	2.57	2.76
		W	1.67	1.60	1.80
		W max	1.83	1.71	2.10
m1	13 (2)	L	3.35	3.03	3.59
		W Tr	1.94	1.68	2.13
		W Ta	2.10	1.92	2.26
	2	HoM		3.52	3.91
m2	8	L	2.84	2.68	2.93
		W Tr	1.91	1.69	2.11
		W Ta	0.93	1.75	2.11
	2*	HoM		2.57	4.00
m3	1 (1)*	L	2.1		
		W Tr	1.3		
Humerus	1(1)	Distal W	5.56		
		Trochlea W	4.33		
		Trochlea H	1.66		
Astragalus	3 (1)	W max	3.16	3.09	2.66**
		Proximal W	2.64	2.55	2.50**
		L max	4.28	4.28	3.92**
		L of lateral facies	2.47	2.49	2.30**
		L of medial facies	1.78	1.40	

posterior to the canine; two smaller ones next to each other, and a bigger one next, posterior of which the mandible is broken. Between the second and the third alveolus, there is a small space. The foramen mentale is large, starting below the large alveolus and forming a deep and long trench ending under the posterior of the small alveoli.

Of the postcranial material, only one distal part of the humerus could be assigned to the Galericinae. The trochlea is quite strong, having a wider lateral side and a rounded wall on the medial side. The entepicondyle is a large and strong knobby flange, including a large elliptical foramen entepicondylaris. The ectepicondyle is larger, but far less protruding, forming a thin flange. Above the trochlea, a shallow fossa is present. In posterior view, the trochlea is saddle-shaped with two clear and wide ridges on each side. The olecranon fossa is large and rather deep. A round fossa is present next to the trochlea on the entepicondyle. The astragalus is rather stout. The trochlea is strongly asymmetric, with the very large lateral ridge reaching much further distal. The groove for the flexor digitorum fibularis tendon is large and bordered by a very prominent bulge. The facies articularis calcanea posterior is very large and bordered by a small ridge. The facies articularis fibularis is narrow; the attachment area of the fibuloastragalar ligament is situated far proximally. It is small and shaped like a wide ellipse. The attachment area of the tibioastragalar filament is shallow, but large. It is bordered by the narrow medial facies articularis tibialis. The facies articularis sustentaculi is large and clearly elevated. The collum of the astragalus is long and wide. The facies articularis navicularis is large. On the medial side, it continues alongside the margin and is confluent with the sustentacular facet. The bone resembles the soricid astragalus, but it is much larger. It is similar to, but a bit larger than, the one assigned to *Galerix exilis* by Ziegler (1983).

Remarks. – The clearly semilunar metaconule of most M1 and M2 place these teeth inside the Galericini Pomel, 1848 (Van den Hoek Ostende 2001). Surprisingly, some teeth lack this feature. Variability of these traits is already known in *Galerix* Pomel, 1848 (Ziegler 1983, 1990a), but is expected to be quite rare. Within the Galericini, the genus *Galerix* is to be expected in this time period (Ziegler 2005, 2006). Presumably, it is an immigrant from Anatolia that entered Europe near the MN 2/MN 3 transition (Van den Hoek Ostende 1992). Given the rather large size of the teeth and the invariably present connection between protocone and metaconule and, with exception of four teeth, also the clear connection between them and the hypocone, the classification should be *Galerix aurelianensis* Ziegler, 1990, as described by Ziegler (1990a). There is no p3 in the Petersbuch 28 material, so the comparison of p2 and p3 is impossible. A second diagnostic trait is the absence of a hypocone on the P3, but there is no P3 preserved in the material. Morphometrically, the teeth are similar to known specimens of *G. aurelianensis* (Fig. 7). The only other possible determination would be *G. remmerti* Van den Hoek Ostende, 2003 described from Spain. This species is very similar to, but smaller than *G. aurelianensis*. Its protocone-metaconule ridge is always present, whereas it is sometimes lacking in *G. aurelianensis*. In the fauna of Petersbuch 28, the ridges are invariably present, but the upper and lower molars exceed *G. remmerti* in size. Given the close morphological resemblance, we consider *G. remmerti* a close southern relative of *G. aurelianensis.* Together, they make up the first European species of *Galerix*. The large size of the molars from Petersbuch 28 are in line with this point of view. For the same reason, we think that the finds from Beaulieu (Aguilar *et al.* 2003), which were described in the same volume as the first description of *G. remmerti* (Van den Hoek Ostende 2003) should be identified as *G. remmerti*. Comparison with the measurements of that species do not only show that the original identification as *G. aurelianensis* should be updated, but also that there is no reason to assume the presence of a second species of Galericinae in the French locality. Likewise, the species from Bouzigues, determined as *Galerix* cf. *aurelianensis* (Sigé *et al.* 1997), might very well be *G. remmerti*.

Discussion

Despite being the last marsupial, *Amphiperatherium frequens* (von Meyer, 1846) is a quite common species from Lower to Middle Miocene deposits in Middle and Western Europe. Germany, especially the southern part, has the richest fossil record of the species. Numerous findings were made in Europe (Aguilar *et al.* 2003; Böttcher *et al.* 2009; Furió *et al.* 2012; Heissig 1989; Legendre 1982; Prieto 2011; Sach & Heizmann 2001; Sigé *et al.* 1997; Ziegler 1990a, 1998, 2000; Ziegler & Fahlbusch 1986; Ziegler & Mörs 2000). The sites range from MN 2 to MN 6. The subspecies ranges are by far less known; more often than not, the subspecies remained undetermined. Typically, the subspecies *A. frequens wintershofense* (von Koenigswald, 1970) is present in faunas of MN 3 (von Koenigswald 1970, Ziegler 1990a, Mein 1989), whereas *A. frequens erkertshofense* (von Koenigswald, 1970) is present in younger assemblages (von Koenigswald 1970; Ziegler 1990a, 1999). The material from Petersbuch 28 can serve as an example for mosaic evolution, because the morphological traits of the upper and lower molars show different states of evolution. The lower molars are highly developed in their reduction of the postcingulid, whereas the upper molars show no anticonus. The reduction of the anticonus would be a typical trait for *A. frequens wintershofense*, a subspecies less derived than *A. frequens erkertshofense*. The lower molars are even further developed in the reduction of the postcingulid than the specimens from the younger locality of Erkertshofen 1 (von Koenigswald 1970, Ziegler & Fahlbusch 1986). The higher reduction demonstrates that the reduction of the postcingulid is a common trend within *Amphiperatherium frequens*, but quite variable between the individual localities.

No M1 from Petersbuch 28 shows signs of the enlarged base of the protocone, another typical trait for *A. frequens wintershofense* (von Koenigswald 1970). *Amphiperatherium frequens erkertshofense* reversed the trend of reducing the anticonus, which is found in half of the M3 from Erkertshofen (von Koenigswald 1970). The assemblages from Petersbuch 28 and Schnaitheim can be interpreted as intermediate stages between *A. frequens wintershofense* and *A. frequens erkertshofense* both in size (Fig. 5) and morphology, with the Petersbuch 28 material being slightly further advanced, because some M1 from Schnaitheim show the enlarged base of the protocone of the M1 (von Koenigswald 1970). The greater size of the teeth, the enlarged base of the protocone of the M1 and the complete reduction of the anticonus in the upper molars of *A. frequens wintershofense* are therefore interpreted as adaptations towards a unique ecological situation which were reversed when the conditions changed again. The material from Petersbuch 28 therefore shows the difficulties of determining the subspecies: *Amphiperatherium frequens* was able to react to changing climatic or dietary conditions quite quickly with changes in size and morphology of its teeth and was therefore prone to develop more or less unique traits in each of its finding sites. Thus, more than the three subspecies described by von Koenigswald (1970) could be expected from different geographic regions, especially regions like France or Spain, where different ecological conditions were found (Furió *et al.* 2012).

The large galericine species is unusual both in appearance and in presence in the discussed time period. A comparable finding occurred in France (Aguilar *et al.* 2003), so the ancestral forms of *Lantanotherium* probably roamed wide areas of Europe during MN 3. Together with the material from Beaulieu, the finding of teeth comparable to

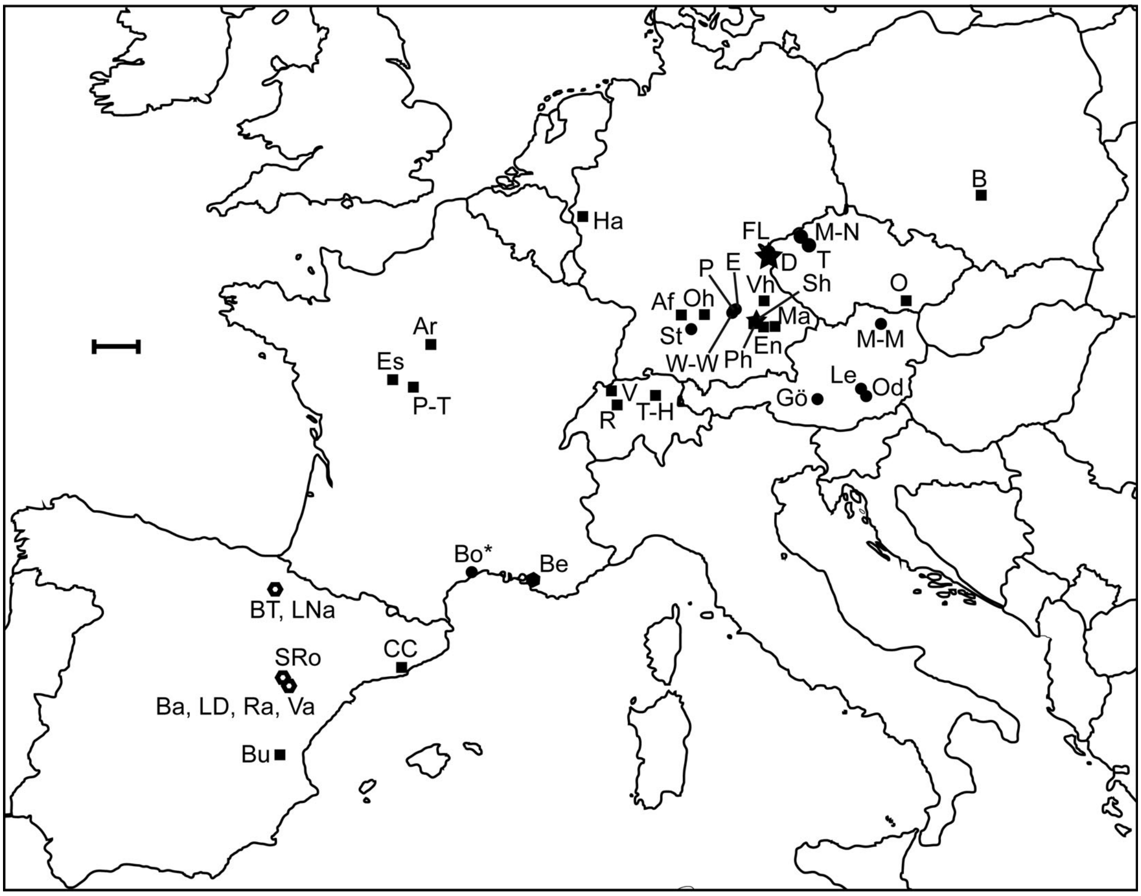


Figure 9. *Lantanotherium* Filhol, 1888, *Galerix aurelianensis* Ziegler, 1990 and *G. remmerti* Van den Hoek Ostende, 2003. The distribution of *Lantanotherium* spp. is only shown from MN 3 to MN 5. The circles represent finding sites of *Galerix aurelianensis*, the squares represent *Lantanotherium* and the star indicates a site where both taxa were found. The open polygons indicate *Galerix remmerti* alone; the filled upright polygon indicates *G. remmerti* and *Lantanotherium*. * = the species from Bouzigues was not identified for sure (Sigé *et al.* 1997); it could belong either to *G. aurelianensis* or to *G. remmerti*. Data from Van den Hoek Ostende *et al.* 2005, Furió *et al.* 2011. Spain: Ba = Bañon, BT = Barranco Tudela, Bu = Buñol, CC = Can Cerdà, LD = La Dehesa, LNa = La Nasa, Ra = Ramblar, SRo = San Roque, Va = Valhondo. France: Ar = Artenay, Es = Esvres, Be = Beaulieu, Bo = Bouzigues, P-T = Pontlevoy-Thenay. Switzerland: R = Rämisgraben, T-H = Tobel-Hombrechtikon, V = Vermes. Germany: Af = Affalterbach, E = Erkertshofen, En = Enghausen, Ha = Hambach, Ma = Maßendorf, Oh = Oggenhausen, Ph = Puttenhausen, P = Petersbuch, Sh = Sandelzhausen, St = Stubersheim, Vh = Viehhausen, W-W = Wintershof-West. Austria: M-M = Mühlbach am Manhartsberg, Le = Leoben, Gö = Göriach, Od = Oberdorf. Czech Republic: D = Dolnice, FL = Františkovy Lázně, M-N = Merkur-North, O = Ořechov, T = Tuchořice. Poland: B = Belchatow.

Lantanotherium Filhol, 1888 indicates that the genus evolution was well on its way. Its rareness may either be due to its rather impressive size, so it was not the preferred prey of the predators responsible for the micromammalian assemblages, or an autecological trait that provided some protection against avian predation. On the other hand, it may also have simply been rare because it was not well adapted towards the environment. Interestingly, the finds from Plakias (Greece, MN 9) also consist of possibly one young individual (Bruijn *et al.* 2012). Young individuals are more likely to be inexperienced and therefore be more easily preyed on by predators than adults, especially in species that are not easily caught by the predator (Temple 1987).

The lack of P3 of *Galerix aurelianensis* Ziegler, 1990, but not of dP3, and the only preserved m3 being still in crypt indicates a rather large amount of subadult individuals within *G. aurelianensis*, too. The material from Petersbuch 28 is therefore useful for any future studies on the age distribution of erinaceids. The high frequency of young individuals can be explained by their inexperience and their need to roam wide areas in search for their own territory.

Based on findings from Petersbuch 28, Petersbuch 2 and Erkertshofen 2, *G. aurelianensis* had an evolutionary trend of shortening the P4 during the time of MN 3 or early MN 4 (Fig. 7). In Petersbuch 28, the upper and lower last premolars are larger than in Petersbuch 2 and Erkertshofen 2, whereas the M3 is relatively small (Fig. 7). Likewise, the lack of the posterior arms of the metaconule on some M1 and M2 is puzzling, for the presence of these arms is typical for the whole tribe Galericini (Van den Hoek Ostende

2001). The posterior arm of the metaconule becomes enlarged in younger species of *Galerix* and in *Schizogalerix* Engesser, 1980 and *Parasorex* von Meyer, 1865 (Van den Hoek Ostende 2001). The enlarged posterior arm of the metaconule was interpreted to be related to a higher amount of frugivory for *Schizogalerix* and *Parasorex* (Van den Hoek Ostende 2001). The reduction of the metaconule posterior arm and the large P4 are probably related to a quite carnivorous diet. Like *Lantanotherium*, *Galerix aurelianensis* (Fig. 9) was present in many European localities (Furió *et al.* 2011). *Galerix remmerti*, the closest relative of *G. aurelianensis*, was found further south (Fig. 9). Like *Amphiperatherium frequens*, *Galerix aurelianensis* demonstrates the adaptive plasticity of mammalian dentition.

Conclusions

The rich site of Petersbuch 28 yielded good material of a rather primitive form of *Amphiperatherium frequens erkertshofense*, which displays a mosaic mode of evolution. The adaptations of *A. frequens wintershofense* from Wintershof-West are seen as reactions towards ecological conditions. *A. frequens* is shown to be variable and likely its "subspecies" reflect local ecological conditions. The Erinaceidae are present in Petersbuch 28 with two galericine species, a previously unknown larger galericine, which is represented by four isolated teeth only, and *Galerix aurelianensis*. *Galerix aurelianensis* has quite large P4 and lacks the posterior arm of the metaconule on some M1 and M2, demonstrating a previously unkown plasticity of the metaconule morphology and a unique ecological situation for Petersbuch 28. Based on its size, the material from Beaulieu should be redetermined as *Galerix remmerti*. Most erinaceid teeth are unworn or only weakly worn, indicating a taphonomical bias towards young individuals. Further studies on the age distribution of fossil erinaceids in different localities may shed light on the taphonomical agents at work.

Acknowledgements

We thank Reinhard Ziegler (Staatliches Museum für Naturkunde Stuttgart, Germany) for giving advice. We are indebted towards Christa Hofmann (Department for Palaeontology, University Vienna, Austria) and Hugh Rice (Department for Geodynamics and Sedimentology, University Vienna, Austria) for granting access to and helping with the SEM. Many thanks to Frank Zachos (Natural History Museum Vienna, Austria) for granting access to the mammal collection and to Alexander Bibl (Natural History Museum Vienna, Austria) for searching the collection and providing everything needed to use it. Many thanks to Norbert Frotzler (Department for Palaeontology, University Vienna, Austria) for doing the line drawings. We thank Thomas Mörs (Swedish Museum of Natural History, Stockholm, Sweden) and Marc Furió (Institut Català de Paleontologia Miquel Crusafont, Barcelona, Spain) for their reviews and for substantially improving the manuscript.

References

Abdul Aziz, H., Böhme, M., Rocholl, A., Prieto, J., Wijbrans, J.R., Bachtadse, V. & Ulbig, A. 2010. Integrated stratigraphy and ^{40}Ar/^{39}Ar chronology of the early to middle Miocene Upper Freshwater Molasse in western Bavaria (Germany). *International Journal of Earth Sciences 99*, 1859–1886. DOI 10.1007/s00531-009-0475-8

Abdul Aziz, H., Böhme, M., Rocholl, A., Zwing, A., Prieto, J., Wijbrans, J.R., Heissig, K. & Bachtadse, V. 2008. Integrated stratigraphy and ^{40}Ar/^{39}Ar chronology of the Early to Middle Miocene Upper Freshwater Molasse in eastern Bavaria (Germany). *International Journal of Earth Sciences 97*, 115–134. DOI 10.1007/s00531-006-0166-7

Aguilar, J.-P., Antoine, P.-O., Crochet, J.-Y., López-Martínez, N., Métais, G., Michaux, J. & Welcomme, J.-L. 2003. Les mammifères du Miocène inférieur de Beaulieu (Bouches-du-Rhône, France), comparaison avec Wintershof-West et le problème de la limite MN3/MN4. *Coloquios de Paleontología, Volumen Extraordinario 1*, 1–24.

Agustí, J., Cabrera, L., Garcés, M., Krijgsman, W., Oms, O. & Parés, J.M. 2001. A calibrated mammal scale for the Neogene of Western Europe. State of the art. *Earth-Science Reviews 52*, 247–260. DOI 10.1016/S0012-8252(00)00025-8

Andrews, P.J. 1990. *Owls, caves and fossils: predation, preservation and accumulation of small mammal bones in caves, with analysis of the Pleistocene cave faunas from Westbury-sub-Mendip, Somerset, UK.* 231 pp. British Museum of Natural History, London.

Aymard, A., 1850. Résponse à M. Robert. *Annales de la Societé d'Agriculture, Sciences, Arts et Commerce du Puy 14*, 80–86.

Baudelot, S. 1972. *Étude des Chiropteres, Insectivores et Ronguers du Miocene de Sansan (Gers.)* 364 pp. PhD thesis, Université Paul Sabatier, Toulouse, France.

Blainville, H.M.D. de 1839. *Osteographie des Mammifères. Tome I, Livraison 6-H, Insectivores.* 155 pp. J.B. Baillière et Fils, Paris.

Böhme, M. 2003. Miocene Climatic Optimum: evidence from Lower Vertebrates of Central Europe. *Palaeogeography, Palaeoclimatology, Palaeoecology 195(3–4)*, 389–401. DOI 10.1016/S0031-0182(03)00367-5

Böhme, M., Gregor, H.-J. & Heissig, K. 2002. The Ries- and Steinheim meteorite impacts and their effect on environmental conditions in time and space, 215–235. *In* Buffetaut, E. & Koeberl, C. (eds) *Geological and biological effects on impact events*. Springer, Berlin.

Bolliger, T. & Rummel, M. 1994. Säugetierfunde in Karstspalten – Die komplexe Genese am Beispiel eines Steinbruchs bei Petersbuch, Südliche Frankenalb (Bayern). *Mitteilungen der Bayerischen Staatssammlung für Paläontologie und historische Geologie 34*, 239–264.

Böttcher, R., Heizmann, E.P.J., Rasser, M.W. & Ziegler, R. 2009. Biostratigraphy and palaeoecology of a Middle Miocene (Karpathian, MN5) fauna of the northern margin of the North Alpine Foreland Basin (Oggenhausen 2, SW Germany). *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 254(1–2)*, 237–260. DOI 10.1127/0077-7749/2009/0011

Bruijn, H. de, Daams, R., Daxner-Höck, G., Fahlbusch, V., Ginsburg, L., Mein, P., Morales, J., Heinzmann, E., Mayhew, D.F., Van der Meulen, A.J., Schmidt-Kittler, N. & Telles Antunes, M. 1992. Report of the RCMNS working group on fossil mammals, Reisensburg 1990. *Newsletters on Stratigraphy 26(2/3),* 65–118.

Bruijn, H. de, Doukas, C.S., Hoek Ostende, L.W. van den & Zachariasse, W.J. 2012. New finds of rodents and insectivores from the Upper Miocene at Plakias (Crete, Greece). *Swiss Journal of Palaeontology 131(1)*, 61–75. DOI 10.1007/s13358-011-0030-7

Butler, P.M. 1948. On the evolution of the skull and teeth in the Erinaceidae, with special reference to fossil material in the British Museum. *Proceedings of the Zoological Society of London 118,* 446–500. DOI 10.1111/j.1096-3642.1948.tb00389.x

Cope, E.D. 1873. Third notice of extinct Vertebrata from the Tertiary of the Plains. *Paleontological Bulletin 16*, 1–8.

Crochet, J.-Y. 1979. Diversité systématique des Didelphidae (Marsupialia) Européens Tertiaires. *Geobios 12(3)*, 365–378. DOI 10.1016/S0016-6995(79)80117-5

Crochet, J.-Y. 1980. *Les Marsupiaux du Tertiaire d'Europe*. 279 pp. Singer-Polignac, Paris.

Daams, R. & Freudenthal, M. 1990. The Ramblian and the Aragonian: limits, subdivision, geographical and temporal extension, 51–59. *In* Lindsay, E.H., Fahlbusch, V. & Mein, P. *European Neogene Mammal Chronology*. Plenum, New York.

Doben-Florin, U. 1964. Die Spitzmäuse aus dem Altburdigalium von Winteshof-West und Eichstätt in Bayern. *Abhandlungen der Bayerischen Akademie der Wissenschaften, mathematisch-naturwissenschaftliche Klasse (Neue Folge) 117*, 1–82.

Doukas, C.S. 1986. The Mammals of the Lower Miocene of Aliveri (Island of Evia, Greece). Part 5. The insectivores. *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen B 89(1)*, 15–38.

Engesser, B. 1980. Insectivora und Chiroptera aus dem Neogen der Türkei. *Schweizerische Paläontologische Abhandlungen 102*, 37–363.

Eronen, J.T. & Rößner, G.E. 2007. Wetland paradise lost: Miocene community dynamics in large herbivorous mammals from the German Molasse Basin. *Evolutionary Ecology Research 9*, 471–494.

Fejfar, O., Dvořák, Z. & Kadlecová, E. 2003. New record of Early Miocene (MN3a) mammals in the open brown coal pit Merkur, North Bohemia, Czech Republic, 163–182. *In* Reumer, J.W.F. & Wessels, W. *Distribution and migration of Tertiary mammals in Eurasia. A volume in honour of Hans de Bruijn. Deinsea 10*.

Filhol, H. 1888. Étude sur les vertébrés fossils d'Issel (Aude). *Mémoirs de la Société géologique de France 3(5)*, 173–174.

Filhol, H. 1879. Étude des mammifères fossils de Saint-Gérand-le-Puy. *Annales des sciences géologiques 10*, 1–253.

Fischer, J.G. 1814. *Zoognosia tabulis synopticis illustrata, in usum praelectionum academiae imperialis medico-chirurgicae Mosquensis edita. Volumen tertium. Quadrupedum reliquorum, cetorum et montrymatum descriptionem continens*. 732 pp. Typis Nicolai Sergeidis Vsevoloszky, Moscow.

Frost, D.R., Wozencraft, W.C. & Hoffmann, R.S. 1991. Phylogenetic Relationships of Hedgehogs and Gymnures (Mammalia: Insectivora: Erinaceidae). *Smithsonian Contributions to Zoology 518*, 1–69. DOI 10.5479/si.00810282.518

Furió, M., Casanovas-Vilar, I. & Hoek Ostende, L.W. van den 2011. Predictable structure of Miocene insectivore (Lipotyphla) faunas in Western Europe along a latitudinal gradient. *Palaeogeography, Palaeoclimatology, Palaeoecology 304(3–4)*, 219–229. DOI 10.1016/j.palaeo.2010.01.039

Furió, M., Ruiz-Sánchez, F.J., Crespo, V.D., Freudenthal, M. & Montoya, P. 2012. The southernmost Miocene occurrence of the last European herpetotheriid *Amphiperatherium frequens* (Metatheria, Mammalia). *Comptes Rendus Palevol 11(5)*, 371–377. DOI 10.1016/j.crpv.2012.01.004

Heissig, K. 1978. Fossilführende Spaltenfüllungen Süddeutschlands und die Ökologie ihrer Huftiere. *Mitteilungen der Bayerischen Staatssammlung für Paläontologie und historische Geologie 81*, 237–288.

Heissig, K. 1997. Mammal faunas intermediate between the reference faunas of MN 4 and MN 6 from the upper freshwater molasse of Bavaria, 537–546. *In* Aguilar, J.P., Legendre, S. & Michaux, J. (eds) *Actes du Congres BiochroM'97. Memoirs et travaux de l'Institut de Montpellier, École Pratique des Hautes Études 21*.

Heissig, K. 1989. Neue Ergebnisse zur Stratigraphie der mittleren Serie der Oberen Süßwassermolasse Bayerns. *Geologica Bavarica 94*, 239–257.

Herán, M.-A., Lécuyer, C. & Legendre, S. 2010. Cenozoic long-term terrestrial climatic evolution in Germany tracked by δ^{18}O of rodent tooth phosphate. *Palaeogeography, Palaeoclimatology, Palaeoecology 285*, 331–342. DOI 10.1016/j.palaeo.2009.11.030

Hoek Ostende, L.W. van den 1992. Insectivore faunas from the lower Miocene of Anatolia. Part 1: Erinaceidae. *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen 94(4)*, 437–467.

Hoek Ostende, L.W. van den 2001. A revised generic classification of the Galericini (Insectivora, Mammalia) with some remarks on their palaeogeography and phylogeny. *Geobios 34(6)*, 681–695. DOI 10.1016/S0016-6995(01)80029-2

Hoek Ostende, L.W. van den 2003. Insectivores (Erinaceomorpha, Soricomorpha, Mammalia) from the Ramblian of the Daroca-Calamocha area, 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 Paléontología, Volumen extr. 1*.

Hoek Ostende, L.W. van den, Doukas, C.S. & Reumer, J.W.F. (eds) 2005. *The Fossil Record of the Eurasian Neogene Insectivores. (Erinaceomorpha, Soricomorpha, Mammalia). Part I. Scripta Geologica, Special Issue 5.* 300 pp. Nationaal Natuurhistorisch Museum, Leiden.

Hooker, J.J. 2001. Tarsals of the extinct insectivoran family Nyctitheriidae (Mammalia): evidence for archontan relationships. *Zoological Journal of the Linnean Society 132(4)*, 501–529. DOI 10.1111/j.1096-3642.2001.tb02473.x

Horovitz, I., Martin, T., Bloch, J., Ladevèze, S., Kurz, C. & Sánchez-Villagra, M.R. 2009. Cranial Anatomy of the Earliest Marsupials and the Origin of Opossums. *Public Library of Science ONE 4(12), e8278*, 1–9. DOI 10.1371/journal.pone.0008278

Huxley, T.H. 1880. On the application of the laws of evolution on the arrangement of the Vertebrata and more particularly of the Mammalia. *Proceedings of the Zoological Society of London 43*, 649–662.

Jong, F. de 1988. Insectivora from the Upper Aragonian and Lower Vallesian of the Daroca-Villafeliche area in the Catalayud-Teruel Basin, 253–285. *In* Freudenthal, M. (ed.) *Biostratigraphy and Paleoecology of the Neogene Micromammalian Faunas from the Calatyud- Teruel Basin. Scripta Geologica, Special Issue 1.*

Klietmann, J. 2013. *Systematic and ecological analysis of Marsupialia and Eulipotyphla from Petersbuch 28 (Germany, Lower Miocene)*. 484 pp. PhD thesis, University of Vienna, Austria.

Koenigswald, W. von 1970. *Peratherium* (Marsupialia) im Ober-Oligozän und Miozän von Europa. *Abhandlungen der Bayerischen Akademie der Wissenschaften, mathematisch-naturwissenschaftliche Klasse, Neue Folge 144*, 1–79.

Kuhlemann, J. & Kempf, O. 2002. Post-Eocene evolution of the North Alpine Foreland Basin and its response to Alpine tectonics. *Sedimentary Geology 152*, 45–78. DOI 10.1016/S0037-0738(01)00285-8

Kurz, C. 2001. Osteologie einer Beutelratte (Didelphimorphia, Marsupialia, Mammalia) aus dem Mitteleozän der "Grube Messel" bei Darmstadt. *Kaupia 11*, 83–109.

Ladèveze, S., Smith, R. & Smith, T. 2012. Reassessment of the morphology and taxonomic status of the earliest herpetotheriid marsupials of Europe. *Journal of Mammalian Evolution 19(4)*, 249–261. DOI 10.1007/s10914-012-9195-0

Legendre, S. 1982. La faune de micromammifères du gisement burdigalien de Port-la-Nouvelle (Aude); complements et indications paleoecologiques. *Bulletin de la Société géologique de France 24(2)*, 383–387.

Mein, P. 1989. Die Kleinsäugerfauna des Untermiozäns (Eggenburgien) von Maigen, Niederösterreich. *Annalen des Naturhistorischen Museums Wien 90 A*, 49–58.

Meyer, C.E.H. von 1846. Mittheilungen an Professor Bronn. *Neues Jahrbuch für Mineralogie, Geognosie, Geologie und Petrefakten-Kunde 1846*, 462–476.

Meyer, C.E.H. von 1865. Briefe an den Herausgeber. *Neues Jahrbuch für Mineralogie, Geologie und Paläontologie 1865*, 215–221.

Müller, A. 1967. Die Geschichte der Familie Dimylidae (Insectivora, Mammalia) auf Grund der Funde aus tertiären Spaltenfüllungen Deutschlands. *Abhandlungen der Bayerischen Akademie der Wissenschaften, mathematisch-naturwissenschaftliche Klasse (Neue Folge) 129*, 1–93.

Pomel, A.N. 1848. Etudes sur les carnassiers insectivores (extrait). Seconde partie, Classification des insectivores. *Archive des Sciences Physiques et Naturelles, Genève 9*, 244–251.

Prieto, J. 2011. The Miocene insectivores and marsupial from Affalterbach (North Alpine Foreland Basin, Germany). *Zitteliana A 51*, 297–301.

Prieto, J., Böhme, M., Maurer, H., Heissig, K. & Abdul Aziz, H. 2009. Biostratigraphy and sedimentology of the Fluviatile Untere Serie (Early and Middle Miocene) in the central part of the North Alpine foreland Basin: implications for palaeoenvironment and climate. *International Journal of Earth Sciences 98*, 1767–1791. DOI 10.1007/s00531-008-0331-2

Rabeder, G. 1973. *Galerix* und *Lanthanotherium* (Erinaceidae, Insectivora) aus dem Pannon des Wiener Beckens. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte 1973*, 429–446.

Rosina, V.V. & Rummel, M. 2012. The bats (Chiroptera, Mammalia) from the Early Miocene of Petersbuch (Bavaria, Southern Germany). *Geobios 45(5)*, 463–478. DOI 10.1016/j.geobios.2011.10.015

Rummel, M. 1993. Neue fossilführende Karstfüllungen der Schwäbisch-Fränkischen Alb. *Documenta naturae 79*, 1–32.

Rzebik-Kowalska, B. 2005. Erinaceomorpha and Soricomorpha (Mammalia) from the Miocene of Belchatow, Poland. IV. Erinaceidae Fischer von Waldheim, 1817 and Talpidae Fischer von Waldheim, 1817. *Acta zoologica cracoviensia 48A(1–2)*, 71–91. DOI 10.3409/173491505783995707

Sach, V.J. & Heizmann, E.P.J. 2001. Stratigraphie und Säugetierfaunen der Brackwassermolasse in der Umgebung von Ulm (Südwestdeutschland). *Stuttgarter Beiträge zur Naturkunde B 310*, 1–95.

Sánchez-Villagra, M., Ladevèze, S., Horovitz, I., Argot, C., Hooker, J.J., Macrini, T.E., Martin, T., Moore-Fay, S., Muizon, C. de, Schmelzle, T. & Asher, R.J. 2007. Exceptionally preserved North American Paleogene metatherians: adaptations and discovery of a major gap in the opossum fossil record. *Biology Letters 2007(3)*, 318–322. DOI 10.1098/rsbl.2007.0090

Sigé, B., Crochet, J.-Y., Sudre, J., Aguilar, J.-P. & Escarguel, G. 1997. Nouveaux sites d'âges variés dans les remplissages karstiques du Miocène inférieur de Bouzigues (Hérault, Sud de la France). Partie I: Sites et faunes 1 (insectivores, chiroptères, artiodactyles). *Geobios, M.S. 20*, 477–483.

Steininger, F.F. 1999. Chronostratigraphy, Geochronology and Biochronology of the Miocene "European Land Mammal Mega-Zones" (ELMMZ) and the Miocene "Mammal-Zones (MN-Zones)", 9–24. *In* Rössner, G.E. & Heissig, K. (eds) *The Miocene land mammals of Europe*. Dr. Friedrich Pfeil, Munich.

Temple, S.A. 1987. Do predators always capture substandard individuals disproportionately from prey populations? *Ecology 68(3)*, 669–674. DOI 10.2307/1938472

Trouessart, E.L. 1879. Catalogue des mammifères vivants et fossiles. Insectivores. *Revue et Magasin de Zoologie, Paris 3(7)*, 219–285.

Waddell, P.J., Okada, N. & Hasegawa, M. 1999. Towards Resolving the Interordinal Relationships of Placental Mammals. *Systematic Biology 48(1)*, 1–5. DOI 10.1093/sysbio/48.1.1

Wied-Neuwied, A.P.M. zu 1826. *Beiträge zur Naturgeschichte von Brasilien. Verzeichnis der Amphibien, Säugthiere und Vögel, welche auf einer Reise zwischen dem 13ten und dem 23sten Grade Südlicher Breite im Östlichen Brasilien beobachtet wurden. II. Abtheilung Mammalia, Säugthiere*. Gr. HS priv. Landes Industrie Comptoirs, Weimar.

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).* 244 pp. PhD thesis, Ludwig-Maximilians-Universität, München, Germany.

ZIEGLER, R. 1989. Heterosoricidae und Soricidae (Insectivora, Mammalia) aus dem Oberoligozän und Untermiozän Süddeutschlands. *Stuttgarter Beiträge zur Naturkunde B 154*, 1–73.

ZIEGLER, R. 1990a. Didelphidae, Erinaceidae, Metacodontidae und Dimylidae (Mammalia) aus dem Oberoligozän und Untermiozän Süddeutschlands. *Stuttgarter Beiträge zur Naturkunde B 158*, 1–99.

ZIEGLER, R. 1990b. Talpidae (Insectivora, Mammalia) aus dem Oberoligozän und Untermiozän Süddeutschlands. *Stuttgarter Beiträge zur Naturkunde B 167*, 1–89.

ZIEGLER, R. 1998. Wirbeltiere aus dem Untermiozän des Lignit-Tagebaues Oberdorf (Weststeirisches Becken, Österreich). 5. Marsupialia, Insectivora und Chiroptera (Mammalia). *Annalen des Naturhistorischen Museums in Wien 99 A*, 43–97.

ZIEGLER, R. 1999. Order Marsupialia. *Amphiperatherium*, the last European Opossum, 49–52. *In* RÖSSNER, G.E. & HEISSIG, K. (eds) *The Miocene land mammals of Europe*. Dr. Friedrich Pfeil, Munich.

ZIEGLER, R. 2000. The Miocene Fossil – Lagerstätte Sandelzhausen, 17. Marsupialia, Lipotyphla and Chiroptera. *Senckenbergiana lethaea 80(1)*, 81–127.

ZIEGLER, R. 2003a. Bats (Chiroptera, Mammalia) from Middle Miocene karstic fissure fillings of Petersbuch near Eichstätt, Southern Franconian Alb (Bavaria). *Geobios 36(4)*, 447–490. DOI 10.1016/S0016-6995(03)00043-3

ZIEGLER, R. 2003b. Shrews (Soricidae, Mammalia) from the Middle Miocene karstic fissure fillings of Petersbuch near Eichstätt, Southern Franconian Alb (Bavaria). *Paläontologische Zeitschrift 77(2)*, 303–322. DOI 10.1007/BF03006944

ZIEGLER, R. 2003c. Moles (Talpidae) from the Middle Miocene of South Germany. *Acta Palaeontologica Polonica 48(4)*, 617–648.

ZIEGLER, R. 2005. Erinaceidae and Dimylidae from the Late Middle Miocene of South Germany. *Senckenbergiana lethaea 85(1)*, 131–152.

ZIEGLER, R. 2006. Miocene Insectivores from Austria and Germany – an overview, 481–494. *In* HOEK OSTENDE, L.W. VAN DEN, NAGEL, D. & HARZHAUSER, M. (eds) *Festschrift für Univ.-Doz. Dr. Gudrun Daxner-Höck gewidmet aus Anlass ihres 65. Geburtstages. Beiträge zur Paläontologie 30.*

ZIEGLER, R. 2007. The nyctitheriids (Lipotyphla, Mammalia) from Early Oligocene fissure fillings in South Germany. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 246(2)*, 183–203.
DOI 10.1127/0077-7749/2007/0246-0183

ZIEGLER, R. & FAHLBUSCH, V. 1986. Kleinsäuger – Faunen aus der basalen Oberen Süßwasser-Molasse Niederbayerns. *Zitteliana 14*, 2–80.

ZIEGLER, R. & MÖRS, T. 2000. Marsupialia, Lipotyphla und Chiroptera (Mammalia) aus dem Miozän des Braunkohlentagebaus Hambach (Niederrheinische Bucht, NW-Deutschland). *Palaeontographica A 257(1–3)*, 1–26.