

Miocene Insectivores from Austria and Germany

– An Overview

by

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ZIEGLER, R., 2006. Miocene Insectivores from Austria and Germany – An Overview. — Beitr. Paläont., 30:481–494, Wien.

Abstract

The Miocene insectivore record of Germany and Austria is evaluated and correlated with the known bio-events. Obviously Africa did not contribute to the Miocene insectivore fauna in Europe. Probably all insectivore immigrations are of Asian origin. The Early to Middle Miocene record is strongly biased in favour of Germany; the Late Miocene is better documented in Austria.

Keywords: Miocene, insectivores, Germany, Austria, correlation, Asian origin, immigration

Kurzfassung

Die miozänen Insektivorenfaunen von Deutschland und Österreich werden mit bekannten Bio-Events korreliert. Nach der gegenwärtigen Datenlage gibt es in der miozänen Insektivorenfauna Europas keine Formen afrikanischen Ursprungs. Wahrscheinlich sind alle zugewanderten Insektivoren aus Asien. Die Insektivorenfaunen von Deutschland und Österreich sind unausgewogen, wobei Unter- und Mittelmiozän in Deutschland und das Obermiozän in Österreich besser dokumentiert sind.

1. Introduction

1.1. Historical background

In Austria and in Germany research on Miocene insectivores has a long history, though finds of insectivores, as those of small mammals in general, have been more or less accidental for most of that period. Private collectors as well as professional naturalists focussed mainly on

large vertebrates. HOFMANN (1892, 1893) was the first to describe insectivore species from several Styrian sites. THENIUS (1949) presented a revision of the insectivores of the Styrian Tertiary, that is the Miocene.

Already in the middle of the 19th century Miocene insectivore species have been described from South German localities. Most of these were authored by Hermann VON MEYER (1859, 1865), the pioneer of German insectivores research. SCHLOSSER referred to the drawings of von Meyer and published them along with the description of new species in his 1887 oeuvre. STROMER (1928, 1940) compiled the knowledge of the Late Miocene fauna from the Munich area, including a couple of insectivores.

From the 1930s on, Samuel Schaub in Switzerland and Florian Heller in Heidelberg were among the first to concentrate their research on small mammals. Systematic search for small mammals by means of screen washing techniques was established in Germany and in Austria only in the middle of the 20th century. The first large scale excavations in Austria, which yielded lots of small mammals, among them insectivores, started in 1955 in the Kohfidisch caves and fissures in Burgenland, and in the 1960s at the Eichkogel site near Mödling in the Vienna Basin. Bachmayer, Zapfe, Thenius and their students, among them Gudrun Höck, initiated and conducted the excavations at these sites. The insectivores have been made known by BACHMAYER & WILSON (1970, 1978, 1980) and by RABEDER (1973). Over the last c. 15 years GUDRUN HÖCK conducted excavations at sites in the Korneuburg Basin, the Styrian Basin, the Vienna Basin of Lower Austria and in the Molasse Basin of Upper Austria. She published a wealth of papers on rodents, thus contributing significantly to our knowledge of rodents and of the biostratigraphy of the sites. The insectivores from these sites have been published by RABEDER (1998a, b) and by the present author (ZIEGLER, 1998, 2003, 2006).

In South Germany the Lower Freshwater Molasse of the Ulm area, the Upper Fresh Water Molasse, the fissure fill sites of the Swabian and Franconian Alb and the Mainz basin yielded small mammals including insectivores. Richard Dehm from Munich and Heinz Tobien from Mainz initiated systematic research on localities in these areas, which were continued by Kurt Heissig and Volker

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Fahlbusch from Munich. In the last c. 20 years Gerhard Storch, Frankfurt and the present author contributed to the knowledge of Miocene insectivores from South Germany (see ZIEGLER et al., 2005 and references therein).

1.2. Palaeogeographic background

In South Germany the Agenian faunas are retrieved from sediments of the Lower Freshwater Molasse and from the Mainz Basin. The only karstic fissure fill sites are Tomerdingen north of Ulm and Weißenburg on the Franconian Alb. In most of the Molasse area the sediments of the Lower Fresh Water Molasse are covered by younger sediments, cropping out only at its northernmost parts near Ulm and at the eastern margins of the Rottenbuch and Murnau synclines. The southernmost Agenian fauna in Southwest Germany is Altheim-Breitenlauh 1, ca. 15 km southwest of Ulm. The sites from the Murnau syncline yielded only Late Oligocene faunas (UHLIG, 1999; UHLIG et al., 2000). The Rottenbuch syncline yielded some Agenian faunas (Rottenbuch 3, 5, 8), but only a commented list of the rodent taxa has been published (FAHLBUSCH & HEISSIG, 1987). East

of the meridian through Munich the Agenian sediments are marine, hence there are no small mammals faunas. At the time of the Upper Marine Molasse (Late Agenian to Early Orleanian) the Swabian and Franconian Alb remained a karstic plateau. There are a couple extremely rich mammals faunas from this time and area. In Austria the only Early Orleanian (MN 3) small mammal fauna is from the Maigen locality, which derives from shallow marine Eggenburgian sediments of the Austrian Molasse area. It yielded no insectivores. At the end of the Orleanian the sea withdrew from the south German Molasse basin, giving place to limno-fluviatile condition. In eastern Austria the Paratethys Sea stayed longer. Fossil mammal localities are situated in the easternmost part of the Molasse area (e.g. Schernham), at the margin of the Styrian basin (Koefflach-Voitsberg lignite area), at the margin of the Bohemian Mass (Mühlbach), or in intramontane basins like the Fohnsdorf Basin with the Apfelberg fauna. The European part of the Paratethys Sea was fully separated from the Mediterranean 11.6 million years ago. Vast parts of the sea ran dry. The refilling of the basins with water in Pannonian times gave rise to the Pannon Lake. The palaeogeographic development of the areas

Neogene Mammal units	German insectivore faunas	Austrian insectivore faunas
MN 11	Dorn-Dürkheim	Eichkogel, Kohfidisch
MN 10		Schernham, Richardhof-Wald, Neusiedl a. See
MN 9-10	Eppelsheim	
MN 9	Munich area (Aumeister, Großlappen, Unterföhring), Hammerschmiede	Götzendorf, Richardhof-Golfplatz, Stix-neusiedl, Vösendorf, Inzersdorf
MN 7-8	Öhningen, Petersbuch 6, 10,18 Petersbuch 31, 35, 48, Steinheim	Bullendorf, Jamm
MN 6	Gallenbach 2b + 2c, Gisseltshausen 1a+1b, Laimering 2, Goldberg Steinberg, Unter-neul 1a, Unterzolling 1	Apfelberg
MN 5/6	Viehhausen, Wannenwaldtobel Hambach 6C	
MN 5	Edelbeuren-Maurerkopf, Engelswies, Schellenfeld 3+4, Randecker Maar, Ma-ßendorf, Niederaichbach, Puttenhausen, Sandelzhausen	Göriach, Leoben, Mühlbach, Grund, Ober-gänserndorf, Teiritzberg 1+2
MN 4	Erkertshofen 1+2, Petersbuch 2 Forsthart, Rembach, Rauscheröd Langenau 1	Oberdorf 3+4 Schönegg, Voitsberg
MN 3	Frankfurt-Nordbassin, Wintershof-West, Schnaitheim and/or Bissingen, Stubers-heim 3	Maigen
MN 2	Budenheim and or Hessler, Haslach, Ulm-Uniklinik, Ulm-Westtangente	
MN 1-2	Eggingen (= Eckingen), Oberer Eselsberg, Fort Eselsberg and Eselsberg	
MN 1	Weisenau, Tomerdingen 1, Lautern 2, Altheim-Breitenlauh 1 Weißenburg 6	

Table 1: Sites with Miocene insectivore faunas in Germany and Austria (only published evidence taken into account).

MN units		German faunas	<i>Galerix aureliensis</i>	<i>Galerix symeonidisi</i>	<i>Galerix exilis</i>	<i>Schizogalerix</i> sp.	<i>Parasorex socialis</i>	<i>Lartantherium sansanense</i>	<i>Lartantherium sanmigueli</i>		<i>Galerix cf. aureliensis</i>	<i>Galerix symeonidisi</i>	<i>Galerix exilis</i>	<i>Galerix</i> sp.	<i>Schizogalerix pristinus</i>	<i>Schizogalerix voesendorfensis</i>	<i>Schizogalerix moedlingensis</i>	<i>Schizogalerix zapfei</i>	<i>Parasorex socialis</i>	<i>Lartantherium aff. sansanense</i>	<i>Lartantherium longirostre</i>	<i>Lartantherium sanmigueli</i>	<i>Lartantherium</i> sp.	Austrian faunas	MN units	
11		Dorn-Dürkheim			●				●							●		●				cf.	●	Kohfidisch		
10																						●		Eichkogel		
																						●		Schernham	10	
																						●		Richardh.-W.		
9																						●		Richardh.-G.		
		München					●								●							cf.		Götzendorf	9	
		Steinheim					●																	Vösendorf		
7/8		Pet. 6,10,18		cf.			●													●				Jamm	7/8	
		Pet. 31,35,48					●																			
		Laimering 2						●																		
		Gissel. 1a, 1b						●																		
6		Gallenbach 2b						●					?												Apfelberg	6
		Steinberg			●																					
		Goldberg			●																					
5-6		Viehhausen			●			aff.																		
		Wannerw.			●																					
		Hambach 6C						aff.																		
		Maßendorf						aff.						●											Teiritzberg 2	
		Puttenham			aff.			aff.						●											Teiritzberg 1	
5		Sandelzhausen			aff.			aff.													●				Leoben	
		Schellenfeld 2			aff.																				Göriach	
		Schellenfeld 4	●												●										Grund	
		Edelbeuren-M.		●							●				●										Mühlbach	
		Langenau 1	●																							
		Schellenf. 4	●																							
4		Niederaichbach	●																							
		Rauscheröd	●																							
		Rembach	●										●												Oberdorf 3	
		Forsthart	●																							
		Erkertshofen 1	●	●																						
		Erkertshofen 2	●	●																						
		Petersbuch 2	●	●																						
3		Wi.-West	●	●																						
		Stubersheim 3	●																							

Table 2: The Galericinae in the Miocene of Germany and Austria.

under study is outlined in RÖGL (1999). The northernmost Miocene small mammal fauna is known from the Lower Rhine Embayment, which is part of the North Sea Basin structure. The fauna is from lignites, which are exploited in open cast mines. The insectivores from the Miocene fauna Hambach 6C have been published by ZIEGLER & MÖRS (2000).

2. Aim and methods

In two previous contributions (ZIEGLER & DAXNER-HÖCK, 2005; ZIEGLER et al., 2005) all published insectivores from the Neogene of Germany and Austria have been listed site by site in stratigraphic order. Here Austrian and German insectivore faunas are compared in order to detect the relationships between them, migrations, and possibly lineages. The sites taken into account are listed in Tab. 1. Note that MN 7/8 means that the former separated units MN 7 and MN 8 are united into one unit (DE BRUIJN et al. 1992). MN 5-6 and MN 9-10 mean that the corresponding faunas cannot be correlated more precisely. In the tables

MN units	German faunas	<i>Amphichrinus edwardsi</i>	<i>Amphichrinus</i> sp.	" <i>Amphichrinus intermedius</i> "	<i>Atelerix depereti</i>	<i>Atelerix oenigensis</i>	<i>Atelerix</i> sp.	<i>Postpalerineaceus vireti</i>	<i>Atelerix</i> sp.	Austrian faunas	MN units
10								●		Schernham	10
9											9
	Öhningen				●						
7/8	Steinheim		●								7/8
	Petersbuch 6,10,18						●				
	Petersbuch 31,35,48						●				
6											6
5-6	Hambach 6C				●						5-6
	Wannerwaldobel	●									
5	Edelbeuren-Maurerkopf	●									
	Puttenham	●						●		Oberganserndorf	5
4	Erkertshofen 2	●									4
	Petersbuch 2	●									
3											3
2											2
1	Altheim-Breitenlauh 1	●									
	Tomerdingen 2	●									1
	Weisenau	●									

Table 3: The Erinaceinae in the Miocene of Germany and Austria.

MN units	German faunas	<i>Plesiosorex</i> cf. <i>soricinoides</i>	<i>Plesiosorex</i> <i>germanicus</i>	<i>Plesiosorex</i> <i>schaaffneri</i>	<i>Plesiosorex</i> <i>roosi</i>	<i>Plesiosorex</i> sp.		<i>Plesiosorex</i> aff. <i>germanicus</i>	<i>Plesiosorex</i> <i>styiicus</i>	<i>Plesiosorex</i> <i>evolutus</i>	<i>Plesiosorex</i> sp.	Austrian faunas	MN units
11													11
										●		Schernham	10
9-10	Eppelsheim				●								9-10
9	Hammerschmiede			●							●	Stixneusiedl	9
	München		●							●		Götzendorf	
7/8	Steinheim					●							7/8
6													6
5-6	Viehhausen		●										5-6
	Hambach 6C		●										
5	Maßendorf		●										
4									●			Schöneegg	
								cf.				Oberdorf 3	4
	Langenau 1		●					●				Oberdorf 4	
									●			Voitsberg	
3													3
2	Ulm-Westtangente	●											2

Table 4: The record of *Plesiosorex* in the Miocene of Germany and Austria.

2-11, which have been prepared on the basis of the faunal lists in the above mentioned papers, the occurrences of the species are shown. Localities are abbreviated where necessary. The Late Miocene samples from Austria are updated according to ZIEGLER (2006).

3. The insectivore record

3.1. Erinaceidae (Tab. 2-3)

In the Agenian the erinaceids are represented exclusively by the Erinaceinae, *Ampechinus edwardsi* being the only species. The earliest undisputed Miocene gymnure is *Galerix aurelianensis* from the Stubersheim 3 fauna. In the slightly younger fauna from Wintershof-West this species is accompanied by a smaller species, *Galerix symeonidisi*, which gradually replaces *G. aurelianensis* in the succession of the faunas from Petersbuch 2 – Erkertshofen 2 – Erkertshofen 1. In the MN 4 faunas of the Molasse area *G. aurelianensis* is not recorded. However, the faunas from Maßendorf and Sandelzhausen include some large teeth, which may represent either *G. aurelianensis* or *G. stehlini* or a transitional form, if the putative lineage *G. aurelianensis* – *G. stehlini* really exists. *Galerix symeonidisi* gradually evolves into *G. exilis* or is replaced by it. The alternative transition, proposed by ZIEGLER (1990a) in view of transitional teeth in the Puttenhausen sample, versus replacement favoured by VAN DEN HOEK OSTENDE & DOUKAS (2003) is discussed in ZIEGLER (2005). The stratigraphic value of both species is independent of the interpretation one adheres. *G. symeonidisi* is typical for MN 4 faunas, *G. exilis* for MN 6 faunas. The latter is replaced by *Parasorex socialis* which is common in faunas correlated with MN 7/8 and is spar-

sely recorded in two MN 9-faunules of the Munich area. They represent the last occurrence of *Galerix* in Central Europe. In Austria *Galerix* is less well-documented, *G. symeonidisi* from Oberdorf 3 being the earliest record. The other records, which are all from MN 5-faunas, are not determinable to species level.

With regard to *Schizogalerix* Germany and Austria differ markedly. This genus obviously avoided Germany largely. There is only one sparse, nevertheless doubtless find in the Late Miocene Dorn-Dürkheim fauna. In Austria it appeared already in the late Early Miocene, was absent in the Middle Miocene, and is represented with three species in the Late Miocene.

Lantanothereum appeared in Central Europe in the late Early Miocene (MN 5) with *L. aff. sansaniense*, which is slightly smaller than *L. sansaniense* from the MN 6-faunas. *Lantanothereum longirostre* is only known from its type locality Leoben in Austria, hence obviously endemic to this area. The small *L. sanmigueli* is a good stratigraphic marker and is characteristic for the Late Miocene faunas. Contrary to the galericines the erinaceines are extremely rare in the Miocene. In the Agenian *Ampechinus edwardsi* is the only known erinaceid at all in south Germany. In the MN4-5 faunas the erinaceines are represented by *Ampechinus*, in the late Middle Miocene (MN 7/8) by species of *Atelerix*. The typical Late Miocene erinaceine is *Postpalerinaceus vireti*, which is known in Central Europe only from the Schernham fauna.

3.2. Plesiosoricidae (Tab. 4)

In Europe plesiosoricids are usually very rare and represented by species of the genus *Plesiosorex*. The Agenian species is *Plesiosorex soricinoides*, which is already

MN units	German faunas	<i>Dimylus paradoxus</i>	<i>Dimylodes stehlini</i>	<i>Dimylodes vireti</i>	<i>Plesiodimylus huerzeleri</i>	<i>Plesiodimylus chantrei</i>	<i>Plesiodimylus bavaricus</i>	<i>Plesiodimylus</i> sp.	<i>Cordylodon haslachensis</i>	<i>Chainodus ulmensis</i>	<i>Chainodus eggingensis</i>	<i>Chainodus sulcatus</i>	<i>Chainodus interdedens</i>	<i>Chainodus</i> sp.	<i>Metacordylodon schlosseri</i>	<i>Plesiodimylus</i> aff. <i>chantrei</i>	<i>Plesiodimylus</i> aff. <i>bavaricus</i>	Austrian faunas	MN units
11	Dorn-Dürk.				●											●		Eichkogel	11
10																●		Schernham	10
																●		Richardh.-W.	
9																●		Richardh.-G.	9
	München				●											●		Götzend.	
7/8	Pet. 6,10,18				●														7/8
	Pet. 31,35,48				●														
6	Gissel. 1a							sp.											
	Gallenb. 2c				●											cf.		Apfelberg	6
5-6	Viehhäusen				●														5-6
	Hambach 6C				●							aff.							
	Maßendorf					●						aff.							
	Puttenh.				●														
5	Sandelzh.							●							aff.				
	Engelswies				cf.												●	Teiritzb. 2	5
	Schellenf. 3				cf.												●	Teiritzb. 1	
	Edelb.-M.							●									●	Obergäns.	
	Rauscheröd				●														
4	Rembach											●							
	Forsth.				●														
	Erk. 1				aff.							●							
	Erk. 2				aff.							●				●		Oberdorf 4	4
	Pet. 2				aff.							●				●		Oberdorf 3	
3	Wi.-West				●							●							
	Stubersh. 3											●							
	Schnait./Biss.				●							●							
	Frankf.-Nord				●							●							
2	Ob. Eselsb.											●							
	Ulm-Uniklinik													●					
	Ulm-Westt.	●		cf.					●										
	Haslach	●						●											
	Hessler													●					
	Bud./Hessler	●																	
	Budenh.	●										●							
1-2	Eggingen	●								●									1-2
1	Lautern 2		●	●					●										
	Weißb. 6		●																1
	Weisenau	●																	

Table 5: The Dimylidae in the Miocene of Germany and Austria.

known in the Late Oligocene of France. According to the record from France this species was present in Europe since the Late Oligocene. It is replaced by *Plesiosorex germanicus* in late Early to Middle Miocene faunas. The Austrian *Plesiosorex styriacus* is a quite similar form. In the Late Miocene faunas the genus is represented by the more advanced species *P. schaffneri* and *P. roosi* in Germany and by *P. evolutus* in Austria. Actually, *P. schaffneri* appeared in Europe already earlier, as evidenced by the sample from the type locality Anwil in Switzerland, which is correlated with MN 7/8 (ENGESSER, 1972). The

evolutionary changes in the lower jaw and molars include an increase in size and the elongation of the m1 trigonid, thus reflecting an optimisation of the cutting function.

3.3. Dimylidae (Tab. 5)

The peak of dimylid diversity lies in the Aagenian. The most common dimylid of this period was *Dimylus paradoxus*, which is accompanied in large faunas by a species of *Chainodus*. The latter is rare in abundance, whereas *D.*

MN units	German faunas	<i>Heterosorex n. neumayrianus</i>	<i>Heterosorex n. subsequens</i>	<i>Heterosorex n. aff. subsequens</i>	<i>Heterosorex</i> sp.	<i>Dinosorex aff. zapfei</i>	<i>Dinosorex sansaniensis</i>	<i>Dinosorex aff. pachygnathus</i>	<i>Dinosorex</i> sp.	<i>Heterosorex n. aff. subsequens</i>	<i>Dinosorex cf. zapfei</i>	<i>Dinosorex engesseri</i>	Austrian faunas	MN units
11	Dorn-Dürkheim								●					
10												●	Schernham	10
												●	Richardhof-Wald	
												●	Neusiedl	
9	Hammerschmiede											●	Richardhof-Golfplatz	9
	München				●							●	Götzendorf	
7/8	Steinheim					●								7/8
	Petersbuch 10							●						
	Petersbuch 6							●						
	Petersbuch 31							●						
	Petersbuch 35,48							●						
6	Gisseltshausen 1a, 1b						●							6
	Gallenbach 2c						●							
	Gallenbach 2b					cf.								
5-6	Viehhausen								●					5-6
	Hambach 6C				●	●								
5	Maßendorf					cf.								
	Randecker Maar								●		●		Teiritzberg 2	5
	Puttenhausen					●					●		Teiritzberg1	
	Sandelzhausen					●					●		Obergänserndorf	
4	Rembach		●							●			Oberdorf 4	4
	Forsthart		●			●				●			Oberdorf 3	
	Erkertshofen 1		●			●								
	Erkertshofen 2		●			●								
	Petersbuch 2		●			●								
3	Wintershof-West		●											3
	Stubersheim 3		●											
2	Ulm-Westtangente	●												2
	Budenheim	●												
1-2	Eggingen	●												1-2
1	Weisenau	●												1
	Lautern 2	●												

Table 6: The Heterosorinae in the Miocene of Germany and Austria.

paradoxus is extremely numerous in some faunas, e.g. Ulm-Westtangente. *D. paradoxus* already is recorded in the Late Oligocene fauna from Gaimersheim. As this is the only Oligocene record and as it is from a karstic fissure filling, we cannot exclude that *Dimylus* is a younger admixture in the Gaimersheim sample. *Chainodus* and the later *Metacordylodon* stand out by their extremely amblyodontous (bulbous) and exodontous teeth, whereas *Dimylus* and *Plesiodymilus* have a more generalised insectivore dentition. The Agenian *Dimylodes* and *Cordylodon* are intermediate in their amblyodonty and, with respect to their not reduced dental formula, less advanced than *Chainodus*. *Dimylus* evolved into *Plesiodymilus huerzeleri*, which itself gave rise to *P. chantrei*, one of the most wide-spread and long-ranging insectivore species in the Miocene of Europe. The lineage *D. paradoxus* – *P. huerzeleri* – *P. chantrei* is well documented in South Germany. Due to the absence of proper Early Miocene sites this lineage is not recognisable in Austria. There are only some scattered, though numerous finds of a species close to *P. chantrei*. *Plesiodymilus bavaricus* is a very rare species, recorded in Germany only at its type locality Maßendorf. A similar form, *P. aff. bavaricus* is known from some roughly coeval faunas from the Korneuburg basin. The *Chainodus* species mainly differ in size, the Agenian species being the largest, and in the degree of amblyodonty

of their teeth. Except *Ch. sulcatus* from the Frankfurt-Nordbassin *Ch. intercedens* is the only amblyodont form in the Early and Middle Orlanian. It evolved into the more amblyodont *Metacordylodon* in the Late Orlanian. In Austria the amblyodont forms are totally absent, *Plesiodymilus* being the only dimylid genus.

3.4. Soricidae (Tab. 6-7)

The only heterosoricine species in the Agenian is *Heterosorex neumayrianus neumayrianus*, which evolved into the Orlanian *H. neumayrianus subsequens*. *Heterosorex n. aff. subsequens* is the most advanced member of this lineage and characteristic for MN 4-faunas. In most MN 4-faunas of South Germany it is accompanied by the newly arrived *Dinosorex aff. zapfei*. *Heterosorex* vanished largely by the end of the Middle Orlanian. There is only one holdover, documented by some scanty finds, in the Hambach 6C fauna. *Dinosorex zapfei* is followed by *D. sansaniensis*, which itself is followed by *D. pachygnathus*. These species with their overlapping ranges do not constitute a single lineage (ENGESSER, 1975), but rather represent immigrations. In Austria *Heterosorex* is represented by the end of the *H. n. neumayrianus* – *H. n. subsequens* lineage. *Dinosorex* from Teiritzberg and Obergänserndorf represent the same

reach South Germany. It seems, however, likely that the material classified as *D. aff. zapfei* from the Munich area (Großlappen) is in fact referable to *D. engesseri*. Unfortun-

Table 7: The non-heterosoricine Soricidae in the Miocene of Germany and Austria.

MN units	German faunas	<i>Mygatalpa</i> aff. <i>arvernensis</i>	<i>Mygalea magna</i>	<i>Mygalea jaegeri</i>	<i>Mygalea antiqua</i>	<i>Asthenoscapter</i> sp.	<i>Storchia quinquecuspdata</i>	<i>Storchia</i> sp.	<i>Archaeodesmana vinea</i>		<i>Storchia biradicala</i>	<i>Archaeodesmana vinea</i>	Austrian faunas	MN units
11	Dorn-Dürkheim							●	●		●	●	Kohfidisch	11
											●	●	Eichkogel	
10											cf.	cf.	aff. Schernham	10
													Richardhof-Wald	
													cf. Neusiedl	
9	Hammerschmiede					●					cf.	cf.	Richardhof-Golfplatz	9
											●	cf.	Götzendorf	
											cf.		Stixneusiedl	
7/8	Petersbuch 6			●										7/8
6											cf.		Apfelberg	6
5-6	Viehhausen		●											5-6
	Hambach 6C			cf.										
5	Randecker Maar				●									5
	Sandelzhausen		●											
4	Langenau 1			cf.										4
3														3
2	Budenheim/Hessler		●											2
	Haslach				●									
	Ulm-Uniklinik			●										
	Ulm-Westtangente				●									
1-2	Eselsberg		●											1-2
1	Tomerdingen 2	●												1
	Lautern 2					●								

Table 8: The Desmaninae in the Miocene of Germany and Austria.

the entire Middle Miocene no soricids are recorded. This gap is due to the fact that there are only three Middle Miocene sites (see Tab. 1) with only a scanty faunal record. The find of three teeth of *Crusafontina* in the Bullendorf sample argues in favour of a Late Miocene correlation. The Late Miocene faunas are characterised by their wealth of *Crusafontina*. *Crusafontina* aff. *endemica* from the Vallesian (MN 9-10) sites is followed by the more advanced *C. kormosi* of the Early Turolian. Given enough material is available, this genus is suitable for distinguishing Vallesian from Turolian faunas. *Petenya dubia* and *Paenelimnocus*

nately, this assumption cannot be corroborated, as the small Munich sample includes only a dentary and a lower incisor, which do not preserve the autapomorphy of the species. The non-heterosoricine soricids, mostly Crocidosoricinae, include a variety of genera and species with widely unknown phylogenetic interrelationships. *Oligosorex* is restricted to the Agenian in South Germany. *Carposorex*, actually an Agenian genus, outlived into the Early Orlanian with one scanty record in the Stubersheim 3 fauna. *Miosorex pusilliformis* from Stubersheim 3 is the first immigrant in the Early Orlanian. *Florinia* and *Paenelimnocus* from Wintershof-West represent a slightly later immigration within the Early Orlanian. In the Middle Orlanian (MN 4) new species were added to the genera that were already present in the Early Orlanian, while *Lartetium* arrived as a new genus. In the Late Orlanian there are no new arrivals. The species, which were established earlier, continued. In Germany *Allosorex* has been recorded only in the Hambach 6C fauna (MN 5-6). But in Austria it already appeared in MN 4. The Late Astaracian (MN 7/8) brought a variety of new soricid genera to Europe: *Petenya*, *Deinsdorfia*, *Alloblarinella*, and *Paenesorex*. In the Vallesian *Crusafontina* appeared in South Germany. *Crusafontina exulta* from the Hammerschmiede may be an endemic species, whereas *C. endemica* and *C. kormosi* have wider distributions. The latter is known in Germany from the Eppelsheim and Dorn-Dürkheim faunas. In Austria the soricid documentation starts with the earliest record of *Allosorex gracilidens*. *Florinia* from Oberdorf 3 and 4 is a member of the second Orlanian immigration. In

repenningi are only scarcely documented but nonetheless characteristic for Late Miocene faunas.

3.5. Talpidae (Tab. 8-11)

Talpids are nowadays represented by relatively few species. However, in the Neogene talpid diversity was much higher. The Agenian Ulm-Westtangente sample yielded eight different talpid species, the Pliocene Wölfersheim fauna even eleven (ZIEGLER, 1990; DAHLMANN, 2001). The highest mole diversity in Austria is found in the Schernham fauna with its ten species (ZIEGLER, 2006). **Desmaninae** (Tab. 8) – The Early to Middle Miocene faunas in South Germany yielded one desmanine species in each case. *Mygatalpa*, a typical Late Oligocene to Agenian genus, has its only Miocene occurrence in Germany in the Tomerdingen fauna. *Mygalea jaegeri*, first described on the basis of the finds from Viehhausen, already appeared in the Agenian. All three *Mygalea* species overlap in their temporal ranges. *Asthenoscapter* is not an exclusive Agenian genus. *Asthenoscapter meini*, the genotypic species, is a Middle Miocene species. The absence of desmans in the MN 4-faunas of Bavaria is intriguing. Possibly, their ecologic role was played by *Desmanodon*. At least, *Desmanodon* and desmans seem to be mutually exclusive, as is, e.g., clear from the absence of desmans in faunas with *Desmanodon*, such as Forsthart, Rauscheröd, Rembach and Puttenhamen. The only marked events are the first appearances of *Storchia* in the Vallesian and of *Archaeodesmana* in the Turolian. *Stor-*

Table 9: The Talpini in the Miocene of Germany and Austria.

MN units	German faunas	<i>Geotrypus montisasin</i>	<i>Geotrypus tomerdingensis</i>	<i>Geotrypus</i> sp.	<i>Scaptomyx</i> cf. <i>edwardsi</i>	<i>Talpa tenuidentata</i>	<i>Talpa minuta</i>	<i>Talpa vallesensis</i>	<i>Talpa gliothi</i>	<i>Talpa minuta</i>	<i>Talpa gliothi</i>	<i>Talpa vallesensis</i>	Austrian faunas	MN units
11	Dorn-Dürkheim						●	●		aff.			Kohfidisch Eichkogel	11
10										aff.		●	Schernham	10
9-10	Eppelsheim							sp.						9-10
9	München			●		●								9
7/8	Petersbuch 6, 10, 18					●								7/8
	Petersbuch 31, 48					●								
6														6
5	Puttenhausen			●										
	Sandelzhausen					●				●			Leoben	5
4	Langenau 1				sp.									
	Rauscheröd			●										
	Rembach			●										
	Forsthart			●						●			Oberdorf 3	4
	Erkertshofen 1		●											
	Erkertshofen 2		●					sp.						
	Petersbuch 2		●			●								
3	Frankfurt-Nordbassin			●		●								3
	Wintershof-West			●		●								
2	Budenheim					cf.								
	Budenheim/Hessler					●								2
	Haslach	●												
	Ulm-Westtangente	●			●									
1	Tomerdingen 2	aff.	●											1
	Lautern 2	aff.												

Table 10: The Urotrichini in the Miocene of Germany and Austria.

MN units	German faunas	<i>Paratalpa brachychir</i>	<i>Paratalpa meyeri</i>	<i>Myxomygale minor</i>	<i>Myxomygale hutchisoni</i>	<i>Myxomygale gracilis</i>	? <i>Urotrichus dolichochoir</i>	<i>Urotrichini</i> gen. et sp. indet.	<i>Tenuibrachiatum storchi</i>		<i>Urotrichus giganteus</i>	<i>Urotrichini</i> gen. et sp. indet.	Austrian faunas	MN units
11	Dorn-Dürkheim										●		Eichkogel	11
10											●	●	Schernham	10
9											●		Götzendorf	9
7-8	Petersbuch 6						●							7-8
	Petersbuch 10					●		●						
	Petersbuch 31							●	●					
6														6
5	Sandelzhausen				●		cf.							5
4	Erkersthofen 1				●									4
	Erkersthofen 2				●									
	Petersbuch 2				●									
3	Wintershof-West				●									3
	Stubersheim 3		?		●									
	Frankfurt-Nordbassin		?											
2	Budenheim/Hessler	●		sp.										2
	Budenheim			sp.										
	Haslach		●											
	Ulm-Westtangente		●	●										
1-2	Eggingen		●											1-2
1	Weisenau	●												1
	Lautern 2			sp.										

chia quinquecuspidata from the Hammerschmiede was described as Desmanella quinquecuspidata by MAYR & FAHLBUSCH (1975). DAHLMANN (2001) noted the similarities with Storchia, but hesitated to refer quinquecuspidata to that genus. ZIEGLER (2006) finally referred the species to Storchia. In the Early Miocene of Austria no desmans

MN units			Scalopini		Talpi(n/d)ae	inc. sed.		Scalopin		Talpi(n/d)ae	inc. sed.				MN units							
	German faunas	<i>Hugueneya primitiva</i>	<i>Proscapanus intercedens</i>	<i>Proscapanus sansaniensis</i>	<i>Proscapanus</i> sp.	<i>Desmanella</i> sp.	<i>Desmanella engesseri</i>	<i>Desmanella stehlini</i>	<i>Desmanella rietscheli</i>	<i>Desmanodon antiquus</i>		<i>Proscapanus cf. intercedens</i>	<i>Proscapanus aff. sansaniensis</i>	<i>Proscapanus minor</i>	<i>Proscapanus austriacus</i>	<i>Desmanella</i> sp.	<i>Desmanella aff. engesseri</i>	<i>Desmanella aff. rietscheli</i>	<i>Desmanodon cf. antiquus</i>	<i>Desmanodon</i> sp.	Austrian faunas	
11																		●			Kohfidisch	11
	Dorn-Dürkheim							●						●	●			●			Eichkogel	
10														●	●			●			Schernham	10
														●				●			Richardhof-Wald	
														●				●			Richardhof-Golf.	
9	München		●													●		●			Götzendorf	9
																●	cf.				Stixneusiedl	
7-8	Steinheim		●																			
	Petersbuch 18							●														
	Petersbuch 10		●																			
	Petersbuch 6							●														
	Petersbuch 31		●	●				●														
	Petersbuch 35,48		●																			
6	Unterzolling 1a		●																			
	Unterneul 1a		●																			
	Laimering 2		●																			
	Gisseltshausen 1a,1b		●																			
	Gallenbach 2b		●																			
	Steinberg		●																			
5-6	Viehhausen		●		●																	
	Wannenwaldtobel		cf.																			
	Hambach 6C		●																			
5	Puttenhausen		●						●			●						●			Obergänserndorf	5
	Sandelzhausen		●	●								●									Teiritzberg 1	
4	Langenau 1		cf.																			
	Rauscheröd		●				●			●												
	Rembach		●				●			●							●		●	●	Oberdorf 4	
	Forsthart		●				●			●		●							●	●	Oberdorf 3	4
	Erkertshofen 1		●																			
	Erkertshofen 2						●															
	Petersbuch 2	cf.	●				●															
3	Wintershof-West						●															
	Stubersheim 3						aff.			?												
	Frankfurt-Nordbassin	?								?												
2	Budenheim/Hessler	●																				
	Budenheim	●																				
	Ulm-Uniklinik	aff.																				
	Ulm-Westtangente					●																
1-2	Eggingen	●																				1-2
1	Altheim-Breitenlauh 1					●																1

Table 11: The Scalopini in the Miocene of Germany and Austria.

have been recorded, though for example the Oberdorf environments yielded suitable habitats for these animals. As in Bavaria, their niche was occupied by *Desmanodon*. *Storchia* obviously appeared in Austria somewhat earlier than in Germany, as indicated by the scanty record from Apfelberg. It should not be emphasised. Possibly, it represents an early push. The scarce record of *Storchia meszaroshi* from the Bonanza site near Devínska Nová Ves in Slovakia, which is also correlated with MN 6, probably represents the same push (SABOL, 2005). In Austria

Archaeodesmana is well documented in Vallesian faunas, hence also earlier than in Germany.
Talpinae (Talpini) (Tab. 9) – In the Agenian this tribe is represented by two species of *Geotrypus*, *G. tomerdingensis* and *G. montisasini*, and by *Talpa tenuidentata*. The earlier part of the Orléanian (MN 3–MN4a) brought only different *Geotrypus* species. In the fauna of the lowermost Upper Freshwater Molasse in Bavaria Forsthart, Rembach and Rauscheröd a form similar to *Scaptonyx edwardsi* had its first appearance in Germany. *Talpa minuta* is an

extremely long-ranging species. In the Early Turolian two new species – *T. gilothi* and *T. vallesensis* – are documented in Germany. In Austria the Talpini are represented by *Talpa* only.

Talpinae (Urotrichini) (Tab. 10) – The Agenian is characterised by the presence of several *Paratalpa* species. The questionable record from Stubersheim 3 can also belong to *Desmanodon*. In the absence of their characteristic humeri *Paratalpa* and *Desmanodon* cannot be distinguished. The humerus from the Frankfurt-Nordbassin, which was referred to *Talpa? meyeri* by STEPHAN-HARTL (1972), certainly does not belong to *Desmanodon*. According to the figure in STEPHAN-HARTL (1972: pl. 5, fig. 1) it is similar to *Hugueneya primitiva*. The genus *Paratalpa* seems to have become extinct at the end of the Agenian.

Myxomygale hutchisoni is obviously an Orleanian immigrant. The genus itself is known in Europe already the Oligocene (*M. antiqua*) and in the Agenian (*M. minor*). In the late Middle Miocene new Urotrichini appeared with *Tenuibrachiatum* and ?*Urotrichus dolichochir*. In the Late Miocene of Germany no Urotrichini have been recorded. In Austria the Urotrichini appeared only in the Late Miocene with the large *Urotrichus giganteus*.

Talpinae (Scalopini) and Talpini/idae incertae sedis (Tab. 11) – *Hugueneya primitiva* is an Agenian scalopine with a possible holdover in the fauna of Frankfurt-Nordbassin. *Desmanella engesseri* is the first Orleanian immigrant in South Germany. The genus itself appeared in the Late Oligocene with some records in the faunas of Eggingen-Mittelhart 1+2 and was present the Agenian as evidenced by occurrences in the faunas of Altheim-Breitenlauh 1 and Ulm-Westtangente. *Proscapanus intercedens* and *Desmanodon antiquus* are Middle Orleanian immigrants. By the end of the Orleanian *P. intercedens* evolved into the more advanced *P. sansaniensis*, which is common in Middle Miocene (MN6-8) faunas. *Desmanella stehlini* appeared in the later Middle Miocene, and *D. rietscheli* in the Late Miocene.

The oldest record of *Proscapanus* in Austria is from Oberdorf 3, and was classified as *P. aff. sansaniensis* (ZIEGLER, 1998). The finds from the somewhat younger localities Teiritzberg and Obergänserndorf were identified as *P. cf. intercedens* (RABEDER, 1998a). Thus the advanced *P. sansaniensis* seems to appear prior to its predecessor, which is highly unlikely. We assume that this is an artefact, due to the difficult discrimination of the two species in scanty material. The absence of *Proscapanus* and *Desmanella* in Middle Miocene faunas from Apfelberg, Bullendorf and Jamm is probably related to the small sample sizes. In the Late Miocene two *Proscapanus* species and *Desmanella rietscheli* appeared.

4. Correlation of the insectivore first appearances with known events

As a matter of principle, it is hardly possible to distinguish lineages from directly successive immigrations, at least in insectivores. FAHLBUSCH (1983) exemplified for the Eomy-

idae the transition from one genus into another, from the Agenian *Pseudotheridomys* to the Orleanian *Ligerimys*. This lineage is based on a wealth of material and on well-delimitable and countable characters. But even this plausible and well-substantiated lineage was challenged (ALVAREZ SIERRA et al., 1987). In insectivore teeth there are no countable crests, which may be long, short or intermediate. The changes of characters are more ambiguous. For the alveolar count we need well-preserved dentaries and one has to take into account that the number of alveoles may be variable, at least to a certain degree. We also have to take into account that the sample sizes differ significantly, the German ones usually being larger, except the Late Miocene faunas, which are larger in Austria. In Austria the whole Middle Miocene is represented by three small samples only – Apfelberg, Bullendorf and Jamm – which together include only about ten specimens. On the other hand, the samples from Middle Miocene Petersbuch fissure fill sites are extraordinarily large, containing thousands of insectivore teeth and jaws.

Having this in mind, it is attempted to place the changes in the German and Austrian insectivore faunas into the known European scenario of events, which have been correlated with the circum-Mediterranean Miocene palaeogeography by RÖGL (1999). In order to avoid confusion I concentrate on the appearances of genera.

In the lower part of the Early Miocene (= Aquitanian, Late Egerian, Agenian – Early Orleanian) the open Tethyan Seaway prevented faunal exchange between Africa and Eurasia. Hence only migrations within Eurasia took place in that time span. Among the large mammals the succession *Hyotherium* (MN 1) – *Xenohyus* (MN 2) – *Anchitherium* (MN 3) indicate three distinct immigrations to Europe.

Early Agenian (MN 1) – This period brought no new erinaceids. The Oligocene galericine genera *Neurogymnurus* and *Tetracus* had become extinct. The only known erinaceine *Amphexinus* already was present in the Late Oligocene, though with species different from the Agenian *A. edwardsi*. Among the plesiosoricids even the Agenian species already is known in the Oligocene of France. *Dimylus*, with its only species *D. paradoxus*, is an Early Agenian immigrant, if we disregard the questionable record from Gaimersheim. The first appearance of *Chainodus* contributed to the Agenian dimylid diversity. An apparent newcomer is *Heterosorex*, which established the lineage *H. neumayrianus neumayrianus* – *H. neumayrianus subsequens* – *H. neumayrianus* aff. *subsequens* ranging from MN 1-MN 4. Among the talpids *Asthenoscapter* is the only Early Agenian newcomer. They may have arrived in Europe along with *Hyotherium*.

Middle Agenium (MN 2) – The soricids *Soricella* and *Carposorex* and the talpids *Mygalea* and *Talpa* appeared with *Xenohyus*.

Early Orleanian (MN 3) – It brought the first undisputed Miocene galericines with *Galerix*, a genus, which turned out to be very successful. The earliest *Galerix* is already known from the Agenian faunas of Kilçak (MN 1) and Harami (MN 2) in Turkey (VAN DEN HOEK OSTENDE, 1992). Thus, Asia Minor is a possible source area for the genus.

Galerix appeared in Europe in two directly successive waves. In the Stubersheim fauna there is only one species, in the slightly younger Wintershof-West sample there are two. *Galerix* arrived Europe along with the dimylid *Plesiodymilus*, a similarly successful genus, and with the soricids *Florinia* and *Paenelimnoecus*. *Riddleria* from some Early Miocene (MN 3) faunas in Spain with its aberrant molar morphology (see VAN DEN HOEK OSTENDE, 2003) obviously is no member of the first immigration. Possibly it descended from an Oligocene galericine on the Iberian Peninsula. The Early Orleanian immigration brought no new talpid genera.

Middle Orleanian (MN 4) – The collision of the Afro-Arabian plates with Anatolia created a land bridge, which afforded a faunal exchange between Africa and Eurasia. The most impressive immigrants from Africa are the proboscideans *Gomphotherium* and *Zygodontomys*, followed immediately by *Deinotherium* and *Archaeobelodon*. *Cricetodon*, *Megacricetodon*, *Democricetodon* and *Eotragus* are immigrants from Asia. There is no evidence that this *Gomphotherium* Land Bridge was used by African insectivores moving into Europe. *Galerix* and *Lantanothereum* rather took the opposite direction. Both genera have been recorded in the Early Miocene fauna of Songhor, *Galerix* also in Rusinga, in Kenya (BUTLER, 1978). The East African *Galerix africanus* may be a descendant of an immigrant from Turkey. *Galerix symeonidisi* spread after its first push in Wintershof-West nearly all over Europe and even arrived in Spain. Obviously all new insectivore genera are of Asian origin: the soricids *Dinosorex*, *Lartetium* and *Allosorex*, and the talpids *Scaptonyx*, *Proscapanus* and *Desmanodon*. There are no unambiguous Late Oligocene records of *Dinosorex* in Europe. The occurrences known thus far either belong to *Quercysorex*, as *Q. huerzeleri* from Rickenbach, or their assignment to *Dinosorex* cannot be corroborated due to scanty material. The first *Dinosorex* beyond doubt is *D. anatolicus* from the Early Miocene (MN 1-3) of Turkey (VAN DEN HOEK OSTENDE, 1995). *Desmanodon* obviously also originated in Turkey, the earliest species being *D. ziegleri* from the MN 2-fauna Harami 1. In the Middle Orleanian it spread all over Europe, even reaching as far as Spain (VAN DEN HOEK OSTENDE, 1997).

Late Orleanian (MN 5) – The immigration of the primate *Pliopithecus* was roughly contemporaneous with the appearance of *Schizogalerix* in Austria and *Lantanothereum* in both Germany and Austria. *Schizogalerix* appeared in South Eastern Kazakhstan (Dzungarian Alatau, MN 4-5), Turkey (Paşalar, MN 5), Greece (Antonios, MN 4-5) and Austria roughly contemporaneous (KORDIKOVA, 2000; ENGESSER, 1980; VASILEIDOU & KOUFOS, 2005). According to the record known thus far it originated possibly also in Anatolia, as shown by the sample from Hisarçik, which is correlated with MN 4 (VAN DEN HOEK OSTENDE & DOUKAS, 2003).

As evidenced by some scanty finds from France and Spain *Lantanothereum* already appeared earlier in the Miocene, in the course of the MN 4-immigration. A further newcomer is *Atelerix*, a small erinaceine.

The Middle Miocene was a period of changing seaways and intermittent land bridges in the Near East. At the base

of the Langhian (= Badenian, MN 6) the terrestrial faunal exchange between Africa and Eurasia was disrupted. The MN 5 immigration from Africa of *Pliopithecus* was prior to this marine transgression. The earliest record of *Griphopithecus* in the Engelswies fauna – the oldest Eurasian hominoid at all – may be correlated with the same immigration (HEIZMANN & BEGUN, 2001).

Early Astaracian (MN 6) – The only insectivore newcomer is *Storchia*, a desman, evidenced by one scanty find from Apfelberg (Austria) and some further finds from the Bonanza site near Devínska Nová Ves in Slovakia (SABOL, 2005). The other insectivore novelties are new species from already established genera, like *G. exilis* and *Dinosorex sansaniensis*.

Later Astaracian (MN 7/8) – The Paratethys was isolated from the open oceans. A seaway from the Mediterranean to the eastern Paratethys prevented direct continental faunal exchange between Africa/Near East and Turkey/Europe (see RÖGL, 1999: fig. 3.5). The insectivore first appearances in Germany are: *Parasorex*, which spread over vast parts of Europe; the soricids *Petenya*, *Deinsdorfia*, *Alloblarnella* and *Paenesorex*; the Urotrichini diversified with the appearances *Urotrichus* and *Tenuibrachiatum*, and new species of *Myxomygale* and *Desmanella*. This apparent wealth of new appearances is partly due to the extremely large samples from the Petersburg fissure fillings.

Early Vallesian (MN 9) – This period is correlated with one of the most remarkable Miocene bio-events, the well-known *Hipparion* event, which marks a distinct sea level drop. *Hipparion* spread all over the northern hemisphere. The erinaceid *Postpalerinaceus*, the soricid *Crusafontina*, and the desman *Archaeodesmana* appeared in the course of this immigration wave. A couple of new species of already present genera also appeared: e.g., the small *Lantanothereum sanmigueli*, *Dinosorex engesseri*, *Desmanella rietscheli*.

Late Vallesian and Early Turolian (MN 10 - MN 11) – This period brought no substantial novelties in the study area. *Crusafontina kormosi* marks a more advanced stage of evolution than its predecessor *C. endemica*. The genus *Crusafontina* was widespread in Europe, from Hungary in the East to Spain in the Southwest, and constituted several lineages (see list in VAN DAM, 2004). Summarising the evidence, there is no compelling evidence that Africa contributed to Miocene insectivore fauna in Central Europe. This may be partly due to the scanty record of this group in Africa and to the apparent absence of typical African forms like chrysochlorids in Europe. Obviously all insectivore immigrations are of Asian origin. We also have to realise that records in Germany and Austria are strongly biased, emphasising the Early and Middle Miocene in Germany and the Late Miocene in Austria. In spite of the efforts in the past 20 years, much remains to be done.

5. Acknowledgements

First of all my sincere thanks are due to Gudrun Höck for the years of good cooperation. I extend my gratitude to the

editors Doris Nagel and Lars van den Hoek Ostende for inviting me to contribute to this volume. Thanks also to Lars van den Hoek Ostende for comments on the first draft and for improving the wording.

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Jahr/Year: 2006

Band/Volume: [30](#)

Autor(en)/Author(s): Ziegler Reinhard

Artikel/Article: [Miocene Insectivores from Austria and Germany - An Overview 481-494](#)