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Erinaceidae and Dimylidae (Lipotyphla) from the Upper Middle Miocene of South Germany

With 8 Text-figures and 6 Tables

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Abstract

The erinaceids and dimylids from the South German fissure fill sites Petersbuch 6, 10, 18, 31, 35 and 48 include at least six species, among them the by far most abundant samples of *Parasorex socialis* known thus far. The phylogenetic relationships of the Miocene galericine genera of Europe are outlined. All genera are characterised by their apomorphic characters. *G. symeonidisi* is the most advanced *Galerix* species. The most conspicuous character of *Deinogalerix* is its gigantism. The genus *Parasorex* is monospecific. As the species *depereti* and *iberica* have an at least incipiently divided mesostyle they are referred to *Schizogalerix*. The apomorph characters of the erinaceine genera *Ampechinus*, *Mioechinus* and *Postpalerinaceus* are outlined. The genus *Mioechinus* is restricted to its type species. The dimylids are extremely rare, *Metacordylodon* aff. *schlosseri* being represented by two specimens of the Petersbuch 35 fauna. *Plesiodimylus chantrei*, a very common dimylid in the Miocene of Europe, is obviously mainly replaced by *Parasorex socialis*. Both species had similar habitat demands and have been vicariants. The composition of the erinaceid and dimylid fauna fits well a late Mid Miocene correlation (MN 7/8), as established by the rodent faunas. The abundance of *Parasorex* and the presence of dimylids indicate a forest component in the environment of the area and the proximity of water.

Key words: Mammalia, Erinaceidae, Dimylidae, Middle Miocene, Germany, Petersbuch, phylogeny, biostratigraphy, palaeoenvironment.

Kurzfassung

[Erinaceidae und Dimylidae (Lipotyphla) aus dem oberen Mittel-Miozän von Süddeutschland.] – Die Erinaceiden- und Dimylidenfauna aus den süddeutschen Karstspaltenfüllungen von Petersbuch 6, 10, 18, 31, 35 und 48 beinhaltet mindestens sechs Arten, darunter die mit Abstand reichsten Stichproben von *Parasorex socialis*. Die phylogenetischen Beziehungen der miozänen Galericine-Gattungen von Europa werden skizziert. Die apomorphen Merkmale aller Gattungen werden aufgelistet. *Galerix symeonidisi* ist die fortschrittlichste Art. Das auffälligste Merkmal von *Deinogalerix* ist seine Großwüchsigkeit. Die Gattung *Parasorex* ist monospezifisch. Das die Arten *depereti* und *iberica* ein zumindest oberflächlich gespaltenes Mesostyl haben, werden sie der Gattung *Schizogalerix* zugeordnet. Die Apomorphien der Erinaceinen-Gattungen *Ampechinus*, *Mioechinus* und *Postpalerinaceus* werden aufgelistet. Die Gattung *Mioechinus* ist monospezifisch. Die Dimyliden sind sehr spärlich vertreten. Von *Metacordylodon* aff. *schlosseri* gibt es nur zwei Exemplare von Petersbuch 35. *Plesiodimylus chantrei*, ein sehr häufiger Dimylide im Miozän von Europa, ist offensichtlich durch *Parasorex socialis* ersetzt. Beide Arten hatten ähnlich Biotopansforderungen und waren Vikarianten. Die Zusammensetzung der Erinaceiden- und Dimylidenfauna spricht für eine mittelmiozäne Korrelation (MN 7/8), wie sie von den Nagern erarbeitet wurde. Die Häufigkeit von *Parasorex* und die Präsenz von Dimyliden zeigen die Nähe von Bäumen und Gewässern an.

Introduction

This contribution is the final portion of a project dealing with the bats and insectivores from the Upper Middle Miocene site Petersbuch in South Germany. The extraordinarily abundant chiropteran samples have been the subject of the first part (ZIEGLER 2003a), the shrews were covered in the second part (ZIEGLER 2003b) and the moles the third (ZIEGLER 2003c). Here the erinaceids and dimylids are presented.

Erinaceids and dimylids in the Miocene of South Germany

The documentation of erinaceids from the Agenian is very poor. If present at all, they were represented by the erinaceine *Amphechinus edwardsi* (FILHOL, 1879), recorded at Tomerdingen near Ulm and in Weisenau in the Mainz Basin (TOBIEN 1939, STORCH 1988, ZIEGLER 1990). Both sites are correlated with MN 1. The Late Agenian (MN 2) is characterised by an erinaceid vacuum. Even in the extremely rich fauna from Ulm-Westtangente, which yielded thousands of insectivore remains, no erinaceids are documented. The Early Orleanian (MN 3) marks the beginning of the success of the genus *Galerix* POMEL, 1848. In the faunas of Stubersheim northeast of Ulm and Wintershof-West near Eichstätt the genus is represented by *G. aurelianensis* ZIEGLER, 1990 (ZIEGLER 1990, 1994). In the Mid Orleanian (MN 4) this species is accompanied and successively replaced by the smaller *Galerix symeonidisi* DOUKAS, 1983. By the end of the Mid Orleanian *G. aurelianensis* either became extinct or possibly evolved into *Galerix stehlini* (GAILLARD, 1929). The transition between these species is not convincingly documented. Some tooth fragments from Maßendorf, referred to *Galerix* sp. by SCHÖTZ (1988), and 22 teeth from Sandelzhausen may represent latecomers of *G. aurelianensis* or intermediates between *G. aurelianensis* ZIEGLER, 1990 and *G. stehlini*. The smaller species, *G. symeonidisi*, ranged from the Mid to the Late Orleanian. In the Late Orleanian it evolved into or, more probably, was replaced by *Galerix exilis* (BLAINVILLE, 1840). The alternative of evolution versus replacement is a matter of debate (see discussion under genus *Parasorex*). Regardless of its origin, *G. exilis* disappeared by the end of the Early Astaracian (MN 6) and *Parasorex* (= *Galerix*) *socialis* VON MEYER, 1865 invaded into Europe. It is the common galericine of faunas correlative with MN 7/8 and is known from a variety of faunas from Central to Southwest Europe. In Southwest Europe it persisted until the Early Vallesian (MN 9), and a closely related form survived in Southwest France until the Late Vallesian (MN 10).

Another galericine, the genus *Lanthanotherium*, is only rarely documented in South Germany. It seems to be a vicariant of *Galerix*. In the Maßendorf fauna *Lanthanotherium* aff. *sansaniense* (LARTET, 1851) is the dominant galericine, whereas *Galerix* is represented by two tooth fragments only. In the fauna from Hambach 6 C (MN 5/6) in the Lower Rhine Embayment *Lanthanotherium* is the only galericine (ZIEGLER & MÖRS 2000). In Puttenhausen, however, *G. aff. exilis* is much more common than *Lanthanotherium* (FAHLBUSCH & WU 1981).

In the time of the dominance of *Galerix* the erinaceines lived a shadowy existence in South Germany and adjacent areas. Their scarce remains are mostly not determinable to species level. An exception is the Oehningen fauna, which yielded the

holotype of *Mioechinus oeningensis* (LYDEKKER, 1886). This species has been recorded nowhere else in South Germany. The only well-known Late Miocene fauna in South Germany, which yielded small mammals and which is published in detail, is from Dorn-Dürkheim in Rheinhessen. The erinaceids are represented by one tooth of *Schizogalerix* sp. and by 10 teeth of *Lanthanotherium* cf. *sanmigueli* VILLALTA & CRUSAFONT, 1944 (STORCH 1978). The Dorn-Dürkheim specimen represents the only record of *Schizogalerix* in South Germany thus far.

The Miocene history of the dimylids is opposite in phase to that of the erinaceids. The Agenian is the time of success for dimylids, concerning diversity as well as abundance. Seven dimylid species are known from the Agenian of South Germany: *Dimylus paradoxus* VON MEYER, 1846, *Cordylodon haslachensis* VON MEYER, 1859, *Chainodus eggingensis* ZIEGLER, 1990, *Chainodus ulmensis* ZIEGLER, 1990, *Chainodus sulcatus* (STEPHAN-HARTL, 1972), *Chainodus intercedens* (MÜLLER, 1967) and *Dimyloides* cf. *vireti* (HÜRZELER, 1944). In the extremely rich fauna from Ulm-Westtangente even three species have been recorded, *D. paradoxus* present with more than 1200 specimens represents the largest sample of a dimylid species ever published (ZIEGLER 1990). The decline of dimylid abundance is clearly contemporaneous with the appearance of *Galerix*. The genus *Plesiodimylus* GAILLARD, 1897 replaced *Dimylus*, the earliest species being *P. huerzeleri* MÜLLER, 1967. In the Early Orleanian faunas, e. g. Wintershof-West, the latter co-occurred with *Chainodus intercedens*. The faunas correlative with MN 4 yielded *C. intercedens* together with *Plesiodimylus chantrei* GAILLARD, 1897. The latter was the dominant and in many samples the only dimylid species, ranging from MN 4 to MN 11. In some faunas it is accompanied by some remains of *Metacordylodon schlosseri* (ANDREAE, 1904). *Plesiodimylus bavaricus* SCHÖTZ, 1985 from Maßendorf has also been identified in Switzerland. In the recent years further species of *Plesiodimylus* have been described: *P. helveticus* BOLLIGER, 1992 from Jona-Tägernaustraße in Switzerland, a fauna correlative with MN 4, *P. johanni* KÄLIN & ENGESSER, 2001 from Nebelberweg (MN 9) in Switzerland, and the smallest species of the genus *P. gaillardi* MEIN & GINSBURG, 2002. In Europe the dimylids became extinct by the Early Turolian (MN 11). From the Late Orleanian to their final demise dimylids were outnumbered by galericines in most faunas.

The site

Petersbuch, which yielded the erinaceid and dimylid remains under discussion, is situated 10 km north of Eichstätt (topographic map 7033, Titting) and ca. 100 km northwest of Munich. The Upper Jurassic quarry of Petersbuch is known for its rich fossiliferous karstic fissure fillings, which have been exploited for more than 30 years. The fissure fillings P6, 10, 18, 31, 35 and 48 yielded rich mammal faunas of late Middle Miocene correlation, including among other insectivores abundant erinaceid material and some dimylids. The first three fissures are located directly adjacent to one another in the southeast corner of the quarry of the SCHÖPFEL company (see BOLLIGER & RUMMEL 1994, fig. 2). The fissures P31 – P48 are situated in the neighbouring quarry of the JUMA company. The GPS coordinates of the fissures (position format Hddd°mm'mmm'', standard for Germany WGS84, precision ±4 m) and the elevation above sea level are listed below.

Fissure	Quarry (company)	latitude	longitude	elevation (m NN)
P6	SCHÖPFEL	48°59'278''	11°11'940''	535
P10	SCHÖPFEL	48°59'284''	11°11'937''	535
P18	SCHÖPFEL	48°59'277''	11°11'943''	535
P31	JUMA	48°59'431''	11°12'049''	540
P35	JUMA	48°59'380''	11°12'027''	540
P48	JUMA	48°59'385''	11°12'021''	518

Methods

All measurements are given in mm. In the terminology of the dental elements and in the measurements of the erinaceids the work of ENGESSER (1980, figs 8-10) is widely followed. For the dimylids I mainly follow MÜLLER (1967, fig. 2-6), but, differing from this author, the i3 is interpreted as canine, the lower canine as p1 and the distolingual cusp of the M1 as metaconule, as discussed by SCHMIDT-KITTLER (1973). When measuring the width of the lower teeth, the entoconid must be exactly vertical in occlusal view. Otherwise the tooth appears distinctly wider.

In the tables, the usual biometric parameters are given. The abbreviations are: n = number of specimens, R = range of measurements, i. e. minimum and maximum value, m = arithmetic mean \pm standard error of the mean (95% probability).

Abbreviations for the measurements of the teeth and post-cranial elements are: L = length, W = width, a = anterior, Hcor = height of the coronoid, p = posterior.

All the material is from the private collection of Dr. MICHAEL RUMMEL (Weissenburg), abbreviated CRW. The figured specimens are now housed in the Naturmuseum Augsburg (Natural History Museum of Augsburg), abbreviated NHMA.

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Systematic palaeontology

Family *Erinaceidae* FISCHER VON WALDHEIM, 1817
Subfamily *Galericinae* POMEL, 1848

Genus *Parasorex* VON MEYER, 1865

Type species: *Parasorex socialis* VON MEYER, 1865

Parasorex socialis VON MEYER, 1865

Figs 1-3

Material (measurements see tab. 1):

Petersbuch 6	NHMA P6-004, 009, 013, 090, 120-123 4 left dentary fragments with teeth, left maxilla fragment with M1-M3, 5 isolated teeth CRW P6-005-008, 010-012, 014-089, 091-119, 124-126 73 dentary fragments with teeth, 37 maxilla fragments with teeth, 431 isolated teeth
Petersbuch 10	NHMA P10-030, 400-405 left maxilla fragment with P3-P4, 6 isolated upper teeth CRW P10-003-029, 031-413 Petersbuch 10, 316 dentary fragments with teeth, 76 maxilla fragments with teeth, 1013 isolated teeth
Petersbuch 18	CRW P18-014-066 27 dentary fragments with teeth, 25 maxilla fragments with teeth, 98 isolated teeth
Petersbuch 31	NHMA P31- 132-134 3 lower molars CRW P31-001-135 123 dentary fragments with teeth, 18 maxilla fragments with teeth, 570 isolated teeth
Petersbuch 35	NHMA P35-31B left p4 CRW P35-001-048 27 dentary fragments with teeth, 4 maxilla fragments with teeth, 343 isolated teeth
Petersbuch 48	CRW P48-001-082 52 dentary fragments with teeth, 11 maxilla fragments with teeth, 509 isolated teeth

Description: The dental morphology of the *Galericinae* has been described in a variety of papers (Engesser 1980, Ziegler 1983, van den Hoek Ostende 1992 and many others). Thus a detailed description of the material under study is dispensable. I confine myself to pointing out the diagnostic characters and to outlining the morphologic variability.

Dentary – The coronoid process is slightly inclined posteriorly. The condyle is situated high above the tooth row. In the vast majority of jaws the mental foramen opens under p3. Its position varies from under p2/3 to below the anterior root of p4.

Lower teeth – Most p1 are single-rooted. In some specimens two roots are fused. p2 is consistently smaller than p3. In all p4 there is a marked paralophid instead of an individualised paraconid. In some unworn specimens the paralophid is notched. The size of the metaconid shows some variability. In most specimens it is a strong cusp, thus forming together with protoconid and paralophid a real trigonid. In six out of 100 p4 from Petersbuch 6 and 23 out of 94 specimens from Petersbuch 31 the metaconid is weaker, but still clearly distinguishable. In the other samples there are only p4 with a well-developed metaconid. The m1 show a marked postcingulid, which usually joins the hypolophid. In some m1 it tapers before reaching the hypolophid. In the m2 the percentage with a shorter hypolophid is somewhat higher. The m3 have no postcingulid at all.

Maxilla – In all samples except Petersbuch 35 there are some maxilla fragments showing the infraorbital foramen opening above the anterior root of P4 or slightly before it and the origin of the zygomatic arch above the full width of M2.

Upper teeth – An important diagnostic character is the presence of a hypocone, the disto-lingual cusp, in all P3 of all samples. The hypocone protrudes more lingually than the protocone. The P3 looks roughly like a diminutive P4. The most characteristic feature of the M1 and M2 is the long posterior arm of the metaconule, which joins the posterior cingulum,

Tab. 1. *Parasorex socialis*, sample statistics of the teeth

loc.	meas.	n	R	m	s	V
Pet. 10	Lp1-m3	2	12.5-14.2	13.35		
Pet. 31	Lp1-m3	1		13.10		
Pet. 10	Lp1-p4	6	5.20-6.60	5.78±0.72	0.626	10.82
Pet. 31	Lp1-p4	2	5.42-6.40	5.92		
Pet. 6	Lm1-m3	8	7.07-7.65	7.35±0.17	0.185	2.52
Pet. 10	Lm1-m3	32	6.50-7.86	7.18±0.16	0.444	6.17
Pet. 18	Lm1-m3	2	7.42-7.50	7.46		
Pet. 31	Lm1-m3	12	7.27-8.15	7.61±0.15	0.231	3.04
Pet. 35	Lm1-m3	1		7.22		
Pet. 48	Lm1-m3	6	7.25-8.11	7.63±0.31	0.280	6
Pet. 6	Hcor	5	10.10-12.1	11.06±1.14	0.820	7.42
Pet. 10	Hcor	3	12.80-13.7	13.17		
Pet. 6	Hum1	23	2.85-3.72	3.28±0.10	0.222	6.75
Pet. 10	Hum1	100	2.51-4.05	3.19±0.06	0.034	10.16
Pet. 18	Hum1	8	3.03-3.46	3.18±0.14		
Pet. 31	Hum1	40	3.00-4.19	3.48±0.08	0.249	7.16
Pet. 35	Hum1	14	3.04-3.50	3.22±0.10	0.169	5.24
Pet. 48	Hum1	32	2.98-3.90	3.39±0.09	0.249	7.35
Pet. 10	Lcinf.	31	1.46-2.06	1.70±0.06	0.157	9.24
	Wcinf.	31	0.59-1.00	0.74±0.04	0.098	13.30
Pet. 6	Lp1	2	1.20-1.23	1.22		
	Wp1	2	0.59-0.64	0.62		
Pet. 10	Lp1	25	0.84-1.20	1.01±0.05	0.087	8.61
	Wp1	24	0.41-0.67	0.54±0.03	0.058	10.82
Pet. 18	Lp1	4	1.12-1.29	1.20		
	Wp1	4	0.55-0.61	0.58		
Pet. 31	Lp1	8	1.07-1.24	1.16±0.05	0.051	4.37
	Wp1	8	0.54-0.67	0.62±0.04	0.043	6.95
Pet. 35	Lp1	4	1.13-1.28	1.21		
	Wp1	4	0.57-0.69	0.61		
Pet. 48	Lp1	9	1.08-1.25	1.18±0.04	0.054	4.62
	Wp1	9	0.54-0.63	0.59±0.02	0.028	4.76
Pet. 6	Lp2	19	1.24-1.54	1.44±0.04	0.079	5.50
	Wp2	19	0.64-0.79	0.72±0.02	0.041	5.62
Pet. 10	Lp2	70	1.02-1.55	1.28±0.03	0.122	9.56
	Wp2	70	0.51-0.82	0.67±0.02	0.074	11.1
Pet. 10	Lp2	7	1.33-1.60	1.46±0.09	0.095	6.47
	Wp2	7	0.61-0.86	0.72±0.09	0.087	12.2
Pet. 31	Lp2	12	1.28-1.51	1.42±0.04	0.062	4.35
	Wp2	12	0.70-0.85	0.76±0.03	0.043	5.70
Pet. 35	Lp2	5	1.34-1.54	1.43		
	Wp2	5	0.70-0.82	0.75		
Pet. 48	Lp2	10	1.34-1.57	1.44±0.07	0.089	6.17
	Wp2	10	0.71-0.79	0.75±0.02	0.030	3.96
Pet. 6	Lp3	25	1.53-1.84	1.66±0.04	0.086	5.20
	Wp3	25	0.81-0.99	0.91±0.02	0.047	5.15
Pet. 10	Lp3	100	1.30-1.94	1.56±0.03	0.145	9.32
	Wp3	100	0.75-1.13	0.89±0.02	0.081	9.09
Pet. 18	Lp3	14	1.46-1.89	1.68±0.06	0.104	6.16
	Wp3	14	0.83-1.02	0.92±0.04	0.061	6.60
Pet. 31	Lp3	51	1.53-1.97	1.74±0.03	0.105	6.03
	Wp3	51	0.82-1.16	0.97±0.02	0.071	7.36
Pet. 35	Lp3	27	1.59-1.81	1.70±0.02	0.059	3.46
	Wp3	27	0.84-1.09	0.97±0.03	0.065	6.66
Pet. 48	Lp3	30	1.60-1.83	1.71±0.03	0.070	4.05
	Wp3	30	0.91-1.12	1.01±0.02	0.050	5.49
Pet. 6	Lp4	41	1.74-2.27	2.00±0.04	0.111	5.53
	Wp4	41	1.12-1.51	1.30±0.03	0.082	6.33
Pet. 10	Lp4	100	1.52-2.36	1.87±0.05	0.227	12.1
	Wp4	100	1.03-1.54	1.25±0.02	0.137	11.0
Pet. 18	Lp4	14	1.63-2.18	1.98±0.08	0.126	6.34
	Wp4	14	1.09-1.42	1.27±0.05	0.086	6.76
Pet. 31	Lp4	85	1.92-2.40	2.13±0.02	0.077	3.61
	Wp4	85	1.23-1.69	1.38±0.02	0.085	6.18
Pet. 35	Lp4	37	1.85-2.12	1.98±0.02	0.065	3.27
	Wp4	37	1.20-1.43	1.30±0.02	0.060	4.65
Pet. 48	Lp4	58	1.69-2.14	1.99±0.02	0.081	4.07
	Wp4	58	1.18-1.52	1.35±0.02	0.076	5.63
Pet. 6	Lm1	100	2.63-3.33	3.04±0.02	0.124	4.07
	Wpm1	100	1.68-2.12	1.94±0.02	0.091	4.67
Pet. 10	Lm1	100	2.62-3.42	2.94±0.04	0.200	6.81
	Wpm1	100	1.64-2.35	1.87±0.03	0.152	8.14
Pet. 18	Lm1	24	2.75-3.27	3.08±0.05	0.118	3.84
	Wpm1	24	1.75-2.14	1.95±0.05	0.110	5.64
Pet. 31	Lm1	92	2.86-3.55	3.18±0.02	0.099	3.11
	Wpm1	92	1.85-2.24	2.04±0.02	0.083	4.09
Pet. 35	Lm1	40	2.67-3.16	2.92±0.03	0.106	3.62
	Wpm1	40	1.78-2.08	1.93±0.02	0.072	3.71
Pet. 48	Lm1	67	2.83-3.34	3.05±0.03	0.111	3.63
	Wpm1	67	1.78-2.20	1.99±0.03	0.102	5.13
Pet. 6	Lm2	87	2.34-2.90	2.51±0.02	0.099	3.95
	Wm2	87	1.57-2.04	1.80±0.02	0.081	4.49
Pet. 10	Lm2	100	2.17-2.83	2.43±0.03	0.174	7.16
	Wm2	100	1.47-2.04	1.75±0.03	0.129	7.35
Pet. 18	Lm2	23	2.37-2.68	2.52±0.04	0.095	3.76
	Wm2	23	1.55-1.90	1.77±0.04	0.094	5.31
Pet. 31	Lm2	100	2.38-3.04	2.62±0.02	0.094	3.58
	Wm2	100	1.58-2.07	1.87±0.02	0.090	4.81
Pet. 35	Lm2	39	2.38-2.70	2.56±0.03	0.078	3.05
	Wm2	39	1.61-2.00	1.80±0.02	0.072	3.99
Pet. 48	Lm2	77	2.40-2.81	2.61±0.02	0.080	3.06
	Wm2	77	1.68-1.99	1.84±0.02	0.069	3.75
Pet. 6	Lm3	32	1.95-2.23	2.08±0.02	0.066	3.17
	Wam3	32	1.21-1.44	1.32±0.02	0.061	4.65
Pet. 10	Lm3	100	1.80-2.34	2.06±0.03	0.137	6.66
	Wam3	100	1.19-1.59	1.31±0.02	0.100	7.64
Pet. 18	Lm3	12	1.97-2.21	2.10±0.06	0.087	4.11
	Wam3	12	1.23-1.40	1.35±0.04	0.055	4.08
Pet. 31	Lm3	68	1.99-2.37	2.20±0.02	0.083	3.76
	Wam3	68	1.14-1.59	1.38±0.02	0.076	5.51
Pet. 35	Lm3	23	1.98-2.17	2.08±0.03	0.063	2.90
	Wam3	23	1.20-1.47	1.33±0.03	0.060	4.53
Pet. 48	Lm3	41	1.97-2.35	2.14±0.03	0.081	3.80
	Wam3	41	1.23-1.50	1.37±0.02	0.062	4.52
Pet. 10	Ld3	3	1.47-1.83	1.68		
	Wd3	2	0.78-1.03	0.91		
Pet. 35	Ld3	6	1.49-1.69	1.65±0.09	0.077	4.69
	Wd3	6	0.69-0.98	0.90±0.12	0.108	12.0
Pet. 48	Ld3	2	1.65-1.66	1.66		
	Wd3	3	0.90-1.02	0.97		
Pet. 10	Ld4	5	1.86-1.97	1.91±0.07	0.051	2.67
	Wd4	5	1.06-1.29	1.15±0.12	0.092	7.99
Pet. 10	Ld4	7	1.61-2.09	1.87±0.18	0.177	9.45
	Wd4	6	0.96-1.28	1.10±0.14	0.125	11.4
Pet. 31	Ld4	5	1.88-2.09	2.01±0.12	0.086	4.30
	Wd4	5	1.15-1.26	1.21±0.06	0.045	3.71
Pet. 35	Ld4	4	1.83-1.88	1.86		

	Wd4	4	1.07-1.14	1.10		
Pet. 48	Ld4	5	1.86-2.14	2.00±0.18	0.127	6.33
	Wd4	5	1.13-1.31	1.21±0.10	0.074	6.07
Pet. 6	LM1-M3	2	5.37-5.54	5.46		
Pet. 10	LM1-M3	3	5.72-6.00	5.84		
Pet. 31	LM1-M3	1		5.94		
Pet. 6	LCsup.	4	1.69-1.79	1.75		
	WCsup.	4	0.76-0.89	0.84		
Pet. 10	LCsup.	26	1.31-1.97	1.58±0.07	0.161	10.2
	WCsup.	26	0.57-0.95	0.76±0.04	0.107	14.1
Pet. 18	LCsup.	3	1.78-1.88	1.82		
	WCsup.	3	0.77-0.97	0.87		
Pet. 31	LCsup.	21	1.58-1.97	1.72±0.05	0.112	6.47
	WCsup.	21	0.69-0.97	0.79±0.03	0.068	8.60
Pet. 35	LCsup.	9	1.53-1.86	1.67±0.11	0.132	7.90
	WCsup.	9	0.71-0.89	0.80±0.05	0.065	8.11
Pet. 48	LCsup.	12	1.50-1.93	1.67±0.09	0.139	8.30
	WCsup.	12	0.69-0.90	0.84±0.04	0.058	6.87
Pet. 6	LP1	1		1.41		
	WP1	1		0.72		
Pet. 10	LP1	17	1.01-1.42	1.17±0.06	0.116	9.93
	WP1	17	0.54-0.76	0.63±0.03	0.064	10.1
Pet. 48	LP1	8	1.04-1.45	1.28±0.14	0.153	11.9
	WP1	8	0.59-0.74	0.69±0.05	0.052	7.47
Pet. 6	LP2	2	1.23-1.40	1.32		
	WP2	2	0.67-0.73	0.70		
Pet. 10	LP2	26	1.09-1.65	1.39±0.05	0.121	8.71
	WP2	26	0.60-0.87	0.74±0.03	0.065	8.72
Pet. 18	LP2	1		1.59		
	WP2	1		0.85		
Pet. 31	LP2	3	1.40-1.52	1.45		
	WP2	3	0.89-0.93	0.91		
Pet. 48	LP2	8	1.29-1.52	1.39±0.06	0.067	4.84
	WP2	8	0.66-0.78	0.74±0.04	0.042	5.61
Pet. 6	LP3	23	1.71-2.29	2.00±0.06	0.144	7.20
	WP3	23	1.53-2.19	1.83±0.08	0.180	10.0
Pet. 10	LP3	76	1.65-2.30	1.98±0.04	0.171	8.63
	WP3	76	1.54-2.17	1.85±0.04	0.183	9.86
Pet. 10	LP3	4	1.89-2.11	1.98		
	WP3	4	1.58-1.95	1.78		
Pet. 31	LP3	31	1.88-2.42	2.12±0.05	0.124	5.84
	WP3	31	1.67-2.15	1.90±0.05	0.124	6.55
Pet. 35	LP3	15	1.78-2.05	1.89±0.04	0.071	3.76
	WP3	15	1.55-2.02	1.77±0.08	0.132	7.43
Pet. 48	LP3	34	1.82-2.15	1.96±0.04	0.101	5.12
	WP3	34	1.65-2.02	1.87±0.03	0.089	4.74
Pet. 6	LP4	62	2.32-2.96	2.59±0.03	0.122	1.12
	WP4	62	2.23-2.76	2.48±0.03	0.115	4.62
Pet. 10	LP4	100	2.05-3.00	2.46±0.06	0.281	11.4
	WP4	100	2.06-2.80	2.40±0.04	0.193	8.06
Pet. 10	LP4	34	2.22-2.81	2.58±0.05	0.133	5.16
	WP4	34	2.25-2.62	2.45±0.03	0.082	3.35
Pet. 31	LP4	48	2.38-2.98	2.69±0.04	0.140	5.20
	WP4	48	1.61-2.83	2.51±0.06	0.221	8.82
Pet. 35	LP4	26	2.25-2.72	2.51±0.05	0.129	5.15
	WP4	26	2.28-2.64	2.46±0.04	0.095	3.84
Pet. 48	LP4	36	2.37-2.76	2.60±0.03	0.089	3.41
	WP4	36	2.30-2.83	2.56±0.04	0.104	4.08
Pet. 6	LM1	93	2.24-2.71	2.50±0.02	0.085	3.39

	WaM1	93	2.67-3.12	2.90±0.02	0.111	3.85
	WpM1	93	2.83-3.36	3.06±0.02	0.116	3.80
Pet. 10	LM1	100	2.18-2.87	2.53±0.03	0.161	6.38
	WaM1	100	2.46-3.31	2.92±0.04	0.223	7.61
	WpM1	100	2.69-3.52	3.11±0.04	0.196	6.31
Pet. 18	LM1	26	2.37-2.73	2.54±0.04	0.103	4.05
	WaM1	26	2.55-3.12	2.92±0.05	0.127	4.36
	WpM1	26	2.90-3.33	3.13±0.04	0.106	3.38
Pet. 31	LM1	76	2.55-2.95	2.71±0.02	0.088	3.24
	WaM1	76	2.82-3.31	3.05±0.02	0.093	3.05
	WpM1	76	3.02-3.66	3.26±0.03	0.114	3.50
Pet. 35	LM1	44	2.41-2.75	2.56±0.02	0.072	2.81
	WaM1	44	2.66-3.05	2.89±0.03	0.097	3.37
	WpM1	44	2.78-3.23	3.06±0.03	0.109	3.57
Pet. 48	LM1	58	2.42-2.81	2.61±0.02	0.089	3.40
	WaM1	58	2.71-3.29	3.00±0.03	0.128	4.28
	WpM1	58	2.86-3.50	3.23±0.04	0.140	4.32
Pet. 6	LM2	77	1.87-2.24	2.07±0.02	0.086	4.16
	WpM2	77	2.67-3.12	2.90±0.03	0.112	3.86
	WpM2	77	2.19-2.86	2.56±0.03	0.125	4.86
Pet. 18	LM2	33	1.84-2.22	2.04±0.03	0.082	4.01
	WpM2	33	2.64-3.07	2.88±0.04	0.097	3.39
	WpM2	33	2.30-2.71	2.53±0.04	0.108	4.24
Pet. 10	LM2	100	1.82-2.31	2.08±0.02	0.124	5.98
	WpM2	100	2.58-3.20	2.91±0.03	0.138	4.74
	WpM2	100	2.36-2.88	2.63±0.02	0.107	4.07
Pet. 31	LM2	62	1.98-2.35	2.19±0.02	0.073	3.34
	WpM2	99	2.71-3.16	2.97±0.02	0.094	3.17
	WpM2	99	2.42-2.98	2.69±0.02	0.107	3.99
Pet. 35	LM2	51	2.00-2.36	2.14±0.02	0.077	3.58
	WpM2	51	2.71-3.09	2.91±0.02	0.081	2.77
	WpM2	51	1.82-2.79	2.57±0.02	0.150	5.83
Pet. 48	LM2	68	1.96-2.32	2.15±0.03	0.078	3.60
	WpM2	68	2.73-3.27	2.99±0.03	0.110	3.68
	WpM2	68	2.32-2.96	2.68±0.03	0.126	4.68
Pet. 6	LM3	5	1.24-1.42	1.32±0.12	0.069	5.23
	WaM3	5	1.76-2.05	1.87±0.18	0.132	7.02
Pet. 10	LM3	31	1.15-1.50	1.34±0.03	0.082	6.09
	WaM3	31	1.90-2.18	2.06±0.03	0.079	3.82
Pet. 18	LM3	6	1.28-1.43	1.37±0.07	0.062	4.50
	WaM3	6	1.97-2.17	2.09±0.09	0.076	3.61
Pet. 31	LM3	35	1.27-1.59	1.42±0.03	0.077	5.46
	WaM3	35	1.82-2.42	2.10±0.04	0.102	4.88
Pet. 35	LM3	20	1.32-1.48	1.39±0.02	0.045	3.21
	WaM3	20	1.88-2.21	2.07±0.02	0.090	4.32
Pet. 48	LM3	40	1.21-1.47	1.38±0.02	0.054	3.89
	WaM3	40	1.86-2.30	2.09±0.03	0.087	4.17
Pet. 10	LD3	4	1.84-2.14	2.05		
	WD3	4	1.22-1.34	1.31		
Pet. 35	LD3	1		1.91		
	WD3	1		1.17		
Pet. 48	LD3	3	1.97-2.20	2.10		
	WD3	3	1.21-1.27	1.24		
Pet. 10	LD4	7	2.28-3.07	2.70±0.34	0.335	12.4
	WD4	7	1.89-2.49	2.25±0.20	0.204	9.08
Pet. 18	LD4	2	2.84-2.88	2.86		
	WD4	2	2.36-2.37	2.37		
Pet. 48	LD4	3	2.56-2.78	2.65		
	WD4	3	2.19-2.29	2.23		

thus connecting to the disto-buccal corner of the tooth. As a consequence the posterior cingulum is bipartitioned. Nearly all M1 and M2 show this character. Only one out of 100 M1 from

Petersbuch 10 and three out of 29 M1 from Petersbuch 18 have a shorter posterior metaconule arm. In these specimens the posterior cingulum is continuous. In most M1 and M2 the pos-

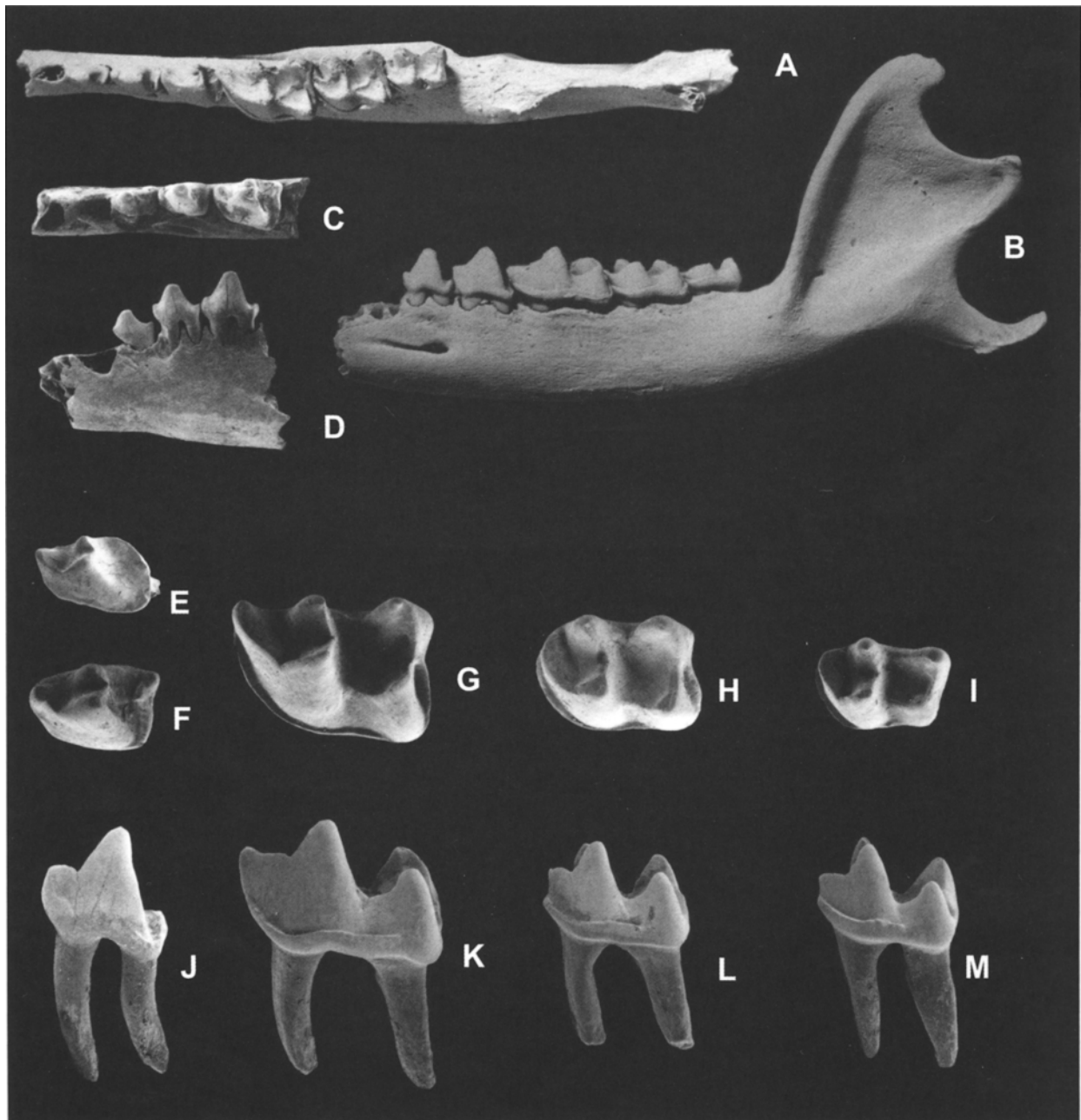


Fig. 1.

A-M. *Parasorex socialis*

- A. Left dentary with p2-m3, NHMA P6-013B1, Petersbuch 6, occlusal view.- Ca. x5.
- B. Left dentary with p3-m3, NHMA P6-013B3, Petersbuch 6, buccal view.- Ca. x5.
- C. Left dentary with p2-p4, NHMA P6-009, Petersbuch 6, occlusal view.- Ca. x5.
- D. Left dentary with p1-p3, NHMA P6-004, Petersbuch 6, buccal view.- Ca. x5.
- E. Left d4, NHMA P6-123D1, Petersbuch 6, occlusal view.- Ca. x10.
- F. Left p4, NHMA P35-31B1, Petersbuch 35, occlusal view.- Ca. x10.
- G. Left m1, NHMA P31-132D1, Petersbuch 31, occlusal view.- Ca. x10.
- H. Left m2, NHMA P31-133C1, Petersbuch 31, occlusal view.- Ca. x10.
- I. Left m3, NHMA P31-134B6, Petersbuch 31, occlusal view.- Ca. x10.
- J. Left p4, NHMA P6-123C1, Petersbuch 6, buccal view.- Ca. x10.
- K. Left m1, NHMA P6-120A1, Petersbuch 6, buccal view.- Ca. x10.
- L. Left m2, NHMA P6-121A2, Petersbuch 6, buccal view.- Ca. x10.
- M. Left m3, NHMA P6-122K1, Petersbuch 6, buccal view.- Ca. x10.

terior arm of the protocone is continuous with the anterior arm of the hypocone, the latter being somewhat weaker. Except for one out of 72 M2 from Petersbuch 48, in which the posterior arm of the protocone connects to the metaconule, there is no connection between protocone and metaconule. All M3 are devoid of a metastylar crest.

Discussion: The Petersbuch samples under study represent by far the most abundant of *P. socialis* ever published. This fact and a publication of VAN DEN HOEK OSTENDE (2001) gives reason to discuss generic allocation of *socialis* and its place among the Galericipini. The species was referred to the genus *Galerix* POMEL, 1848 by ENGESSER (1972). This allocation was accepted by most authors since that time except BUTLER (1980). VAN DEN HOEK OSTENDE (2001) considers the

differences between *G. exilis* (BLAINVILLE, 1839) and *P. socialis* sufficient to warrant a generic separation and exhumed the name *Parasorex*. In the following text, I try to outline the phylogenetic relationships between the Galericipini, which include the four fossil genera *Galerix*, *Parasorex* VON MEYER, 1865, *Schizoglaerix* ENGESSER, 1980 and the giant erinaceid from the Gargano peninsula *Deinogalerix* FREUDENTHAL, 1972 (fig. 3). Therefore it is necessary to unambiguously distinguish derived and primitive dental characters. As most galericine species are only known from teeth and jaw fragments, I confine myself to dental characters. As out-groups the Miocene genus *Lanthanotherium* FILHOL, 1888 and the Oligocene genus *Neurogymnurus* FILHOL, 1877, which belongs to the tribe Neurogymnurini BUTLER, 1948, are chosen. The choice of two out-groups helps to certainly identify the polarity of characters.

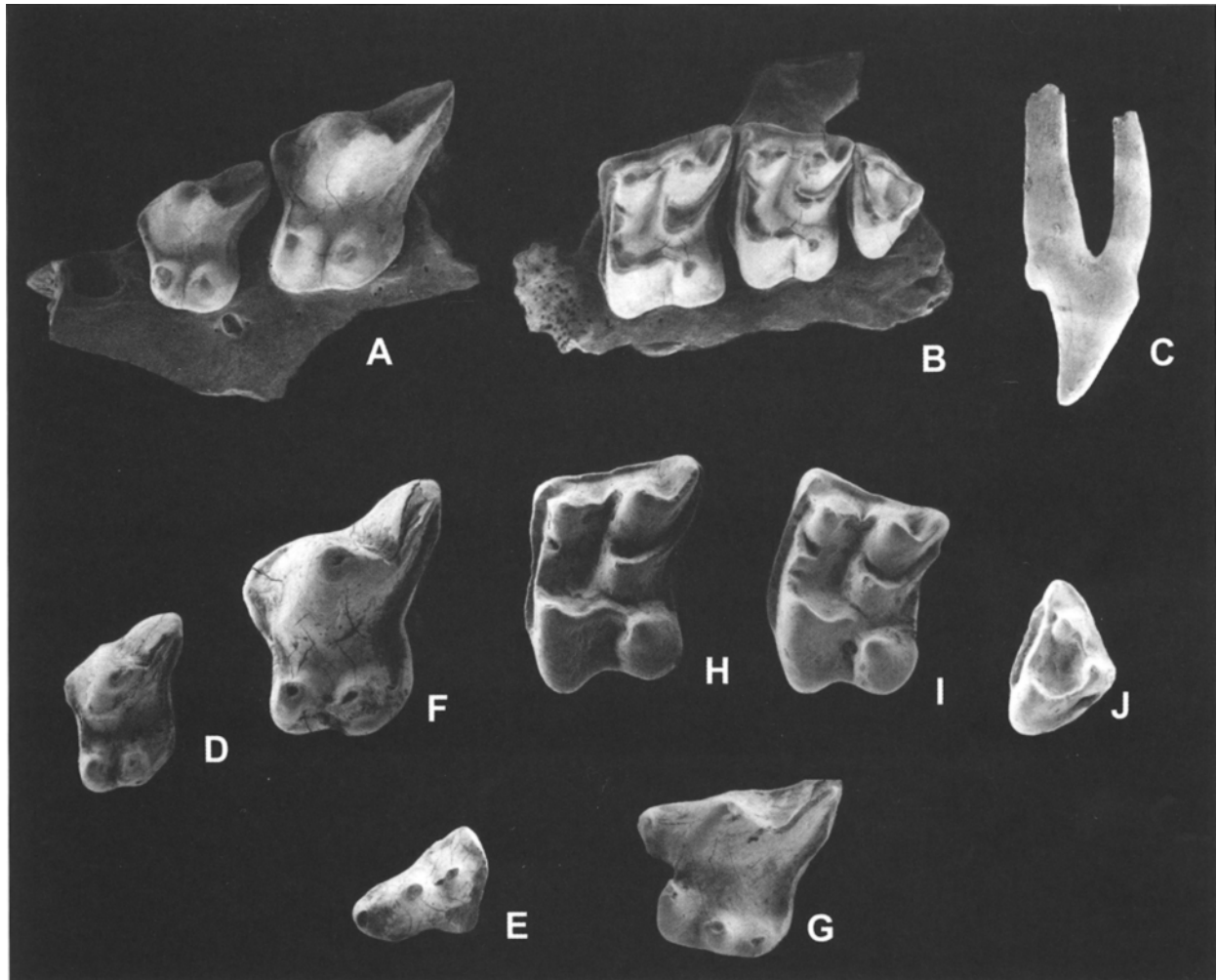


Fig. 2. A-J. *Parasorex socialis*
 A. Left maxilla fragment with P3-P4, NHMA P10-030, Petersbuch 10, occlusal view.
 B. Left maxilla fragment with M1-M3, NHMA P6-090, Petersbuch 6, occlusal view.
 C. Right C sup., NHMA P10-405A11, Petersbuch 10, labial view.
 D. Left P3, NHMA P10-400B1, Petersbuch 10, occlusal view.
 E. Left D3, NHMA P6-123E1, Petersbuch 6, occlusal view.
 F. Left P4, NHMA P10-401A1, Petersbuch 10, occlusal view.
 G. Left D4, NHMA P6-123-F2, Petersbuch 6, occlusal view.
 H. Left M1, NHMA P10-402A4, Petersbuch 10, occlusal view.
 I. Left M2, NHMA P10-403D1, Petersbuch 10, occlusal view.
 J. Left M3, NHMA P10-404B5, Petersbuch 10, occlusal view.
 All ca. x10

In the outgroup taxa the P3 has only a small lingual flange, which carries no cusps. Additionally, the p4 has a low cone-shaped paraconid and, if at all, only a very small metaconid. These characters are plesiomorphic with respect to the ingroup. The polarity of the size relation $p2/p3$ cannot be unambiguously assessed, because of insufficient information from the outgroup. In *Lanthanotherium* the anterior premolars are all reduced in size. In *Neurogymnurus cayluxi* FILHOL, 1877 there are dentaries with $p2=p3$ and with $p2<p3$ (CROCHET 1974, tab. 5). In *Neurogymnurus indricotherii* LOPATIN, 1999 $p2$ and $p3$ are of the same size (LOPATIN 1999). However, the evidence is extremely scanty. A $p3$ reduced in size seems to be rather a derived character. In all of the in-group genera the P3 has an extended lingual flange carrying at least a protocone and the p4 has a stronger metaconid. Both characters are autapomorphies of the in-group and they originated only once. The other characters are obviously convergent, i. e. they originated several times. The *Galerix* species have P3 without hypocone, except *G. symeonidisi*. The group *Parasorex* and *Schizogalerix* is characterised by the invariable presence of a hypocone in P3, a long posterior arm of the metaconule joining the posterior cingulum and a p4 with a paralophid and a strong metaconid. The autapomorph character of *Schizogalerix* is an at least incipient division of the mesostyle. In the early species such as *S. iliensis* KORDIKOVA, 2000 from the Early Miocene of Kazakhstan, *S. pasalarensis* ENGESSER, 1980 from the Early Miocene of Turkey and *S. pristinus* Ziegler, 2003 from the early Middle Miocene of Austria the anterior arm of the metacone shows a protrusion, which marks the first steps towards a divided mesostyle. In the later, more evolved species *S. moedlingensis* (RABEDER, 1973) from Austria it is deeply divided. *G. depereti* CROCHET, 1986 and *G. iberica* MEIN & MARTÍN SUÁREZ, 1993 are characterised by $p2<p3$, p4 with paralophid, P3 with hypocone and M1/2 with an at least superficially divided mesostyle (see CROCHET 1986: 151, pl. 1, fig. 1; MEIN & MARTÍN SUÁREZ 1993: 726, fig. 5b, c). As the latter is an autapomorphy of *Schizogalerix* they are referred to this genus. The hypocone in P3 obviously originated twice. It is also developed in *G. symeonidisi* DOUKAS, 1983 (see DOUKAS, 1986). Since the M1/2 of this species have a confluent mesostyle and a short posterior arm of the metaconule it cannot be referred to *Parasorex* nor to *Schizogalerix*.

The evolution within the genus *Galerix* is less clear. A variety of species has been described, which differ from one another in size and morphological details. Common to all is a $p3$ reduced in size. ZIEGLER & FAHLBUSCH (1986) postulated a lineage *G. symeonidisi* – *G. exilis*, which is documented in South Germany. The proposed transition between the species is characterised by increase in size and by a successive loss of the hypocone in P3. This transition is documented in several samples with different percent-

ages of P3 with and without hypocone and by intermediate P3 with a rudimentary hypocone. In samples correlated with MN 4 there is *G. symeonidisi*, and in MN 5 faunas we find transitional forms. The transition is completed by the early Mid Miocene (MN 6) with the occurrence of unambiguous *G. exilis*. I interpreted this as an anagenetic process, with *G. symeonidisi* as the most primitive species. All of the other *Galerix* species have lost the hypocone of P3 and thus have been interpreted as more derived. This view was challenged by VAN DEN HOEK OSTENDE (2001) and VAN DEN HOEK OSTENDE & DOUKAS (2003). They argue in favour of a replacement instead of transition. According to the replacement hypothesis the hypocone is not lost in the *Galerix* species except *G. symeonidisi*, but it is a new acquisition in the latter. Consequently, *G. symeonidisi* is more derived than *G. exilis* and the other species. Given this assumption is correct, a derived species (*G. symeonidisi*) is replaced by a less derived one (*G. exilis*). Both interpretations raise some problems. We cannot dismiss the transitional P3 with rudimentary hypocone. On the other hand, according to this transition hypothesis *Galerix* must have developed a hypocone in P3 in a first step and then lost it again. The first stage is represented only by *G. symeonidisi*, the other by the remaining *Galerix* species. This is no parsimonious explanation. Summarising all arguments, I tend to prefer the replacement hypothesis.

There are some *Galerix* species with a long posterior arm of the metaconule in some but not all of their M1/2 (*G. rutlandae* MUNTHE & WEST, 1980, *G. saratji* VAN DEN HOEK OSTENDE, 1992, *Deinogalerix freudenthali* BUTLER, 1980). Only the invariable presence of this character is a synapomorphy for *Parasorex* and *Schizogalerix*.

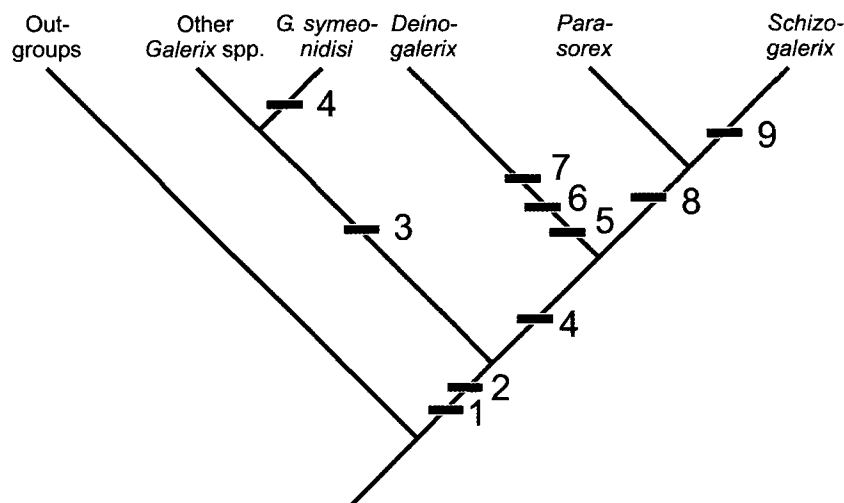


Fig. 3. Cladogram showing the possible phylogenetic relationships of the Miocene Galerixini based on dental characters. The out-groups are *Neurogymnurus* and *Lanthanotherium*.

The nodes mean:

1. P3 with extended lingual flange and protocone.
2. p4 with \pm marked metaconid.
3. $p3<p2$.
4. P3 with hypocone. It is a convergent character.
5. gigantism.
6. $p3/4$ and $P3/4$ enlarged.
7. Trigonid of m1 enlarged.
8. M1 and M2 with invariably long postmetaconuluscrista and bipartitioned posterior cingulum.
9. Mesostyle at least incipiently divided.

Deinogalerix is clearly defined by its large size, the enlarged p3/4 and P3/4, the hypocone of P3 and the enlarged trigonid of m1.

The above cladogram (fig. 3) shows that *Deinogalerix*, *Schizogalerix* and *Parasorex* are closely related groups. *Parasorex* is monospecific with *P. socialis* being the only species. The relationships between the *Galerix* species are far from being clear.

All samples from the Petersbuch fissures belong to *P. socialis* without any doubt. However, there are considerable size differences in the teeth. All teeth from the Petersbuch 10 sample except the upper molars are somewhat smaller on average than in the other samples. They are even smaller than in the sample from the type locality Steinheim. These size differences reflect the variability and are without any taxonomic consequences. The exclusive occurrence of one galericine is not unusual. In all Early Miocene faunas from south Germany, correlative with MN 4 and MN 5, except Niederaichbach (SCHÖTZ 1988) we find two species of *Galerix* (see ZIEGLER 1990, 2000). But in the time spanning MN 6 *G. exilis* seems to be the only galericine. In the later Mid Miocene (MN7/8) it is replaced by *P. socialis*. In Central Europe this species seems to be confined to the Mid Miocene (MN 7/8), in Spain it is also recorded from the Early Vallesian (MN 9), in the faunas of Carrilenga 1 and Pedregueras 2A (DE JONG 1988). *P. aff. socialis* from the Late Vallesian fauna of Montredon represents the latest occurrence (CROCHET & GREEN 1982).

Subfamily Erinaceinae FISCHER VON WALDHEIM, 1817

In the Petersbuch faunas under study the Erinaceinae, the spiny hedgehogs, are much rarer than the gymnures. In spite of their scarcity in all samples two species are represented, a large one and a distinctly smaller one. The generic allocation of the Miocene erinaceines is a matter of continuing debate. In the Miocene of Europe three erinaceine genera are known since the 19th century: *Amphechinus* AYMARD 1850, *Mioechinus* BUTLER 1948 and *Postpalerinaceus* CRUSAFONT & VILLALTA, 1947. Recently MEIN & GINSBURG (2002) recorded two species of *Atelerix* POMEL, 1848 in the La Grive fauna. In the last 30 years a variety of erinaceine species have been described. Most authors did not discuss the generic affiliation of these species. Many of these species are not sufficiently characterised nor delimited from other species. In most cases this is a hopeless venture. The above mentioned genera are best characterised by craniologic criteria, which cannot be studied in a sample with isolated teeth. Another drawback is the extreme scarcity of many erinaceine samples. Even a painstaking revision of Miocene Erinaceinae, needed for a long time, will not help to correctly allocate isolated teeth and jaw fragments. Consequently, the affiliation of the samples under study can only be provisional.

Genus "*Mioechinus*" BUTLER, 1948

Type species: *Erinaceus oeningensis* LYDEKKER, 1886

"*Mioechinus*" sp.

Fig. 4

Material (measurements see tab. 2):

Petersbuch 6	NHMA P6-002-003 right maxilla fragment with M1, 8 isolated teeth CRW P6-001-003 Petersbuch 6, left dentary fragment with c, p4, m1-trigonid, 10 isolated teeth
Petersbuch 10	CRW P10-001 2 maxilla fragments with P2, 6 isolated teeth
Petersbuch 18	NHMA P18-002-003 left dentary fragment and left maxilla fragment with teeth CRW P18-001-012 left dentary fragment and two right maxilla fragments with teeth, 7 isolated teeth
Petersbuch 31	NHMA P31-136A2 left c inf CRW P31-136 edentulous left dentary fragment, 9 isolated teeth
Petersbuch 35	CRW P35-049-050 right dentary fragment with p4, 52 isolated teeth
Petersbuch 48	CRW P48-083 4 isolated teeth

Description: Dentary – Only the samples from Petersbuch 6, 18 and 35 yielded dentary fragments which preserved at least the mental foramen. It is situated below the posterior root of p4. In the Petersbuch 18 and 35 samples there is a distinctly smaller additional foramen under the trigonid of m1. The ascending ramus elevates almost perpendicular to the horizontal ramus. The condyle is situated high above the level of the tooth-row. According to its alveolus, the i2 was small, short-rooted, and sandwiched between i1 and the canine. The myphysis extends to below p3.

Lower dentition – In the Petersbuch 35 sample there are 7 chisel-shaped single-rooted teeth, which represent the i2, the smaller ones possibly the id2 or belonging to the smaller erinaceine. They compare well with the first canines of the extant European hedgehog.

i3 and c inf. are quite similar morphologically, the latter being distinctly larger. There is one strong root, directed posteriorly and an anterior, nearly horizontal crest. In a fresh i2 a faint labial cingulid is preserved. The single-rooted p3 is not preserved.

In the p4 the paraconid, either a conical cusp or fused with the ledge-like paralophid, is lower than the protoconid. The metaconid is only a faint inflation of the disto-lingual crest. The talonid is short and bordered by a faint postcingulid, which may terminate in a disto-lingual cuspule. There are no further cingulids.

In the m1 the trigonid is distinctly longer than the talonid, the protoconid higher than the hypoconid. In an unworn specimen the paralophid is superficially notched. There is a broad but faint ectocingulid and a marked postcingulid, which ascends the entoconid. In the m2 the trigonid is shorter than in the m1 and the talonid is narrower than the trigonid. The weak postcingulid either joins the posterolophid or terminates just below it. In the m3 the talonid is fully eliminated. The trigonid morphologically fits well with the trigonid of a diminutive m2.

Maxilla – The Petersbuch 6 and 18 samples yielded some maxilla fragments with the lacrimal foramen above the posterior root of P4, outside the orbit and well visible in side view. There is no vestige of a pre-lachrymal flange. The infraorbital foramen is situated between the posterior root of P3 and the anterior one of P4. The zygomatic arch originates above M1/M2.

Tab. 2. "Mioechinus" sp., sample statistics of the teeth

loc.	meas.	n	R	m
Pet. 18	Lm1-m3	1		12.4
Pet. 18	Lp4-m3	1		15.5
Pet. 6	Hum1ling.	1		6.62
Pet. 18	Hum1ling.	2	6.86-7.00	6.93
Pet. 35	Hum1ling.	1		6.17
Pet. 6	Li3	1		2.43
	Wi3	1		2.05
Pet. 10	Li3	1		2.31
	Wi3	1		1.90
Pet. 18	Li3	1		2.33
	Wi3	1		1.95
Pet. 35	Li3	1		2.55
	Wi3	1		1.95
Pet. 6	Lcinf.	3	3.31-3.38	3.35
	Wcinf.	3	2.09-2.37	2.19
Pet. 18	Lcinf.	2	3.56-3.58	3.57
	Wcinf.	2	2.42-2.46	2.44
Pet. 31	Lcinf.	2	3.37-3.52	3.45
	Wcinf.	2	2.07-2.15	2.11
Pet. 35	Lcinf.	3	3.00-3.06	3.04
	Wcinf.	3	1.84-1.86	1.85
Pet. 48	Lcinf.	1		3.02
	Wcinf.	1		1.98
Pet. 6	Lp4	1		3.76
	Wp4	1		2.45
Pet. 18	Lp4	1		3.76
	Wp4	1		2.45
Pet. 35	Lp4	2	3.52-3.91	3.72
	Wp4	2	2.32-2.62	2.45
Pet. 6	Ld4	1		3.48
	Wd4	1		2.00
Pet. 6	Lm1	1		5.79
	Wam1	1		3.70
	Wpm1	2	3.67-3.85	3.76
Pet. 18	Lm1	2	5.49-5.71	5.60
	Wam1	2	3.32-3.37	3.35
	Wpm1	2	3.31-3.40	3.36
Pet. 35	Lm1	1		5.62
	Wam1	1		3.42
	Wpm1	1		3.42
Pet. 6	Lm2	3	4.42-4.98	4.63
	Wam2	3	3.09-3.30	3.20
	Wpm2	3	2.95-3.08	3.02
Pet. 10	Wam2	1		3.32
Pet. 18	Lm2	1		4.46
	Wam2	2	3.08-3.12	3.10
	Wpm2	1		2.96
Pet. 35	Lm2	6	4.41-4.72	4.59
	Wam2	7	2.92-3.12	3.05
	Wpm2	8	2.75-3.08	2.95
Pet. 48	Wam2	1		2.99
Pet. 6	Lm3	1		2.18
Pet. 6	Lm3	1		2.18
	Wam3	1		1.69
Pet. 18	Lm3	1		2.02
	Wam3	1		1.60
Pet. 31	Lm3	2	2.02-2.14	2.08
	Wam3	2	1.53-1.65	1.59
Pet. 35	Lm3	4	2.10-2.34	2.21
	Wam3	4	1.66-1.74	1.72
Pet. 6	LI3/Csup.	1		3.21
	WI3/Csup.	1		1.87
Pet. 35	LI3/Csup.	5	2.42-2.66	2.55
	WI3/Csup.	5	1.62-1.84	1.73
Pet. 48	LI3/Csup.	1		2.80
	WI3/Csup.	1		1.71
Pet. 10	LP2	2	2.49-2.67	2.58
	WP2	2	1.57-1.73	1.65
Pet. 18	LP2	2	2.57-2.88	2.73
	WP2	2	1.82-2.02	1.92
Pet. 31	LP2	1		2.23
	WP2	1		1.68
Pet. 35	LP2	1		2.31
	WP2	1		1.52
Pet. 6	LP3	1		2.52
	WP3	1		2.38
Pet. 18	LP3	2	2.35-2.47	2.41
	WP3	2	2.22-2.30	2.26
Pet. 31	LP3	1		2.53
	WP3	1		2.15
Pet. 6	LP4	1		4.83
	WP4	2	4.33-4.51	4.42
Pet. 18	LP4	2	4.80-4.92	4.86
	WP4	2	4.25-4.40	4.33
Pet. 31	LP4	1		4.51
	WP4	1		4.32
Pet. 35	LP4	4	4.32-4.70	4.55
	WP4	3	3.94-4.44	4.15
Pet. 6	LbM1	1		4.76
	LIM1	1		4.62
	WaM1	1		5.53
	WpM1	1		5.67
Pet. 10	LbM1	1		4.76
	LIM1	2	4.32-4.42	4.37
	WaM1	1		5.20
	WpM1	1		5.48
Pet. 31	LbM1	2	3.62-4.12	3.87
	LIM1	2	3.08-4.02	3.55
	WaM1	2	3.55-4.18	3.70
	WpM1	2	3.97-4.79	4.38
Pet. 35	LbM1	1		4.90
	LIM1	1		4.42
	WaM1	1		5.27
	WpM1	1		5.32
Pet. 48	LbM1	1		5.11
	LIM1	1		4.46

	WaM1	1		4.91
	WpM1	1		4.98
Pet. 6	LbM2	1		4.02
	LIM2	1		3.29
	WpM2	1		4.70
	WpM2	2	3.62-3.70	3.66
Pet. 10	LbM2	1		4.07
	LIM2	1		3.35
	WpM2	1		4.82
	WpM2	1		3.57
Pet. 31	LbM2	1		3.52
	LIM2	1		3.36
	WpM2	1		4.18
	WpM2	1		3.35
Pet. 35	LbM2	7	3.62-4.04	3.91
	LIM2	7	3.05-3.42	3.25
	WpM2	7	4.35-4.92	4.73
	WpM2	7	3.46-3.88	3.61
Pet. 6	LM3	2	1.43-1.43	1.43
	WaM3	2	2.96-3.02	2.99
Pet. 10	LM3	1		1.51
	WaM3	1		3.06
Pet. 35	LM3	4	1.29-1.47	1.37
	WaM3	4	2.83-3.04	2.93

Upper dentition – The upper teeth anterior to P3 are available only as isolated teeth. The I3, which is double-rooted in *Amphechinus edwardsi* (Filhol, 1879) (see Viret 1938, fig. 6) and in *Mioechinus tobieni* Engesser, 1980 (see Engesser 1980, fig. 23) is not distinguishable with certainty from the upper canine, which is higher in the latter species. The teeth under discussion are all of similar, moderate height and have a posterior crista, which terminates in a conule. There is no cingulum. The crown is broadened anteriorly.

The P2 differs from the I3/C in its smaller size.

The P3 has two buccal and one lingual root and a lingual talon with a small cusp. The buccal roots can be fused or nearly fused. The parastyle does not project anteriorly.

The P4 is slightly molariform and has a main cusp and two lingual conules. The mesio-lingual one (protocone) is higher than the distal one (hypocone). The latter extends more lingually. A long notched ledge runs from the main cusp to the disto-buccal margin. The parastyle does not project. The cingulum along the distal margin may be interrupted. There are no further cingula.

In the M1 the postmetacrista extends far disto-labially. Hence the tooth is wider distally than mesially. The mesiolingual crista of the protocone ends abruptly before the paracone. A small protoconule is differentiated as a widening of this crista. The postprotocrista extends disto-lingually and terminates in a small metaconule, which is susceptible to wear. The M1 is surrounded by a cingulum, which is buccally strong, weaker mesially and distally and very thin lingually.

The M2 has a trapezoidal outline, being wider mesially than distally. The postprotocrista is distinctly stronger than the mesial crista of the hypocone and terminates abruptly before the metacone. The metaconule is absent in all specimens. There is a strong mesial cingulum above the parastyle, which

fades on its lingual course. The distal cingulum is restricted to the median part.

The M3 has a weak paracone and a somewhat stronger protocone. The mesial cingulum is stronger than the distal one. The two roots are fused, at least the base.

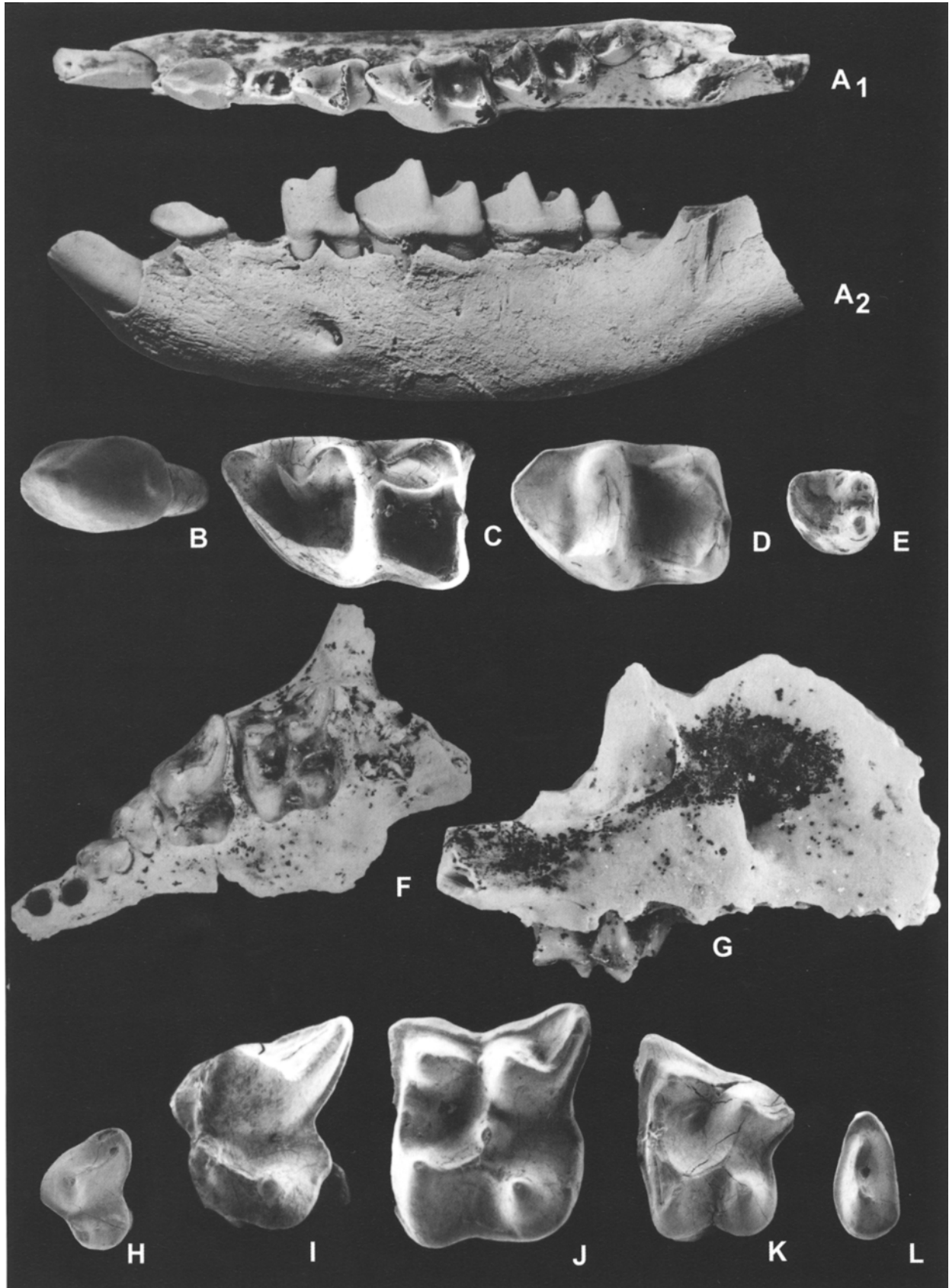
Discussion: In a sample from the Middle Miocene of Europe we expect two erinaceine genera: *Amphechinus* AYMARD, 1850 and *Mioechinus* BUTLER, 1948. We also have to take into account *Postpalerinaceus* CRUSAFONT & VILLALTA, 1947, which according to the record known thus far appeared in the early Late Miocene. Finally, we have to be aware of *Atelerix* POMEL, 1848, which was recorded in the Middle Miocene fauna of La Grive by MEIN & GINSBURG (2002). *Amphechinus* is characterised by nearly vertical ascending ramus of the dentary, the absence of a basisphenoid groove, a P4 situated under the orbit and a lacrimal foramen, which opens into the orbit, thus not being visible in side view. *Mioechinus* is characterised by the presence of a basisphenoid groove, a P4 situated anterior to the orbit and a lacrimal foramen visible in side view. The latter characters cannot be verified on the genotype skull from Öhningen as it is dorsally embedded in matrix. These characters are preserved in *Mioechinus tobieni* (see ENGESSER 1980: 87, fig. 22). *Postpalerinaceus* has no basisphenoid groove, the lacrimal foramen opens into the orbit (as far as can be seen from fig. 1 in CRUSAFONT & VILLALTA, 1947), and the alveolar margin and the ascending ramus form an obtuse angle.

In many species of *Amphechinus* described so far, the diagnostic characters are not preserved. Their generic allocation is more or less ambiguous. Without any doubt *A. arvernensis* (BLAINVILLE, 1840), the type species from the Late Oligocene of Cournon, and *A. edwardsi* (FILHOL, 1879) from the Agenian of Saint-Gérard-le-Puy are correctly assigned to *Amphechinus*.

Amphechinus rusingensis BUTLER, 1956 from the Miocene of Kenya has a lacrimal foramen opening into the orbit and a P4 situated under the orbit. The coronoid process makes almost a right angle with the line of the teeth (see BUTLER 1956: 54 f, fig. 16). It is also correctly allocated. However, in all the European species, except the above mentioned, the assignment to *Amphechinus* is not substantiated.

In the species from the Miocene of Spain, *A. baudelotae* GIBERT, 1975, *A. robinsoni* GIBERT, 1975 and *A. golpae* GIBERT, 1975, no features characteristic of *Amphechinus* are preserved (GIBERT 1975).

A. intermedius (GAILLARD, 1899), at first described as *Palaeoerinaceus intermedius* by GAILLARD (1899), was referred to *Amphechinus* by BAUDELLOT (1972) and listed in a faunal list of La Grive as *Postpalerinaceus intermedius* by MEIN (in DE BRUJN ET AL. 1992). This allocation was substantiated by MEIN & GINSBURG (2002). The important character is the lateral position of the lacrimal foramen outside the orbit. However, this character only excludes the allocation with *Amphechinus*. Given the position of the lacrimal foramen is drawn correctly in CRUSAFONT & VILLALTA (1947, fig. 1) the species *intermedius* is not referable to *Postpalerinaceus*. *Mioechinus* also comes into question. We cannot even exclude *Atelerix* in which the lacrimal also opens on the face. The differences in dental morphology and size are no more than specific differences. For the correct generic allocation we cannot do without the key cranial characters, e. g., the basisphenoid groove, the extension of the palate posterior to the transverse crest. I fear the new generic



allocation of *intermedius* is not sufficiently substantiated.

A. ginsburgi BAUDELLOT, 1972 from Sansan is known from a dentary fragment and isolated teeth. Since the ascending ramus

stands upright on the horizontal ramus we can exclude *Postpalerinaceus* (BAUDELLOT 1972, fig. 74). The allocation with *Amphexhinus* or with *Mioechinus* cannot be substantiated.

Tab. 3. Erinaceinae gen. et.sp. indet., sample statistics of the Teeth

loc.	meas.	n	R	m
Pet. 31	Li3	1		1.55
	Wi3	1		1.00
Pet. 35	Lcinf.	3	2.06-2.16	2.10
	Wcinf.	3	1.49-1.79	1.61
Pet. 48	Lcinf.	1		2.25
	Wcinf.	1		1.31
Pet. 31	Lp4	2	1.95-2.29	2.12
	Wp4	2	1.20-1.42	1.31
Pet. 35	Lm2	2	3.41-3.45	3.43
	Wam2	2	2.29-2.32	2.31
	Wpm2	2	2.25-2.29	2.27
Pet. 31	Lm3	1		1.38
	Wam3	1		1.06
Pet. 35	Lm3	1		1.49
	Wam3	1		1.19
Pet. 35	LI3/Csup.	1		2.12
	WI3/Csup.	1		1.26
Pet. 35	LD2	1		2.17
	WD2	1		1.68
Pet. 10	LP2	1		1.58
	WP2	1		0.96
Pet. 35	LP2	2	1.93-2.02	1.98
	WP2	2	1.30-1.34	1.32
Pet. 18	LP3	1		1.80
	WP3	1		1.54
Pet. 31	LP3	1		2.03
	WP3	1		1.76
Pet. 35	LP3	1		2.01
	WP3	1		1.81
Pet. 18	LbM1	1		>3.0
	LIM1	1		2.76
	WaM1	1		3.09
	WpM1	1		>3.3

Pet. 31	LbM1	5	2.55-3.00	2.74
	LIM1	5	2.41-2.62	2.51
	WaM1	5	2.76-3.00	2.84
	WpM1	5	2.90-3.30	3.08
Pet. 35	LbM1	2	3.20-3.23	3.22
	LIM1	3	2.95-3.05	3.00
	WaM1	2	3.23-3.31	3.27
	WpM1	3	3.57-3.74	3.66
Pet. 6	LbM2	2	2.71-2.75	2.73
	LIM2	2	2.29-2.43	2.36
	WpM2	2	3.13-3.26	3.20
	WpM2	2	2.52-2.62	2.57
Pet. 10	LIM2	1		2.57
	WpM2	1		2.80
Pet. 18	LbM2	1		>2.4
	LIM2	1		2.45
	WpM2	1		3.15
	WpM2	1		2.44
Pet. 31	LbM2	4	2.00-2.43	2.26
	LIM2	5	1.80-2.26	2.05
	WpM2	4	2.53-3.00	2.80
	WpM2	5	2.02-2.32	2.21
Pet. 35	LbM2	4	2.61-3.02	2.77
	LIM2	5	2.24-2.55	2.44
	WpM2	4	3.21-3.63	3.48
	WpM2	5	2.52-2.93	2.69
Pet. 48	LbM2	1		2.55
	LIM2	1		2.33
	WpM2	1		3.17
	WpM2	1		2.50
Pet. 31	LM3	1		0.84
	WaM3	1		1.71
Pet. 48	LM3	1		0.97
	WaM3	1		2.19

◀ Fig. 4. A-L. "*Mioechinus*" sp.

- A. Left dentary fragment with i₂, p₂, p₄-m₃, NHMA P18-002, Petersbuch 18, in occlusal (A₁) and buccal (A₂) views.- Ca. x4
 B. Left C inf., NHMA P31-136A2, Petersbuch 31, occlusal view.- Ca. x8.
 C. Right m₁, NHMA P6-003B1, Petersbuch 6, occlusal view, inverted.- Ca. x8.
 D. Left m₂, NHMA P6-003B3, Petersbuch 6, occlusal view.- Ca. x8.
 E. Left m₃, NHMA P6-003F4, Petersbuch 6, occlusal view.- Ca. x8.
 F. Left maxilla fragment with P2-M1, NHMA P18-003, Petersbuch 18, occlusal view.- Ca. x4.
 G. Right maxilla fragment with M1 and the lacrimal foramen, NHMA P6-002, Petersbuch 6, lateral view, inverted.- Ca. x4.
 H. Left P3, NHMA P6-003C3, Petersbuch 6, occlusal view.- Ca. x8.
 I. Right P4, NHMA P6-003C2, Petersbuch 6, occlusal view, inverted.- Ca. x8.
 J. Left M1, NHMA P6-003D1, Petersbuch 6, occlusal view.- Ca. x8.
 K. Left M2, NHMA P6-003E1, Petersbuch 6, occlusal view.- Ca. x8.
 L. Right M3, NHMA P6-003F1, Petersbuch 6, occlusal view, inverted.- Ca. x8

We face the same problems with some Asian species referred to *Ampechinus*, e. g. *A. asekapensis* LOPATIN, 1999 and *A. gigas* LOPATIN, 2002 (see LOPATIN 1999, 2002).

The situation is not much better with *Mioechinus*. The type species *M. oeningensis* (LYDEKKER, 1886) is represented only by a skull from Öhningen.

The species *sansaniensis* from La Grive was tentatively referred to *Mioechinus* by BUTLER (1948). However, important craniologic characters cannot be controlled and there is a taxonomic confusion. DEPÉRET (1887) identified the small erinaceine from La Grive with "*Erinaceus sansaniensis*" LARTET, 1851 from Sansan. As this name refers to *Lanthanotherium* and as there is no small erinaceine in the Sansan fauna, this allocation is not correct. Consequently, the small erinaceine from La Grive has no valid species name (ENGESSER 1980: 86). Therefore the name *Mioechinus sansaniensis* has been used only with some reservation. MEIN & GINSBURG (2002) named the small erinaceine from La Grive *Atelerix depereti*. They synonymised *Mioechinus* with *Atelerix*. However, there are some differences that should be appreciated. In *Atelerix*, which has a basisphenoid groove like *Mioechinus*, the lacrimal foramen opens on the face, this means that it is visible in side view. But the palate extends for a considerable distance behind the transverse crest (see BUTLER 1948, fig. 5). This is not the case in *Mioechinus oeningensis*. In *Mioechinus* the condyle is laterally excavated for the condylar foramen. I prefer to retain the genus for the type species only.

"*Mioechinus*" *tobieni* ENGESSER, 1980 from the Miocene of Turkey was tentatively referred to *Mioechinus* on the basis of the following characters: position of the lacrimal foramen in front of the orbit (not preserved in the *M. oeningensis* skull) above the posterior root of P4, position of the infraorbital foramen above the anterior root of P4, presence of a metaconule in M1 and M2 (see ENGESSER 1980, figs 22, 24). This allocation can only be tentative as no basisphenoid groove is preserved in the Turkish species and as the lacrimal foramen is not preserved in *Mioechinus*. We cannot exclude the affiliation with *Atelerix*. Except for the type species, all species previously referred to *Mioechinus* should be named "*Mioechinus*" + species name.

I fear even a thorough revision of all species referred to *Ampechinus* or *Mioechinus* will result in a lot of species, not referable to any genus, because of their scanty preservation.

The material under study is assigned to "*Mioechinus*",

because of the position of the lacrimal foramen in the maxilla fragments from Petersbuch 6 and 18. As the teeth of all samples are similar in size and because of temporo-spatial proximity, I assume that all samples under study represent one species. In size they are intermediate between *Atelerix depereti* (= *M. sansaniensis*) and *M. oeningensis* and better correspond to *Postpalerinaceus intermedius* (GAILLARD) from La Grive. The material under study cannot be assigned to one of these species because of the above-mentioned suite of characters. It obviously represents a new species. I think we should not describe any new erinaceine species before a revision of the European Erinaceinae has been developed. This is far beyond the scope of this contribution. Therefore I content myself with the determination "*Mioechinus*" sp.

Erinaceinae gen. et sp. indet.

Fig. 5

Material (measurements see tab. 3):

Petersbuch 6	NHMA P6-119/3 left M2 CRW P6-119 2 M2
Petersbuch 10	CRW P10-002 right P2, right M2
Petersbuch 18	NHMA P18-013 right maxilla fragment with P3 CRW P18-013 Petersbuch 18, right M1, right M2
Petersbuch 31	CRW P31-137 5 isolated teeth NHMA P31-137 11 isolated teeth
Petersbuch 35	NHMA P35-051 7 isolated teeth CRWP35-051 13 isolated teeth
Petersbuch 48	NHMA P48-084 left c inf., right M2, right M3

Description: Except one maxilla fragment with P3 but without foramina from Petersbuch 18, this small erinaceine is represented by isolated teeth only. As most erinaceines are

► Fig. 5. A-Q. Erinaceinae gen. et sp. indet.

- A. Right C inf., NHMA P35-051A1, Petersbuch 35, occlusal view, inverted.
 - B. Left C inf., NHMA P48-084/1, Petersbuch 48, occlusal view.
 - C. Left p4, NHMA P31-137A3, Petersbuch 31, occlusal view.
 - D. Left p4, NHMA P31-137A2, Petersbuch 31, buccal view.
 - E. Right m2, NHMA P35-051B2, Petersbuch 35, occlusal view, inverted.
 - F. Left. P3, NHMA P35-051E1, Petersbuch 35, occlusal view.
 - G. Right maxilla fragment with P3, NHMA P18-013, Petersbuch 18, occlusal view, inverted.
 - H. Right P3, NHMA P31-137A5, Petersbuch 31, occlusal view, inverted.
 - I. Left M1, NHMA P31-137A6, Petersbuch 31, occlusal view, ?3rd erinaceine species.
 - J. Left M1, NHMA P35-051F1, Petersbuch 35, occlusal view.
 - K. Right M1, NHMA P35-051G2, Petersbuch 35, occlusal view, inverted.
 - L. Left M2, NHMA P31-137B3, Petersbuch 31, occlusal view.
 - M. Left M2, NHMA P35-051H3, Petersbuch 35, occlusal view.
 - N. Right M2, NHMA P35-051K1, Petersbuch 35, occlusal view, inverted.
 - O. Right M2, NHMA P48-084/2, Petersbuch 48, occlusal view, inverted.
 - P. Left M2, NHMA P6-119/3, Petersbuch 6, occlusal view.
 - Q. Right M3, NHMA P48-084/3, Petersbuch 84, occlusal view, inverted.
- All ca. x10.

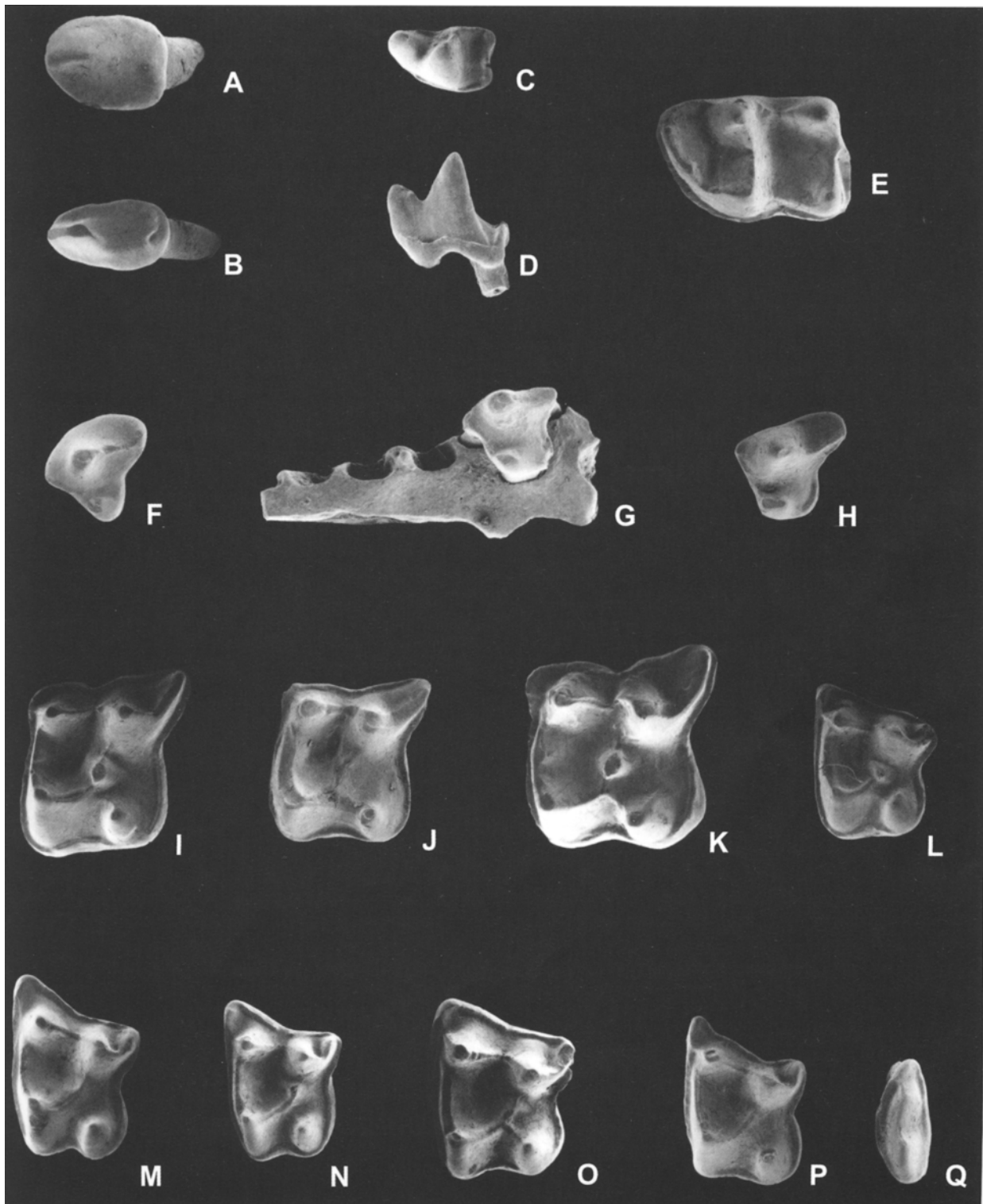
quite similar in their dental morphology I refrain from describing all teeth. Instead the peculiar characters of the samples under study are outlined.

Lower dentition – There are two p4 in the Petersbuch 31 sample with a conical paracone. In one specimen there is a well-differentiated metaconule, in the smaller one the metaconule is bud-shaped. Both have an ectocingulid and a marked postcingulid.

In both m2 from the Petersbuch 35 sample the postcingulid joins the posteristid.

The two m3 from the Petersbuch 31 and 35 samples are reduced to their trigonids. The marked ectocingulid joins the weaker postcingulid.

Upper dentition – In the small P3 from Petersbuch 18 the lingual talon is long, whereas it is somewhat shorter in the larger specimens from Petersbuch 31 and 35.



One longer and narrower tooth from Petersbuch 35 with the crown morphology of a P3 is interpreted as D2 due to its splayed roots. Between the roots there is enough space for the cusp of the erupting P2.

In the Petersbuch 18 sample there is one M1 with an isolated metaconule. The distal crest of the protocone tapers off without labial curvature. The M2 of the sample has a well-developed metaconule situated at the end of the distobuccal arm of the protocone. Probably both molars belong to one individual. In the Petersbuch 31 sample four of five M1 and two of five M2 are provided with a metaconule. In Petersbuch 35 three M1 have a metaconule. A very small M1 (2.57x2.46x2.77x2.87) without metaconule possibly represents a third, very small erinaceine. It is not included in the sample statistics in Tab. 3. Two of five M2 from the same sample have metaconule. The Petersbuch 6 sample has one M2 with and two without metaconule, Petersbuch 10 and 48 have one M2 each without metaconule.

There are only two M3. The Petersbuch 31 specimen has two separated roots, the one from Petersbuch 48 a very broad one.

Discussion: The teeth characterised above are lumped together because of their small size. They do not necessarily represent the same genus or even the same species. As is shown above presence/absence of a metaconule on M1 and M2 is a quite variable feature. It is neither a generic nor a specific character.

As there are no cranial fragments with some preserved foramina even the genus cannot be firmly determined.

Most of the teeth listed above are somewhat smaller than in *Atelerix depereti* MEIN & GINSBURG, 2002 (= *Mioechinus sansaniensis*) from La Grive (see MEIN & GINSBURG 2002, tab. 2), than *A. aff. depereti* from Verme 2 (see ENGESSER ET. AL. 1981: 908) and smaller than "*Mioechinus*" *tobieni* ENGESSER, 1980 from Yeni-Eskihisar in Turkey (see ENGESSER 1980: 84 f). Consequently, the teeth under study are distinctly smaller than those of the type species *Mioechinus oeningensis* (LYDEKKER, 1886), which is the largest species of the genus.

QIU (1996) described a small erinaceine on the basis of 90 isolated teeth from the upper Middle Miocene deposits Moergen II and Tunggur in Inner Mongolia and named it *Mioechinus? gobiensis*. He followed ENGESSER (1980) in recognising the presence or absence of metaconules in M1+2 to distinguish *Ampechinus* and *Mioechinus*. However, the metaconule is not a sufficient characteristic to distinguish both genera. According to BUTLER (1948: 481) a metaconule is present on the M1 of *Mioechinus*. It is absent on most M2 of *Mioechinus* (see ENGESSER 1980, fig. 24) and it is not necessarily absent in the M1 of *Ampechinus*. In Late Oligocene *A. arvernensis* (BLAINVILLE, 1840) and *A. robustus* (LAVOCAT, 1951) from South German localities it is present in the M1 (ZIEGLER 1998). The Moergen II species has a distinct metaconule on M1 and M2 each. Regardless of its morphology it is much smaller than all the specimens under discussion.

„*Mioechinus*" *butleri* CRUSAFONT, VILLALTA & TRUYOLS, 1955 from the Late Burdigalian of San Mammet in Spain is a poorly known species, represented by an upper jaw fragment with p3-M3. There the M1 has a distinct metaconule and all teeth are smaller than in the samples under study.

I include in the comparisons some species which have been referred to *Ampechinus*.

Ampechinus baudelotae GIBERT, 1975 from Valtorres (MN 4) is represented by isolated teeth only. The M1 and M2 have a well-developed metaconule, the paralophid of the m2 extends to the basis of the metaconid. The m2 is smaller than the specimen from Petersbuch 35 and the other teeth are larger, at least wider than the Petersbuch specimens.

Ampechinus golpae GIBERT, 1975 from Hostalets (MN 7/8) is represented by a dentary fragment with teeth and by some isolated teeth, which are larger than in the erinaceine under discussion.

Ampechinus robinsoni GIBERT, 1975 from Manchones I and II (MN 7/8) is a large-sized species with metaconules in M1 and M2. It cannot be confused with the Petersbuch specimens.

The affiliation of these Spanish species with *Ampechinus* is not warranted.

The Oligocene *Ampechinus* species of Europe – *A. arvernensis* (BLAINVILLE, 1840), *A. robustus* LAVOCAT, 1951 – the Agenian *A. edwardsi* (FILHOL, 1879), and the Middle Miocene *A. ginsburgi* BAUDELLOT, 1972 and *A. intermedius* (GAILLARD, 1899), which is now called *Postpalerinaceus intermedius* (see previous chapter), have distinctly larger teeth than the Petersbuch specimens. In all these taxa the M1 has a metaconule.

There are a couple of *Ampechinus* species from North America, Africa and Asia. The very small *A. kansuensis* BOHLIN, 1942 and *A. minimus* BOHLIN, 1942 from the Late Oligocene of western Kansu, China, have metaconules in M1 and M2 (QIU 1996). *A. bohlini* BI, 2000 from the Early Miocene of the North Junggar Basin in China is only represented by dentaries and lower teeth, which are also small (BI 2000). *A. microdus* LOPATIN, 1999 from the Early Miocene of Kazakhstan is distinctly smaller than the Petersbuch specimens and has M1 and M2 without metaconules. The other Kazakhstan species *A. asekapensis* LOPATIN, 1999 and the Mongolian *A. gigas* LOPATIN, 2002 are distinctly larger.

A metaconule is also present in the M1 and M2 of *A. rus-ingensis* BUTLER, 1956 from the Miocene of Kenya. But there the skull shows unambiguous *Ampechinus* characters, as the lachrymal foramen opens into the orbit. This means that the presence/absence of a metaconule in M1 and M2 is no generic character.

As a consequence, the material under study is not determinable to the genus level. Because of the above mentioned uncertainties I prefer to leave the determination open. The smallest M1 of the Petersbuch 35 sample (2.57x2.46x2.77x2.87, not included in the sample statistics, tab. 3) has no metaconule and possibly represents a third erinaceine species, which also is not determinable more precisely. It is even smaller than *Atelerix rhodanicus* MEIN & GINSBURG, 2002, the smallest erinaceine from La Grive (see MEIN & GINSBURG 2002, tab. 3).

Family Dimylidae SCHLOSSER, 1887

Genus *Metacordylodon* SCHLOSSER, 1911

Type species: *Cordylodon schlosseri* ANDRAE, 1904

Metacordylodon aff. *schlosseri* (ANDRAE, 1904)

Fig. 6

Material and measurements:

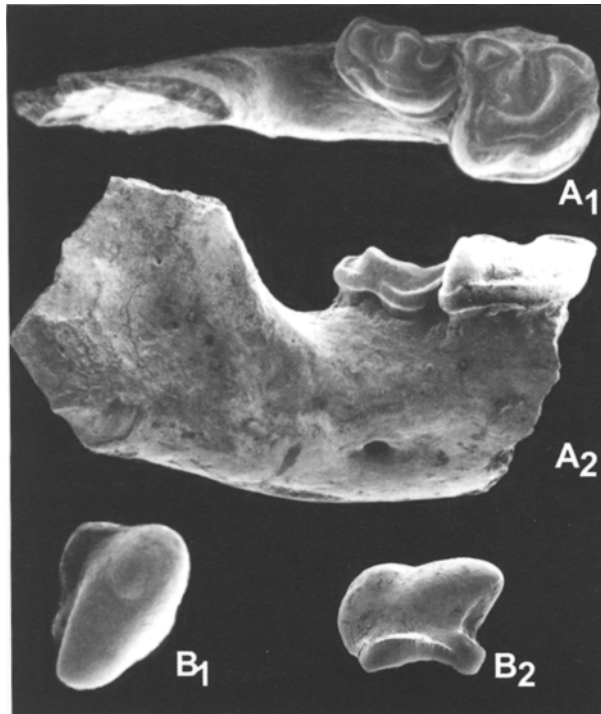


Fig. 6. A-B. *Metacordylodon* aff. *schlosseri*, Petersbuch 35.
A. Right dentary fragment with m1-m2, NHMA P35-060/2, Petersbuch 35, in occlusal (A₁) and buccal (A₂) views.- Ca. x10.
B. Right p4, NHMA P35-60/1, Petersbuch 35, in occlusal (B₁) and posterior (B₂) views.- Ca. x10.

Petersbuch 35	NHMA P35-60/1-2
	1. right p4: 2.14x2.50
	2. right dentary fragment with m1-m2: Lm1-m2 3.94; m1 2.16x2.00; m2 1.95x1.15

Description: Dentary – Only a short fragment of horizontal ramus carrying m1 and m2 and the basis of ascending ramus is preserved. The mental foramen is situated below the trigonid of m2 in the ventral third of the dentary.

Teeth – The p4 has an inflated crown with a lobe directed postero-buccally and a weak posterior cingulid. This specimen is obviously aberrant. Usually the p4 has an antero-buccal lobe. As the posterior cingulid yields a good criterion for posterior I can exclude that the orientation of the tooth was misidentified.

The m1 is amblyodontous (inflated) and exoedaenontontous, i. e. it is overlapping the dentary. The crown is heavily worn, trigonid and hypoconid from a conjoint wear-facet. There is a broad and continuous cingulid from beneath the paraconid alongside the buccal crown-base to below the entoconid.

The m2 is similarly worn and thus shows no morphological details. Its small size, which is typical for the genus, is mainly due to the reduced talonid.

Discussion: *Metacordylodon* with its only species *M. schlosseri* is extremely rare. Without exception it is recorded in small numbers. The teeth under study are smaller than in the type from Opole (Poland), which according to KOWALSKI (1989, tab. 1) is correlative with MN 6. The holotype was

figured and measured by FAHLBUSCH (1989, fig. 1). It is also smaller than in the samples from La Grive and Anwil (MÜLLER 1967, tab.39-41). In *Metacordylodon* aff. *schlosseri* from Franzensbad, which is also bigger, the mental foramen is situated more anteriorly. Along with the four isolated teeth from Sandelzhausen, referred to *M. aff. schlosseri*, it represents the earliest record of the species. The m1 from the present sample best fits the Sandelzhausen m1. There are no more comparable measurements available. Due to their small size, the Petersbuch specimens are referred to *M. aff. schlosseri*.

Genus *Plesiodimylus* GAILLARD, 1897

Type species: *Plesiodimylus chantrei* GAILLARD, 1897

Plesiodimylus chantrei GAILLARD, 1897

Fig. 7

Material (measurements see tab. 4):

Petersbuch 6	NHMA P6-177/4 right dentary fragment with p3-m2 CRW P6-177/1-3 3 dentary fragments with teeth
Petersbuch 18	CRW P18-757 left maxilla fragment with P2
Petersbuch 31	NHMA P31-172 5 isolated teeth CRW P31-172 3 dentary fragments with teeth, right maxilla fragment with P4-M1, 7 isolated teeth
Petersbuch 35	CRW P35-59 right M1
Petersbuch 48	NHMA P48-89/2-4 3 isolated teeth CRW P48-89/1 right dentary fragment with m2

Description: *Plesiodimylus* with its species has been described in a variety of papers (e. g., MÜLLER 1967, ENGESSER 1972, 1980, SCHÖTZ 1985, BOLLIGER 1992, KÄLIN & ENGESSER 2001). Hence, a redescription is not necessary. I will confine myself to highlighting the peculiar characters.

From the dentary only fragments of the horizontal ramus are preserved. The mental foramen is situated between the roots of m1 at somewhat variable height. In Petersbuch 6/1077.1-3 it lies the upper third of the dentary, in Pet. 6/1077.4 and Pet. 31/172A2 at half height. Obviously the level of the mental foramen is not dependent on the age of the animal. According to the wear of the teeth, all have been at least subadult.

In the M1 and M2 there is no mesostyle.

Plesiodimylus chantrei is one of the most common insectivore species in the Mid and early Late Miocene of Europe with a very long stratigraphic range. The earliest records are correlative with MN 4, for example Rauscheröd and Rembach in Lower Bavaria (MN 4, ZIEGLER & FAHLBUSCH 1986), the latest is known from Montredon (MN 10, CROCHET & GREEN 1982). STORCH (1978) identified a similar form, *P. cf. chantrei*, in the Dorn-Dürkheim fauna and MEIN (1999) in Ambérieu, both correlated with MN 11. Geographically it was very

Tab. 4. *Plesiodimylus chantrei*, sample statistics of the teeth

loc.	meas.	n	R	m
Pet. 31	Li3	1		1.55
	Wi3	1		1.00
Pet. 35	Lcinf.	3	2.06-2.16	2.10
	Wcinf.	3	1.49-1.79	1.61
Pet. 48	Lcinf.	1		2.25
	Wcinf.	1		1.31
Pet. 31	Lp4	2	1.95-2.29	2.12
	Wp4	2	1.20-1.42	1.31
Pet. 35	Lm2	2	3.41-3.45	3.43
	Wam2	2	2.29-2.32	2.31
	Wpm2	2	2.25-2.29	2.27
Pet. 31	Lm3	1		1.38
	Wam3	1		1.06
Pet. 35	Lm3	1		1.49
	Wam3	1		1.19
Pet. 35	LI3/Csup.	1		2.12
	WI3/Csup.	1		1.26
Pet. 35	LD2	1		2.17
	WD2	1		1.68
Pet. 10	LP2	1		1.58
	WP2	1		0.96
Pet. 35	LP2	2	1.93-2.02	1.98
	WP2	2	1.30-1.34	1.32
Pet. 18	LP3	1		1.80
	WP3	1		1.54
Pet. 31	LP3	1		2.03
	WP3	1		1.76
Pet. 35	LP3	1		2.01
	WP3	1		1.81
Pet. 18	LbM1	1		>3.0
	LIM1	1		2.76
	WaM1	1		3.09
	WpM1	1		>3.3

Pet. 31	LbM1	5	2.55-3.00	2.74
	LIM1	5	2.41-2.62	2.51
	WaM1	5	2.76-3.00	2.84
	WpM1	5	2.90-3.30	3.08
Pet. 35	LbM1	2	3.20-3.23	3.22
	LIM1	3	2.95-3.05	3.00
	WaM1	2	3.23-3.31	3.27
	WpM1	3	3.57-3.74	3.66
Pet. 6	LbM2	2	2.71-2.75	2.73
	LIM2	2	2.29-2.43	2.36
	WpM2	2	3.13-3.26	3.20
	WpM2	2	2.52-2.62	2.57
Pet. 10	LIM2	1		2.57
	WpM2	1		2.80
Pet. 18	LbM2	1		>2.4
	LIM2	1		2.45
	WpM2	1		3.15
	WpM2	1		2.44
Pet. 31	LbM2	4	2.00-2.43	2.26
	LIM2	5	1.80-2.26	2.05
	WpM2	4	2.53-3.00	2.80
	WpM2	5	2.02-2.32	2.21
Pet. 35	LbM2	4	2.61-3.02	2.77
	LIM2	5	2.24-2.55	2.44
	WpM2	4	3.21-3.63	3.48
	WpM2	5	2.52-2.93	2.69
Pet. 48	LbM2	1		2.55
	LIM2	1		2.33
	WpM2	1		3.17
	WpM2	1		2.50
Pet. 31	LM3	1		0.84
	WaM3	1		1.71
Pet. 48	LM3	1		0.97
	WaM3	1		2.19

widespread, from Spain in the west, to Austria and Poland in the east (VILLATA & CRUSAFONT 1944, ENGESSER 1972, RZEBIK-KOWALSKA 1996, ZIEGLER 1998). During the long time interval spanning MN 4 to MN 11 *P. chantrei* obviously did not change noticeably. Hence, this species is of no use for precise stratigraphic correlation.

Plesiodimylus n. sp.

Fig. 8

Material and measurements:

Petersbuch 10 NHMA P10-626/1
left maxilla fragment with M1-M2;
M1 3.55x>2.17x2.56; M2 1.85x2.82
CRW P10-626/2-3
2. P1-3 1.29x0.89
3. P1-3 1.17x0.89

Description: There are two maxilla fragments with extraordinary large M1 and M1-M2 respectively. The specimen from Petersbuch 31 has been separated from the *Plesiodimylus chantrei* sample because of its large size and because of its mesostyle. In Petersbuch 10 M1 and M2 of the maxilla fragment have no mesostyle. They are distinctly larger than

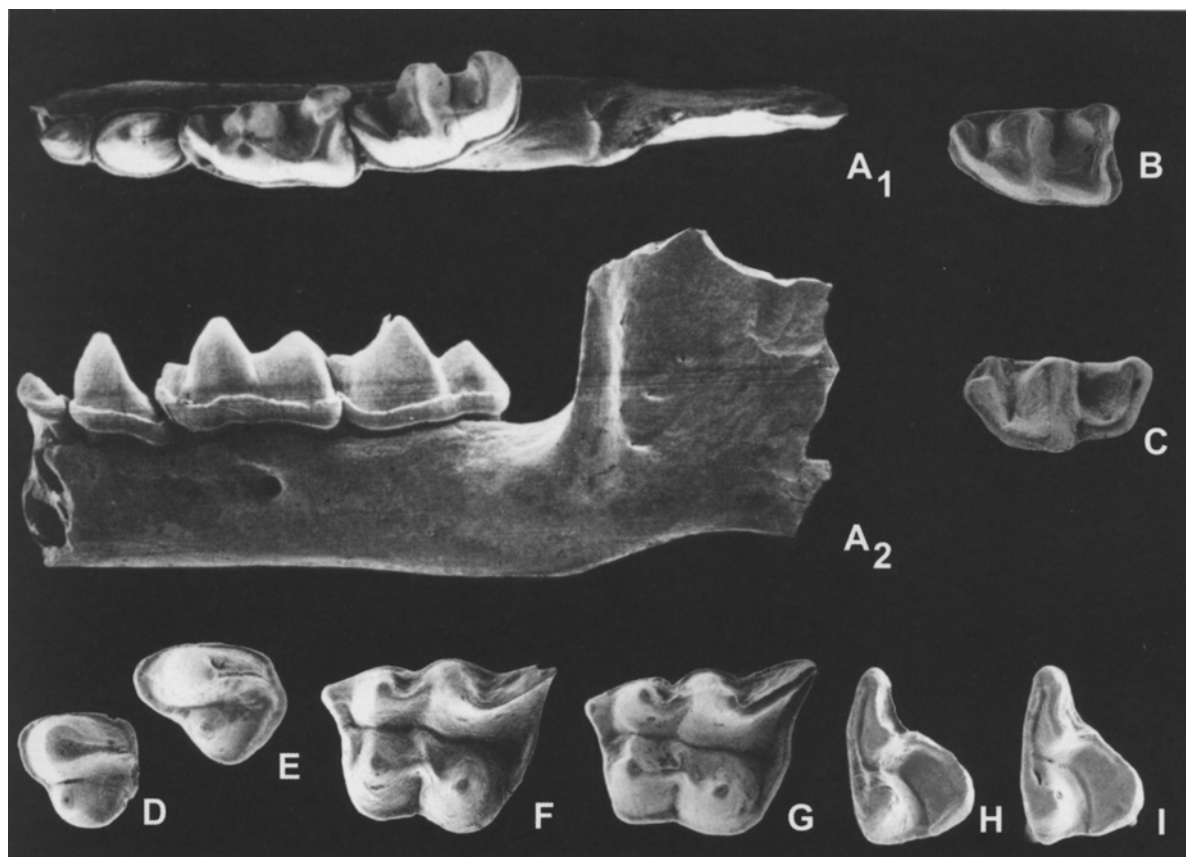


Fig. 7. A-I. *Plesiodimylus chantrei*

- A. Right dentary fragment with p3-m2, NHMA P6-177/4, Petersbuch 6, in occlusal (A₁) and buccal (A₂) views, inverted.- Ca. x10.
 B. Right m1, NHMA P31-172A5, Petersbuch 31, occlusal view, inverted.- Ca. x10.
 C. Left m2, NHMA P31-172A4, Petersbuch 31, occlusal view.- Ca. x10.
 D. Right P4, NHMA P31-172B1, Petersbuch 31, occlusal view, inverted.- Ca. x10.
 E. Right P4, NHMA P48-95/2, Petersbuch 48, occlusal view, inverted.- Ca. x10.
 F. Right M1, NHMA P31-172B3, Petersbuch 31, occlusal view, inverted.- Ca. x10.
 G. Right M1, NHMA P48-095/3, Petersbuch 48, occlusal view, inverted.- Ca. x10.
 H. Left M2, NHMA P31-172D1, Petersbuch 31, occlusal view.- Ca. x10.
 I. Left M2, NHMA P48-95/4, Petersbuch 48, occlusal view.- Ca. x10.

all known upper molars of *P. chantrei* (compare measurements with ENGESSER 1980, fig. 7; SCHÖTZ 1985, fig. 5). The teeth are even larger than *P. bavaricus* SCHÖTZ 1985 from Maßendorf. The two upper anteromolars from Petersbuch 10 have been included because I do not expect that they repre-

sent a second dimylid species in the Petersbuch 10 sample. Possibly the large teeth listed above represent a new species. As the evidence is insufficient I refrain from describing a new species.

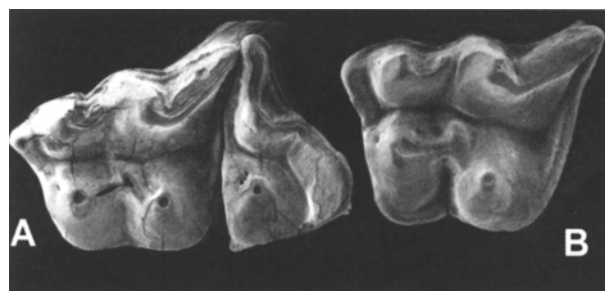


Fig. 8. A-B. *Plesiodimylus* n. sp.

- A. Left maxilla fragment with M1-M2, NHMA P10-626/1, Petersbuch 10, occlusal view.- Ca. x10.
 B. Left M1, NHMA P31-173, Petersbuch 31, occlusal view.- Ca. x10

Conclusions

Composition of the insectivore samples

(see table 5, 6)

In table 6 the numbers of the specimens (n_s) and the numbers of the most common element (n_c) are listed. The latter is roughly double the minimum number of individuals as left and right specimens are counted. In large samples the n_s tends to exaggerate the most common species compared to the less common species. In Petersbuch 6 the erinaceids represent 77% of the specimens, but only 56% of the most common elements. In the n_c the effect of different tooth formulas in different taxa is eliminated. Therefore I consider the n_c a more appropriate means for quantitative faunal comparisons.

Table 5. List of the erinaceid and dimylid species of the six Petersbuch 6-48 fissure fills (n_s =number of specimens, n_c =number of most common element)

Species	P 6		P 10		P 18		P 31		P 35		P 48	
	n_s	n_c	n_s	n_c	n_s	n_c	n_s	n_c	n_s	n_c	n_s	n_c
Erinaceidae												
Galericinae												
<i>Parasorex socialis</i>	551	124	1381	279	178	37	719	122	375	57	572	77
Erinaceinae												
" <i>Mioechinus</i> " sp.	20	3	8	2	12	4	11	2	48	8	4	1
Erinaceinae gen. et sp. indet.	3	3	2	1	3	1	16	5	20	5	3	1
Dimylidae												
<i>Metacordylodon</i> aff. <i>schlosseri</i>									2	1		
<i>Plesiodimylus chantrei</i>	4	4			1	1	16	4	1	1	4	1
<i>Plesiodimylus</i> sp.			3	1			1	1				
Σ	578	134	1394	283	194	43	763	134	446	72	583	80

Regardless of what you count, the erinaceids represent the vast majority of the insectivores in most but not in all samples. In Petersbuch 18 there are more specimens from erinaceids (193) than from soricids (73) but in the n_c the erinaceids (42) are outnumbered by the soricids (52). The predominance of the erinaceids in most samples is due to the abundance of *Parasorex socialis*, which is without exception the most common insectivore species.

The predominance of erinaceids among the insectivores is conspicuous but not unique for the Petersbuch samples. There are other Miocene faunas with a remarkable erinaceid share: for example Rauscheröd (58%, ZIEGLER & FAHLBUSCH 1986, tab. 14), Rembach (51%, ZIEGLER & FAHLBUSCH 1986, tab. 14), Sansan (50%, calculated from BAUDELLOT 1972) and Nebelbergweg (62%, calculated from KALIN & ENGESSER 2001). In these faunas too the abundance of erinaceids is due to one galericine species.

Biostratigraphic considerations

Erinaceids are not usually appropriate for precise stratigraphic correlation. This counts without reservation for the erinaceines. There are also too many taxonomic uncertainties. *Para-*

sorex socialis is a good terminus ante quem non, since it does not appear in Europe prior to the Middle Astaracian (MN 7). In central Europe it seems to be restricted to faunas correlative with MN 7/8. However, there are hardly any MN 9 faunas known. In the Nebelbergweg fauna, which is correlated with MN 9, the galericines are represented by *Schizogalerix* aff. *voesendorfensis*. In southwest Europe *Parasorex socialis* has been recorded until Vallesian times.

Plesiodimylus chantrei is totally unsuitable for biostratigraphic correlation. Its stratigraphic range covers nearly two thirds of the whole Miocene.

Metacordylodon schlosseri is too rare to be a stratigraphic guide. The records known thus far are correlative with MN 6-MN7/8. Similar forms have been recorded from earlier faunas (MN 5).

Recapitulating the evidence, the faunas under study with some certainty can be correlated with MN 7/8.

Palaeoenvironmental aspects

All the extant galericines mainly inhabit forest environments in southeast Asia often close to water (Nowak 1991). Consequently, we can assume a similar environment for the Miocene galericines. Sometimes it is argued that the present day distribution is only a relic and that in Miocene times the galericines probably had a wider range of habitat preferences (VAN DEN HOEK OSTENDE 2001). It is true that many species now restricted to Southeast Asia once had a wider distribution. But this can also mean that their habitats had a wider distribution.

Family	P 6		P 10		P 18		P 31		P 35		P 48	
	n_s	n_c	n_s	n_c	n_s	n_c	n_s	n_c	n_s	n_c	n_s	n_c
Erinaceidae	574	130	1391	282	193	42	746	129	443	71	579	79
Talpidae	64	27	456	107	29	10	164	71	33	14	32	13
Dimylidae	4	4	3	1	1	1	17	5	3	2	4	1
Soricidae	106	73	85	55	73	52	100	46	24	14	36	15
Σ	748	234	1935	445	296	105	1027	251	503	101	651	108

Table 6. Shares of the insectivore families in the Petersbuch fissure fillings (n_s =number of specimens, n_c =number of most common element)

The karstic area of the Swabian and Franconian Alb was a dry area throughout the Miocene. However, the Petersbuch site is situated only some tens of kilometres from the Molasse area with its many rivers and lakes during the time of the Upper Freshwater Molasse. There have been enough suitable habitats within the range of the owls that preyed on *Parasorex socialis*. JUNG & MAYR (1980) who correlated the leaf floras of the Upper Freshwater Molasse with the corresponding MN units identified two periods of forest development (MN 4-5 and MN 7-9) interrupted by a period of open vegetation (MN 5-6). The faunas under study fall within the second period.

The extant erinaceines inhabit a variety of habitats, ranging from desert to forests. Since we cannot relate our erinaceine species to any Recent one, we cannot infer their environmental demands.

The same is true for the dimylids. As an extinct family they have no Recent relatives. Their peculiar dentition with the bulbous teeth overlapping the dentary, especially in *Metacordylodon*, indicates a durophagous feeding habit. The dimylids are said to have fed on snails (HÜRZELER 1944, MÜLLER 1967). Consequently it is often inferred that dimylids lived in moist environments (SCHÖTZ 1985, VAN DEN HOEK OSTENDE 2001). However, snails do not only thrive in moist environments. In the Mediterranean area there are also snails that live under dry conditions, subsisting on the water from dew. There is a different argument for moist environments. Often deposits yielding many dimylids are of fluvatile origin or are of coaly composition. This per se suggests a moist environment. *Plesiodimylus* with its less specialised dentition probably fed on insects like erinaceids and many talpids.

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