

# **A record of *Macroneomys brachygnathus* FEJFAR, 1966 (Mammalia, Insectivora, Soricidae) in the early Middle Pleistocene (late Biharian) locality of Voigtstedt (Germany) and the history of the genus *Macroneomys***

Lutz MAUL and Barbara RZEBIK-KOWALSKA

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**Abstract.** The Middle Pleistocene locality of Voigtstedt is the sixth with a record of *Macroneomys*. Two mandibles from there, although fragmentary, increase the understanding of the variability of this taxon. Morphological and metrical comparisons with the previous finds are followed by discussions on palaeoecology, stratigraphical range and the origin of *Macroneomys*.

**Key-words:** Insectivora, Soricidae, *Macroneomys*, Middle Pleistocene, Central Europe

Lutz MAUL, Bereich Quartärpaläontologie Weimar, Institut für Geowissenschaften, Friedrich-Schiller Universität Jena, Steubenstr. 19a, D-99423 Weimar, Germany, e-mail: lutz.maul@gast.uni-weimar.de; Barbara RZEBIK-KOWALSKA, Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Sławkowska 17, 31-016 Kraków, Poland, e-mail: rzezik@isez.pan.krakow.pl

## **I. INTRODUCTION**

In 1966 FEJFAR described a new soricid species from the karst sediments of the cave C 718 near the village Koněprusy in Bohemia. This locality is well known for yielding abundant small mammal faunas from 15 superposed horizons representing various climatic oscillations during the early Middle Pleistocene, in particular successive changes from cold to temperate and back again to cold conditions (FEJFAR 1961, 1966). The new species was a neomyin shrew which differed so markedly from the hitherto known species of *Neomys* that the creation of a new genus was necessary. The crucial features of this new form, named *Macroneomys brachygnathus*, are massive teeth and a high mandible (FEJFAR 1966)

Although this shrew belongs to a distinctly robust species, and although since that time hundreds of new Pleistocene small mammal faunas with soricids have been excavated in Europe, only a single incisor from Kövesvár in Hungary (JÁNOSSY 1963), a nearly complete mandible from La Fage in France (JAMMOT 1975) and a fragment of mandible from Kozi Grzbiet in Poland (RZEBIK-KOWALSKA 1991) belonging to *Macroneomys* have been found. JAMMOT (in CLOT et al. 1976) also

mentioned this form (as *Soriculus brachygnathus*) from Montoussé 3 in France, although without giving any data on the nature or number of specimens.

More recently, the sixth record, from the locality of Voigtstedt in Thuringia (Central Germany) can be added. This is one of the most important early Middle Pleistocene localities of Central Europe because it provides various information for dating: a stratigraphically homogenous fauna of large and small mammals, records of mollusca, pollen, glacial geological evidence (KAHLKE 1965) and paleomagnetic data (WIEGANK 1975).

The first description of small mammals from Voigtstedt was made by KRETZOI (1965 – rodents and lagomorphs) and JÁNOSSY (1965 – insectivores). Later on, additional material not available for the monograph edited by KAHLKE (1965) was discovered. Among the shrews, STUART (1981) mentioned two mandibles of *Neomyini* ? sp. nov. and MAUL, in an unpublished thesis (1990) identified them as *Macroneomys brachygnathus*.

Because of the still limited number of records of *Macroneomys brachygnathus* each new find enlarges our knowledge of the morphological variation of this taxon. That is why we have decided to describe the remains from Voigtstedt in more detail, and to compare them with previously described specimens of this rare taxon and with extant *Neomys fodiens* (PENNANT, 1771) considered by FEJFAR (1966) to be the most closely related form.

**A c k n o w l e d g m e n t s.** We are indebted to Dr. A. TURNER (Liverpool) for discussions and improvements in the English, Dr. B. MÖSER (Weimar) for scanning microscopy, and to Dr. R. ANGERMANN (Berlin) for loaning samples of the recent *Neomys fodiens* and *Neomys anomalus*.

## II. SYSTEMATIC PART

Family: Soricidae FISCHER VON WALDHEIM, 1817

Subfamily: Soricinae FISCHER VON WALDHEIM, 1817

Tribe: Neomyini MATSCHIE, 1909

Genus *Macroneomys* FEJFAR, 1966

*Macroneomys brachygnathus* FEJFAR, 1966

**M a t e r i a l f r o m V o i g t s t e d t.** Fragment of the right mandible without teeth, specimen no. IQW 1966/8074 (Voi. 3566), Fig. 1 a-d, in the text named specimen 1. Its horizontal ramus is broken anterior to the distal root of the  $P_4$ . The superior part of the coronoid process is lacking and its buccal surface destroyed. The medial part of the lower articular facet is also damaged and the angular process broken.

A fragment of the right mandible with  $M_2$ , specimen no. IQW 1966/8186 (Voi. 3532), Fig. 1 e-h, in the text named specimen 2. Its horizontal ramus is broken before the second molar, the angular process is lacking.

The material from Voigtstedt is housed in the collection of the Weimar Quaternary Palaeontology branch of the Institute of Geosciences of the Friedrich-Schiller University of Jena.

**Description of the material.** For nomenclature of the elements and measuring points see REUMER (1984).

Both specimens are of brown colour. The well preserved coronoid process of specimen 2 is extremely massive and makes an angle of c.  $90^\circ$  with the horizontal ramus. It resembles the coronoid

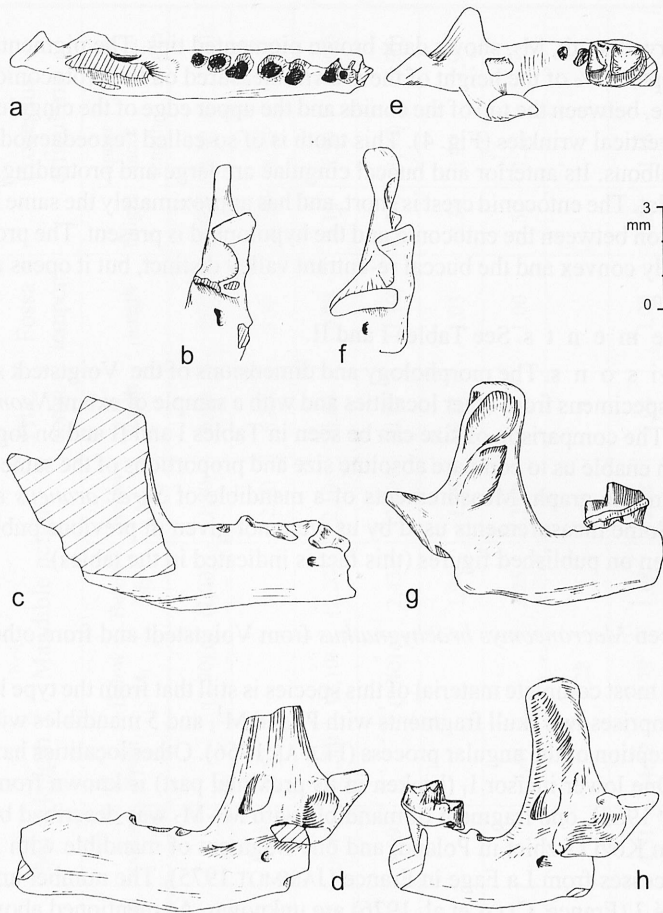


Fig. 1. *Macroneomys brachygnathus* FEJFAR, 1966 from Voigtstedt; a-d: right mandible fragment without teeth – IQW 1966/8074 (Voi. 3566) – specimen 1; e-h: right mandible fragment with  $M_2$  – IQW 1966/8186 (Voi. 3532) – specimen 2; a, c: dorsal view; b, f: caudal view of the articular process; c, g: buccal view; d, h: lingual view.

process in the subgenus *Sorex* (*Drepanosorex*). Its tip, bent lingually, is very large and its base (on the level of the upper sigmoid notch) is relatively narrow. It is, therefore, of nearly the same width over its whole height (the anterior and posterior margins are nearly parallel). The preserved lower part of the coronoid process of the specimen 1 is even broader than in the specimen 2. Its upper part was obviously also larger. The external temporal fossa extends below the upper sigmoid notch. The coronoid spicule is long and protruding. It points towards the upper condylar facet and divides the deep external temporal fossa into two almost equal parts. The upper sigmoid notch forms a right angle. A pterygoid spicule is present. The condyloid process is of *Neomys*-type. Its upper facet is short and narrow, the lower one much longer, broader and slightly concave buccally. Both facets are inclined lingually. They are not parallel, but slightly divergent from each other. The interarticular area is very narrow. The internal temporal fossa is very small, in the shape of a triangle. An single mandibular foramen is located centrally underneath the internal temporal fossa (spec. 2), or a little more to the rear (spec. 1). In comparison to other soricids with similar mandibular length, the horizontal ramus is rather high. The mental foramen is located below the alveolus of the anterior root of the  $M_1$ .

The only preserved tooth,  $M_2$ , shows dark brown pigmented tips. The pigmentation covers approximately the upper 80% of the height of the crown (measured on the protoconid and hypoconid from the buccal side, between the top of the conids and the upper edge of the cingulum). The enamel surface has slight vertical wrinkles (Fig. 4). This tooth is of so-called "exoedaenodont" type, being rather short and bulbous. Its anterior and buccal cingulae are large and protruding, and the lingual one also large but flat. The entoconid crest is short, and has approximately the same height as the hypolophid. An incision between the entoconid and the hypolophid is present. The protoconid and hypoconid are buccally convex and the buccal re-entrant valley distinct, but it opens at some distance above the cingulum.

**M e a s u r e m e n t s.** See Tables I and II.

**C o m p a r i s o n s.** The morphology and dimensions of the Voigtstedt specimens are to be compared with specimens from other localities and with a sample of extant *Neomys fodiens* from Central Germany. The comparison of size can be seen in Tables I and II and on log-diagrams (Figures 6 and 7) which enable us to compare absolute size and proportions of the same elements of different specimens in one graph. Measurements of a mandible of *Sorex araneus* are used here as reference values. Some measurements used by us were not given in previous publications. In this case they were taken on published figures (this fact is indicated in the tables).

Comparison between *Macroneomys brachygnathus* from Voigtstedt and from other localities

The richest and most complete material of this species is still that from the type locality of Koněprusy C 718. It comprises two skull fragments with  $P^4$  and  $M^1$ , and 5 mandibles with teeth and processes with the exception of the angular process (FEJFAR 1966). Other localities have yielded much scarcer material. One lower incisor  $I_1$  (broken in its proximal part) is known from Kővesvárad in Hungary (JÁNOSSY 1963), one fragment of mandible with  $M_1$ - $M_2$  was described by RZEBIK-KOWALSKA (1991) from Kozi Grzbiet in Poland, and one fragment of mandible with  $P_4$ - $M_3$ , coronoid and condyloid processes from La Fage in France (JAMMOT 1975). The number and kind of specimens in Montoussé 3 (France, CLOT et al. 1976) are unknown. As mentioned above, in Voigtstedt two mandibular fragments with  $M_2$ , coronoid and condyloid processes were present.

The specimen from La Fage (JAMMOT 1975) represents the most massive horizontal ramus. Others (from Voigtstedt, Kozi Grzbiet and Koněprusy) are smaller and their dimensions overlap each other (RZEBIK-KOWALSKA 1991, FEJFAR 1966). The coronoid process is rather similar in shape and size in all preserved specimens of *M. brachygnathus*, although some differences are visible. For example, the coronoid process of the specimen 2 from Voigtstedt is similar to those from the type locality of Koněprusy, but that from La Fage is more enlarged and not inclined forwards (Fig. 2). The damaged specimen 1 from Voigtstedt probably resembled this from La Fage. Because of differences between specimens from the type locality and La Fage, JAMMOT (1975) was not sure that the mandible from La Fage was conspecific with the type specimen and described it as *M. cf. brachygnathus*. However, the two differently formed coronoid processes from Voigtstedt show that this feature can vary in one locality. Moreover, the width of the coronoid process, as well as its angle of inclination, vary also in *Neomys fodiens* (Fig. 2h). These differences, in our view, have no taxonomic value either in *N. fodiens* or in *M. brachygnathus*. The coronoid spicule, upper sigmoid notch and external temporal fossa in the Voigtstedt specimens are similar to these from other localities. The internal temporal fossa, not clearly limited in its upper part in specimens from Koněprusy and La Fage, is characterised in the Voigtstedt material by clear limitation. The axes of the upper and lower facets of the condyloid process are parallel in specimens from Koněprusy (Fig. 3a-b) but slightly inclined in specimens from La Fage and Voigtstedt (Fig. 3c-e). The pterygoid spicule is hardly visible in specimens from Koněprusy, and in La Fage and Voigtstedt it is well developed. According to FEJFAR (1966) the mandibular foramen in the typical material is situated below the posterior corner of the internal temporal fossa, whereas in the mandible from La Fage (JAMMOT



Table I

## Measurements of mandibles of various soricids

Taxon	Kat.no.resp. collection	locality/area	Mandible length		M1-3 length		Mandible height			Proc. coron.	Fossa tempor.	Processus articularis		
			total	cardinal	coron.	alveol.	Below M <sub>1</sub>	Below M <sub>2</sub>	Below M <sub>3</sub>			height	upper facet length	lower facet length
<i>Macroneomys brachygnathus</i> <sup>1</sup>	64532 Holotype	Koneprusy <sup>1</sup>	14.50	11.80			(1.90)	(2.00)	1.90	6.50	0.95	1.95	1.42	(1.80)
<i>Macroneomys brachygnathus</i> <sup>1</sup>	64694	Koneprusy <sup>1</sup>			5.00	4.53			2.10	6.83	1.15	2.12	1.50	
<i>Macroneomys brachygnathus</i> <sup>1</sup>	64697	Koneprusy <sup>1</sup>	15.30	12.50	(4.80)	(4.30)	(2.10)	(2.20)	2.10	6.60	0.90	2.10	1.50	(2.10)
<i>Macroneomys cf. brachygnathus</i>	LF (1) 5201	La Fage <sup>2</sup>		(13.50)	5.09		(2.40)	2.43	(2.30)	6.78	(1.10)	(2.70)	(1.50)	(1.90)
<i>Macroneomys brachygnathus</i>	(Voi. 3532)	Voigtstedt						1.94	1.89	6.32	1.03	2.36	1.22	1.97
<i>Macroneomys brachygnathus</i>	(Voi. 3566)	Voigtstedt				4.44		2.25	2.19		1.00	2.50	1.25	
<i>Macroneomys brachygnathus</i>	MF/1925	Kozi Grzbiet <sup>3</sup>					2.28							
<i>Neomys fodiens</i> (mean)	ZM Berlin	C-Germany	14.06	11.37	4.51	4.12	1.79	1.68	1.68	5.03	1.08	2.23	1.18	1.74
<i>Sorex araneus</i>	IQW S.a.01	C-Germany	12.15	9.86	3.82	3.47	1.36	1.36	1.28	4.72	1.19	1.56	0.75	1.36

Data from: <sup>1</sup> FEJFAR 1966; <sup>2</sup> JAMMOT 1975; <sup>3</sup> RZEBIK-KOWALSKA 1991. Values in brackets indicate approximately data taken from figures. Illustration of data in log diagram see Fig. 5.

Table II

## Measurements of lower molars of various soricids

Taxon	Kat.no. resp. collection	Locality/area	M <sub>1-3</sub>		M <sub>1</sub>				M <sub>2</sub>				M <sub>3</sub>			
					Length (with cingulum)		Width		Length (with cingulum)		Width		Length (with cingulum)		Width	
			cor.	alv.	total	trig.	tal.	trig.	tal.	total	trig.	tal.	total	trig.	tal.	tal.
<i>Macroneomys brachygnathus</i>	64532 Holotype	Koneprusy <sup>1)</sup>			2.10			(1.40)	1.50							
<i>Macroneomys brachygnathus</i>	64694	Koneprusy <sup>1)</sup>	5.00	4.53	2.15				1.65	1.85			1.30		1.00	
<i>Macroneomys brachygnathus</i>	64697	Koneprusy <sup>1)</sup>	(4.80)	(4.30)	2.25			(1.54)	1.50	(1.90)	(1.40)	(1.30)	(1.30)		(0.90)	(0.90)
<i>Macroneomys cf. brachygnathus</i>	64697	Koneprusy <sup>1)</sup>			2.30				1.40	1.95		1.35				
<i>Macroneomys brachygnathus</i>	LF (1) 5201	La Fage <sup>2)</sup>	5.09	4.48	(2.20)	(1.20)	(1.00)	(1.60)	(1.70)	(1.90)	(1.50)	(1.40)	1.28	(0.80)	(1.00)	(0.80)
<i>Macroneomys brachygnathus</i>	(Voi. 3532)	Voigtstedt								1.75	1.03	0.72	1.28	1.14		
<i>Macroneomys brachygnathus</i>	MF/1925	Kozi Grzbieł <sup>3)</sup>			(4.40)	2.10	1.21	0.86		1.70	(0.90)	(0.70)				
<i>Neomys fodiens</i> (mean)	ZM Berlin	Germany	4.51	4.12	1.72	1.00	0.71	0.95	1.07	1.51	0.84	0.67	0.93	1.01	0.54	0.60
<i>Sorex araneus</i>	IQW S.a.1	Weimar	3.82	3.47	1.53	0.97	0.56	0.89	0.92	1.25	0.75	0.50	0.83	0.81	0.39	0.44

Data from: <sup>1)</sup> FEJFAR 1966; <sup>2)</sup> JAMMOT 1975; <sup>3)</sup> RZEBIK-KOWALSKA 1991

Values in brackets indicate approximately data taken from figures.

Illustration of data in log diagram see Fig. 6.

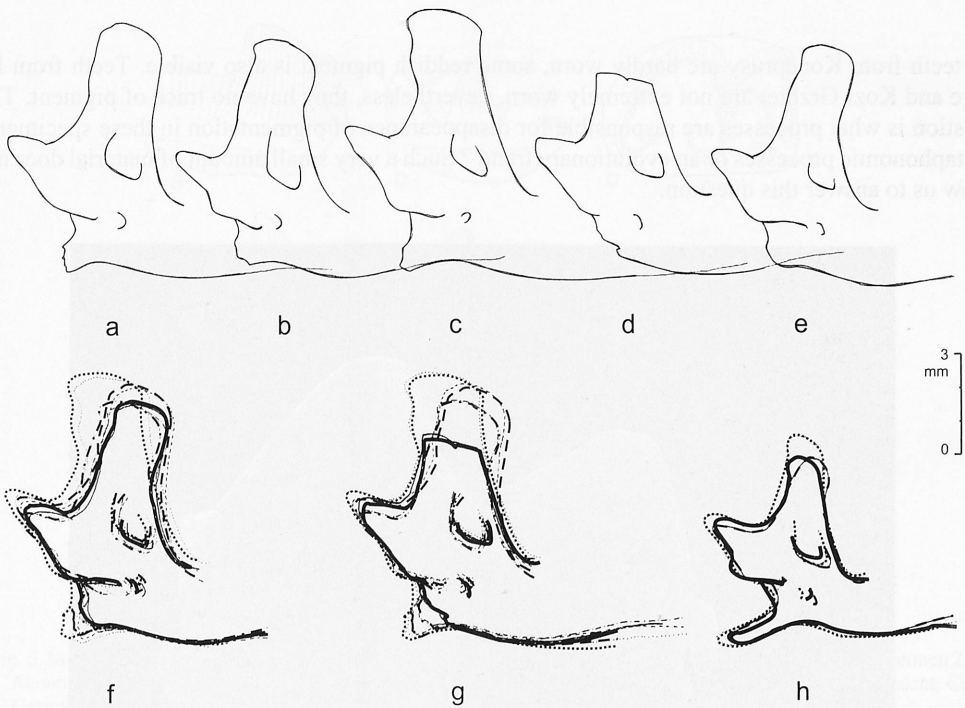


Fig. 2. Views of the distal portion of the mandible of *Macroneomys brachygnathus* FEJFAR, 1966 (a-g) and of *Neomys fodiens* (PENNANT, 1771) (h); a, b: Koněprusy C718 (redrawn from FEJFAR 1966); c: La Fage (redrawn from JAMMOT 1975); d: Voigtstedt specimen 1; e: Voigtstedt specimen 2; f: specimen 2 from Voigtstedt (continuous line) overlaying the specimens of La Fage (dotted line), Koněprusy (bared and bared/dotted lines); g: as Fig. f with specimen 1 from Voigtstedt; h: variation of three specimens of *Neomys fodiens* (recent, Central-Germany).

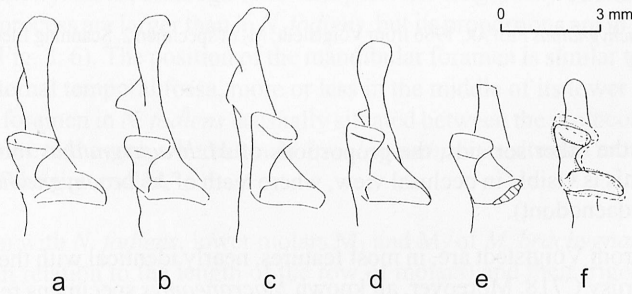


Fig. 3. Views of the articular processes of *Macroneomys brachygnathus* FEJFAR, 1966 (a-e) and of *Neomys fodiens* (PENNANT, 1771) (f); a, b: Koněprusy C718 (redrawn from FEJFAR 1966); c: La Fage (redrawn from JAMMOT 1975); d: Voigtstedt specimen 2; e: Voigtstedt specimen 1; f: variation of three specimens of *Neomys fodiens* (recent, Central-Germany).

1975) it lies more forwards, below the middle of its lower margin. In one specimen (spec. 1) from Voigtstedt it is placed more posteriorly, in the other just in the middle of the lower margin of the internal temporal fossa. In all specimens the mental foramen is visible under the protoconid of  $M_1$ .

According to FEJFAR (1966) the enamel of the convex buccal walls of the teeth is slightly sculpted. This is also the case for the specimens from Voigtstedt (Fig. 4), but not for those from Kozi Grzbiet and La Fage. As mentioned above, the tooth from Voigtstedt is pigmented. Although

the teeth from Koněprusy are hardly worn, some reddish pigment is also visible. Teeth from La Fage and Kozi Grzbiet are not extremely worn, nevertheless, they have no trace of pigment. The question is what processes are responsible for disappearance of pigmentation in these specimens, the taphonomic processes or an evolutionary trend? Such a very small amount of material does not allow us to answer this question.

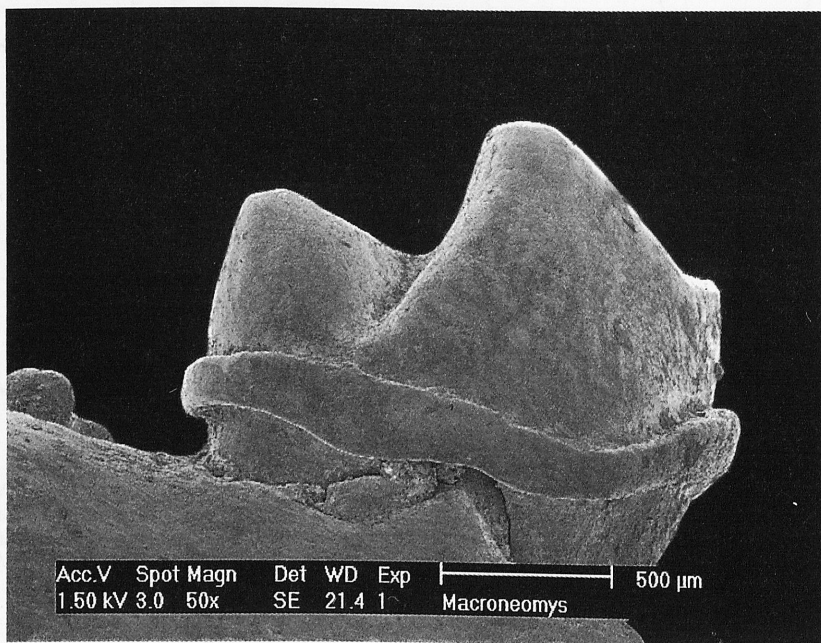


Fig. 4. *Macroneomys brachygnathus* FEJFAR, 1966 from Voigtstedt;  $M_2$  of specimen 2. Scanning Electron Microscope photograph by B. MÖSER.

Compared with the other soricids, the proportions of *M. brachygnathus* molars are markedly different (Fig. 5). This is visible in occlusal view, where teeth of *M. brachygnathus* appear rounded and truncated (exoedaenodont).

The mandibles from Voigtstedt are, in most features, nearly identical with the material from the type locality Koněprusy C718. Moreover, all known *Macroneomys* specimens resemble each other very much. Only the mandible from La Fage shows some differences and larger measurements (Tables I and II, Figures 6 and 7). This may be the result of variability, which would not be greater than in the sample of *Neomys fodiens* used for comparison. It may, however, display a trend of size enlargement with geological time. This phenomenon is known in many species of shrews.

#### Comparison between *Neomys fodiens* and *Macroneomys brachygnathus*

In comparison with *Neomys fodiens*, the horizontal ramus of *M. brachygnathus* is much higher, not only absolutely but also proportionally to the total and cardinal length of the mandible and to the length of the row of molars (see Fig. 6 mandible height). The same is true in the case of the coronoid process. It is much higher than in *N. fodiens*. It is also larger, absolutely and in relation to the length of mandible and the molar row (Fig. 6). The coronoid spicule is much better developed than in



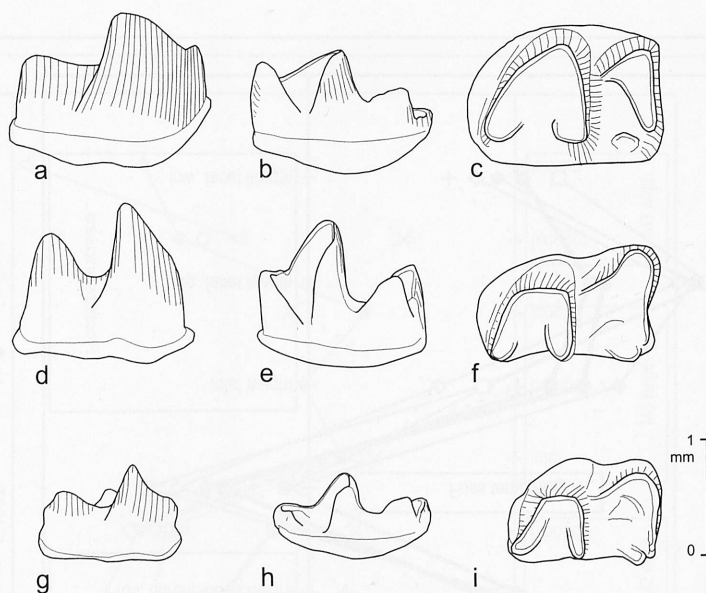


Fig. 5.  $M_2$  of various soricid species; a – c: *Macroneomys brachygnathus* FEJFAR, 1966 from Voigtstedt – specimen 2; d – f: *Neomys fodiens* (PENNANT, 1771) (recent, Central-Germany); g – i: *Sorex araneus* LINNAEUS 1758 (recent, Central-Germany); a, d, g: buccal view; b, e, h: lingual view; c, f, i: occlusal view.

*N. fodiens* and the upper sigmoid notch less open than in the latter species (although the angle of c.  $90^\circ$  occurs also in *N. fodiens* – see Fig. 2h, but with a lower frequency). The internal temporal fossa is similar to that in *N. fodiens*, although its antero-posterior length may be smaller. The dimensions of the condyloid process are larger than in *N. fodiens*, but its proportions are in the range of variation of the last form (Fig. 3, 6). The position of the mandibular foramen is similar to this in *N. fodiens*. It lies below the internal temporal fossa, more or less in the middle of its lower margin. On the other hand, the mental foramen in *N. fodiens* is usually situated between the protoconid/hypoconid valley of  $M_1$  or a little more to the rear, whereas in *M. brachygnathus* it is situated more anteriorly, below the protoconid of the first molar.

In comparison with *N. fodiens*, lower molars  $M_1$  and  $M_2$  of *M. brachygnathus* are much longer (absolutely and in relation to the length of the row of molars) and their trigonids and talonids are much wider in relation to their length, and the  $M_3$  is relatively shorter in comparison with  $M_1$  and  $M_2$  (Fig. 7).

**S y s t e m a t i c p o s i t i o n a n d d i s t r i b u t i o n.** Two specimens from Voigtstedt described above fit morphologically, in absolute size and proportions, to *Macroneomys brachygnathus* and are different from *Neomys fodiens* (Figures 2-7). Small differences in their size and morphology (e. g. in a shape of the coronoid process) express the variation of *Macroneomys brachygnathus*. These differences also indicate that the specimen from La Fage considered by JAMMOT (1975) as *M. cf. brachygnathus* lies, without doubt, within the range of variation of this species.

The geographical distribution of 6 localities in which *Macroneomys brachygnathus* has been so far recorded is given in Fig. 8.

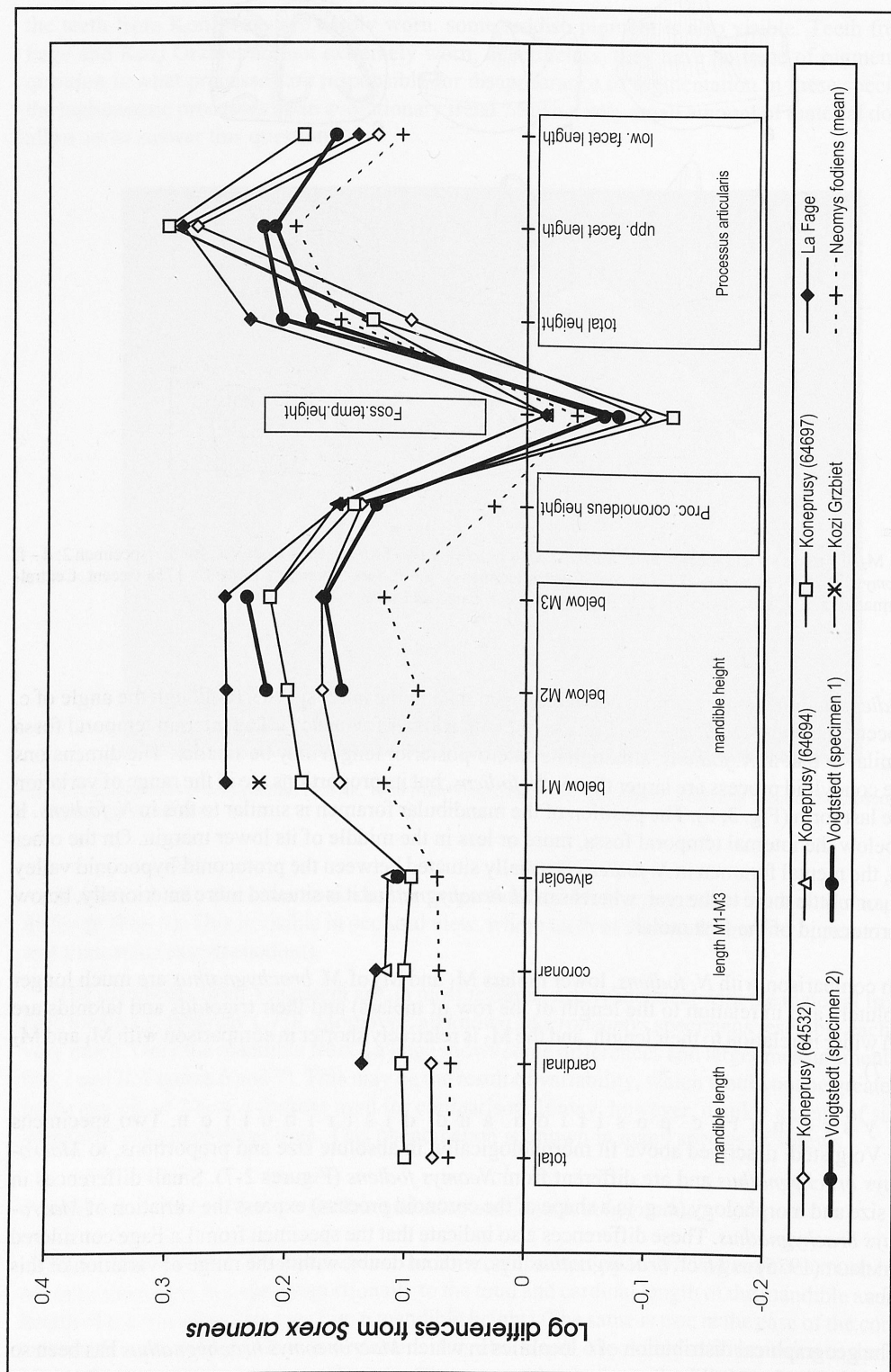


Fig. 6. Log-diagram showing the absolute and relative sizes of the measured mandible elements of *Macroneomys brachygnathus* FEJFAR, 1966, and of *Neomys fodiens* (PENNANT, 1771) (recent, Central-Germany). Values of *Sorex araneus* LINNAEUS, 1758, serve as reference. For measurements see Table I.

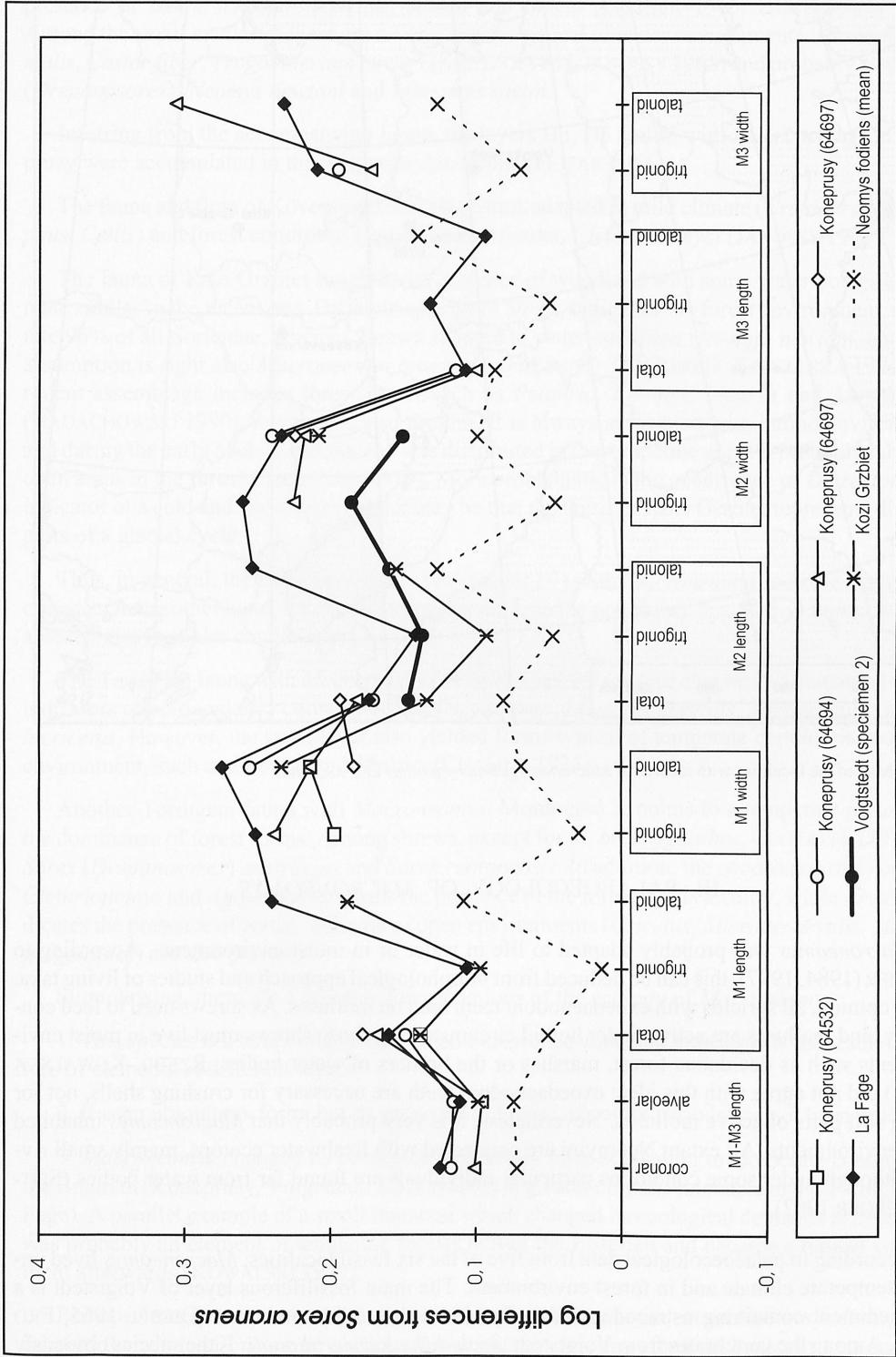


Fig. 7. Log-diagram showing the absolute and relative sizes of the measured molar elements of *Macroneomys brachynathus* FEJFAR, 1966, and of *Neomys fodiens* (PENNANT, 1771) (recent, Central-Germany). Values of *Sorex araneus* LINNAEUS, 1758, serve as reference. For measurements see Table II.

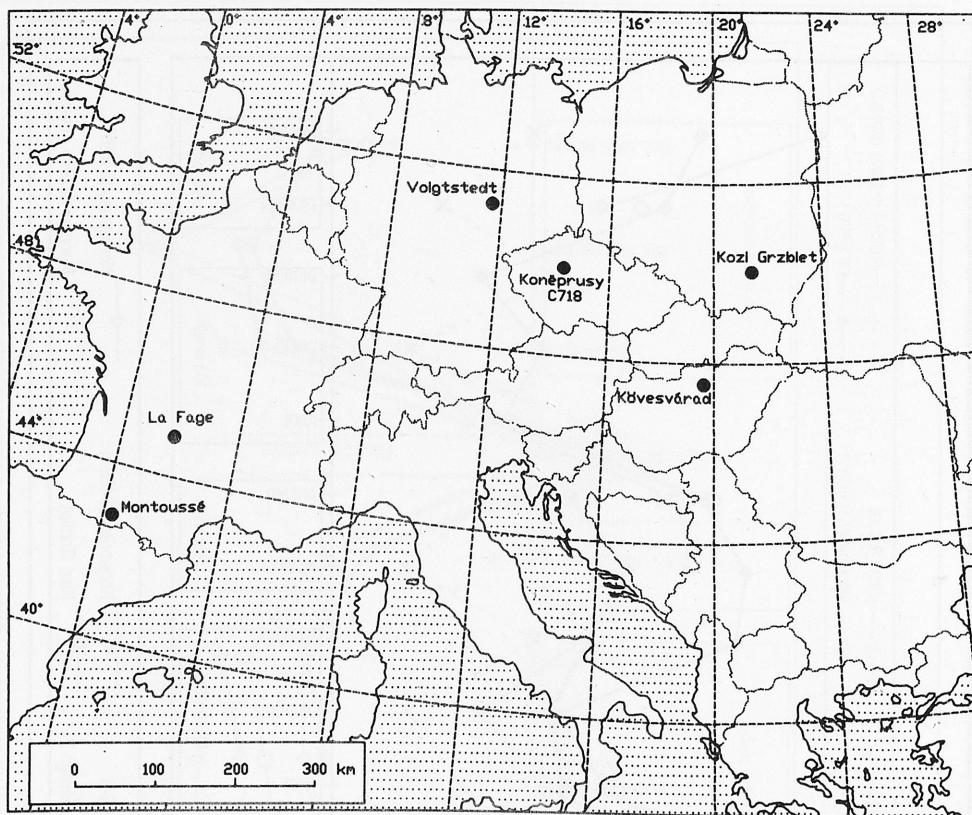


Fig. 8. Map of the localities with records of *Macroneomys brachygnathus* FEJFAR, 1966.

### III. PALAEOECOLOGY OF *MACRONEOMYS*

*Macroneomys* was probably adapted to life in water or in moist environments. According to REUMER (1984, 1997), this can be deduced from morphological approach and studies of living taxa. In his opinion, all soricids with exoedaenodont teeth feed on molluscs. As shrews need to feed constantly, and molluscs are active under humid circumstances, those shrews must live in moist environments such as deciduous forest, marshes or the borders of water bodies. RZEBIK-KOWALSKA (1994) did not agree with this idea: exoedaenodont teeth are necessary for crushing shells, not for eating soft parts of active molluscs. Nevertheless, it is very probably that *Macroneomys* inhabited such environments. All extant Neomyini are connected with freshwater ecotops, mainly small rivers, although under some conditions particular individuals are found far from water bodies (SPITZENBERGER 1982).

According to palaeoecological data from five of the six fossil localities, *Macroneomys* lived under a temperate climate and in forest environment. The main fossiliferous layer of Voigtstedt is a clay sediment containing ostracodes and pollen indicating mild conditions (DIEBEL 1965, ERD 1965). Among the vertebrates from Voigtstedt, *Archidiskodon meridionalis* is the species obviously adapted to temperate climate (THENIUS 1976). Moreover, forest conditions are indicated by the



presence of *Bison schoetensacki*, *Sus scrofa* and others (FISCHER 1965, HÜNERMANN 1965). Among the small mammals there are several species typical of water environments: *Desmana thermalis*, *Castor fiber*, *Trogontherium cuvieri* (KRETZOI 1965, JÁNOSSY 1965) and probably also *Sorex* (*Drepanosorex*), *Neomys newtoni* and *Mimomys savini*.

Inferring from the accompanying fauna, the layers H3, H5 and f5 with *Macroneomys* in Koněprusy were accumulated in the temperate conditions (FEJFAR 1966).

The fauna and flora of Kövesvárad includes forms adapted to mild climate (*Crociodura*, *Rhinolophus*, *Celtis*) and forest conditions (large *Ursus*, *Myoxus*, *Clethrionomys*) (JÁNOSSY 1963).

The fauna of Kozi Grzbiet suggests the presence of woodland with some water bodies and climate similar to the recent one. Different species of *Sorex*, typical of the forest environment, constitute 96% of all Soricidae, whereas shrews adapted to water condition (*Neomys newtoni*, and if the assumption is right also *Macroneomys brachygnathus* itself) 3% (RZEBIK-KOWALSKA 1994). The rodent assemblage includes forest forms such as *Petauria*, *Eliomys*, *Myoxus* and *Muscardinus* (NADACHOWSKI 1990). *Lemmus* is also present. It is always associated with humid environments and during the early Middle Pleistocene was distributed in the temperate zone. It probably inhabited open areas in the forest (KOWALSKI 1977). More problematic is the occurrence of *Dicrostonyx*, an indicator of a cold and dry climate, and it may be that the fauna of Kozi Grzbiet represents different parts of a glacial cycle.

Thus, in general, the Biharian faunas (see chapter IV) with *Macroneomys* indicate a temperate climate. On the other hand, we cannot definitely exclude the possibility that *Macroneomys* was also able to exist in colder conditions.

The Toringian fauna with *Macroneomys* of layer 5 in La Fage (see chapter IV) contained typical indicators of cold and arid climate such as *Dicrostonyx*, *Microtus gregalis*, *Spermophilus* and *Allocricetus*. However, the same layer also yielded forms typical of temperate conditions and forest environment, such as *Eliomys* and *Myoxus* (CHALINE 1975).

Another Toringian fauna with *Macroneomys*, Montoussé 3, points to a temperate period with the dominance of forest forms. Among shrews, except for *M. brachygnathus*, CLOT et al. (1976) list *Sorex* (*Drepanosorex*) *austriacus* and *Sorex runtonensis*. In addition, the occurrence of *Erinaceus*, *Clethrionomys* and *Apodemus* confirms the presence of the forest in this locality, while *Arvicola* indicates the presence of water. Animals of open environments (*Cricetus*, *Microtus arvalis*, *Microtus gregaloides*) are also present.

Summarising, there are 3 possible interpretations of the ecology of *Macroneomys*:

1. This species is a temperate form. The co-occurrence with cold indicators is the result of mixture of elements of different layers.

2. It is an ubiquitous form, but its presence in faunas of colder periods has not been noted.

3. *Macroneomys* changed its ecological characters from adaptation to temperate conditions in the Biharian (Koněprusy, Voigtstedt, Kövesvárad) to greater climatic tolerance in the Toringian (La Fage). A parallel example of a small mammal which changed its ecological demands is *Lemmus*. It was probably an element of temperate forests before the Elsterian and became a typical cold element afterwards (KOWALSKI 1977).

Perhaps *Macroneomys* occupied similar ecological niches to the extant *Neomys fodiens*, which inhabits the whole of Europe up to its northernmost part, hunting along the bank of rivers and lakes (SPITZENBERGER 1982).

#### IV. STRATIGRAPHIC POSITION OF THE RECORDED SPECIMENS OF *MACRONEOMYS*

Implications for the stratigraphic range of *Macroneomys* in Europe are based mainly on the arvicolids in the accompanying faunas. The large-sized rooted vole *Mimomys savini* occur in the Biharian faunas of Koněprusy, Kövesvárad, Kozi Grzbiet, and Voigtstedt, whereas in the Toringian faunas of La Fage and Montoussé 3 *Arvicola* was already present.

The term "Biharian" sometimes leads to confusion, because since its introduction by KRETZOI (1941) it has been used in many different ways. We use the terms *sensu* FEJFAR and HEINRICH (1989). According to these authors the Biharian spans the time of the co-occurrence of the arvicolid genera *Microtus* and *Mimomys*, while the Toringian is defined by the co-occurrence of *Arvicola* and *Microtus*. Moreover, these authors have divided both stratigraphical units into several zones (see below).

In the fauna of Untermassfeld, which is dated close to the Jaramillo event, *Mimomys pusillus* is recorded but *Microtus* species (*sensu stricto*) are absent (MAUL *in press*). Because true *Microtus* taxa are recorded in Koněprusy, Kövesvárad, Kozi Grzbiet and Voigtstedt, these faunas must be younger than the Jaramillo event. On the other hand, they are younger than the Elsterian faunas because *Arvicola* appears in the last interglacial before this glaciation (VAN KOLFSCHOTEN 1990). These three faunas, as well as that from Voigtstedt, lack *Mimomys pusillus*. They are therefore younger than the *Mimomys savini*/*Mimomys pusillus* rodent zone of FEJFAR and HEINRICH (1989) and thus belong to the *Mimomys savini* zone (Fig. 9).

The fossiliferous layer of Voigtstedt is a clayey sediment underlying gravels and a moraine of Elsterian age. The finds therefore must be dated to a pre-Elsterian. Vertebrates and pollen indicate a temperate phase – very probably an interglacial. The fossiliferous layer is of normal paleomagnetism. Therefore it must be an interglacial within the Cromer complex. From the faunal content it resembles very much that of the type Cromerian from West Runton (STUART 1981). According to TURNER (1974) interglacial I, II, and III should be excluded. The age of Voigtstedt should thus correlate with  $\delta^{18}\text{O}$  stage 13, 15, or 17, which means a possible age limit between c. 500 and 700 ky B.P.

The bone bearing unit 2 of Kozi Grzbiet shows great resemblance to that of Voigtstedt (NADACHOWSKI 1990). This is in agreement with datings based on fluoro-chloro-apatite and collagen of 0.63-0.56 My (WYSOCHAŃSKI-MINKOWICZ 1969), and the referral to the Brunhes normal magnetic epoch (GLAZEK *et al.* 1976, 1977a, b).

In Koněprusy C 718 fifteen fossil mammal-bearing horizons represent a climatic succession from cold to warm and again to cold conditions (FEJFAR 1961, 1966). These faunas as well as that from Kövesvárad, comprise arvicolids such as *Microtus arvalinus* and *Microtus ratticepoides*, being at a similar evolutionary stage as the *Microtus* species of Voigtstedt. Koněprusy and Kövesvárad cannot be much older than the latter locality.

CLOT *et al.* (1976) consider the fauna of Montoussé 3 as belonging to the Mindel and Mindel-Riss complex (but before Riss), so it must be younger than these mentioned above. Thus, and because of the presence of *Arvicola* in this fauna, this locality could be dated to the early Toringian.

The fauna of La Fage (layer 5) is still younger. Many students (CHALINE 1972, 1975, JAMMOT 1975, MOURER-CHAUVIRÉ 1975, JEANNET in BARTOLOMEI *et al.* 1975) assign it to the Riss complex. What is considered in France as the Riss complex probably does not correlate entirely with the Central-European Saalian ( $\delta^{18}\text{O}$  stage 6-8) but may also include older  $^{18}\text{O}$  stages. Moreover in layer 5 *Pliomys lenki relictus* CHALINE, 1975 was recorded together with cold elements (see palaeoecology). On the other hand *Arvicola*, which shows an evolutionary tendency to an increase in

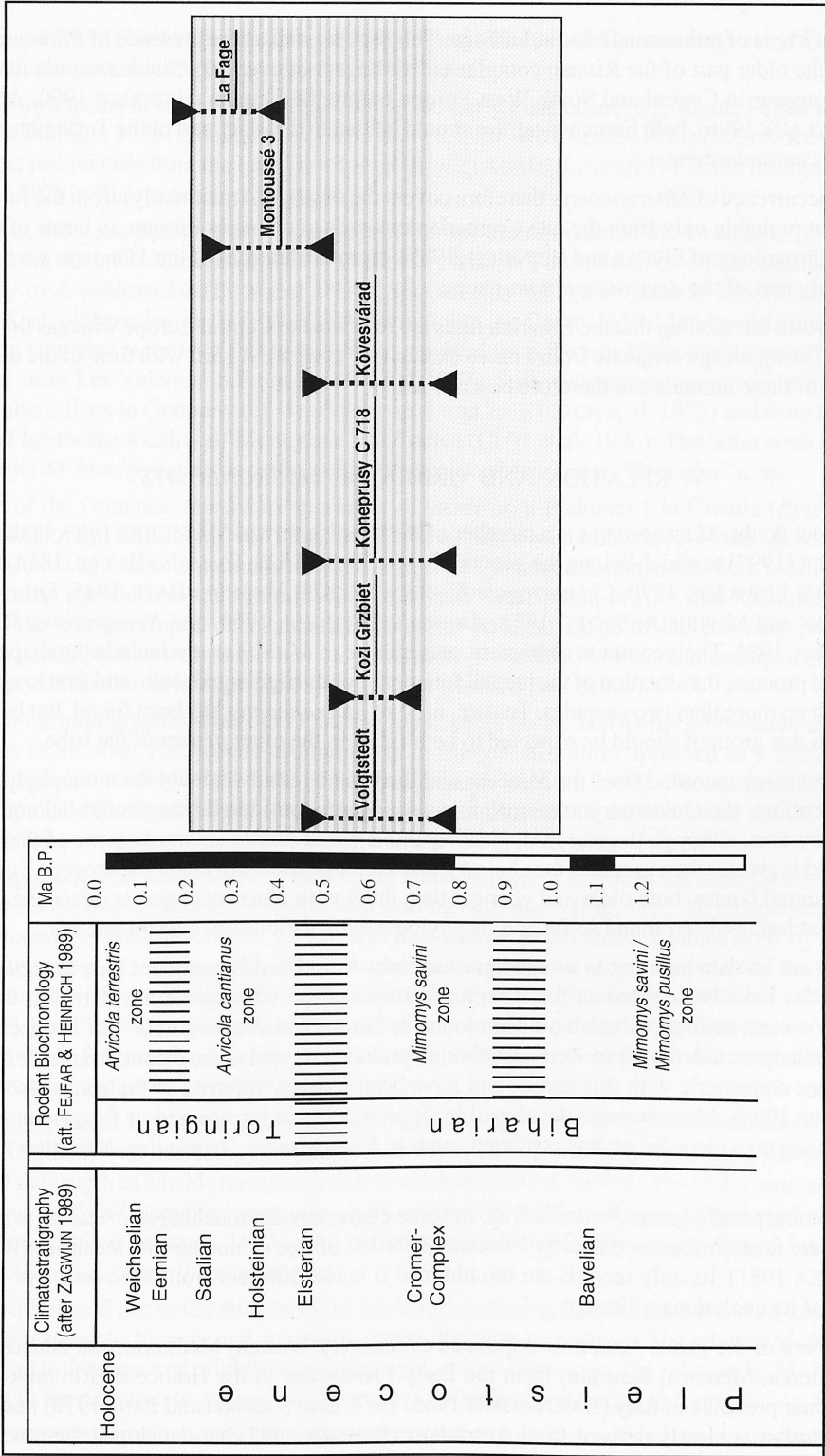


Fig. 9. Maximal (grey background) and assumed (horizontal bars) stratigraphic range of *Macroneomys brachygnathus* FEJFAR, 1966, according to the age of the relevant faunas.



size of its  $M_1$  is of rather small size at La Fage. This fact, as well as the presence of *Pliomys*, could indicate the older part of the Rissian complex ( $\delta^{18}O$  stage 8 or even 10). Since *Arvicola terrestris* does not appear in Central and South West Europe before the Eemian (HEINRICH 1990, ABBASSI and DESCLAUX 1996), both French localities should belong to the older part of the Toringian, i.e. the *Arvicola cantianus* zone.

The occurrence of *Macroneomys* therefore covers the time span (maximally) from the Jaramillo Event, but probably only from the late Cromerian onwards to the early Rissian, in terms of the rodent biochronology of FEJFAR and HEINRICH (1989): from the late part of the *Mimomys savini* zone to the early part of the *Arvicola cantianus* zone.

It is worth mentioning that the Biharian finds are restricted to Central Europe whereas the specimens of Toringian age originate from France exclusively (Fig. 8). A shift with time of the distribution area of these animals can therefore be assumed.

## V. RELATION AND ORIGIN OF *MACRONEOMYS*

Without doubt, *Macroneomys* is a member of the tribe Neomyini MATSCHIE, 1909, in the sense of REUMER (1997) to which belong the genera *Neomys* KAUP, 1829, *Soriculus* BLYTH, 1854, *Nectogale* MILNE-EDWARDS, 1870, *Chimarrogale* ANDERSON, 1877, *Nesiotites* BATE, 1945, *Episoriculus* ELLERMAN and MORRISON-SCOTT, 1951, *Asoriculus* KRETZOI, 1959, and *Neomyosorex* RZEBIK-KOWALSKA, 1981. Their common characters, present also in *Macroneomys* include the shape of the condyloid process, the situation of the mental foramen, lightly pigmented teeth, and first lower incisor  $I_1$  with no more than two cuspules. To date, no  $I^1$  of *Macroneomys* has been found, but based on referral to this group it should be expected to be bifid as in the other genera of the tribe.

Neomyini are recorded since the Miocene and there is no reason to doubt the monophyly of this tribe. Therefore, the Quaternary ancestor of *Macroneomys* considered here should belong to this group. However, although the morphological resemblance of *Macroneomys* to some of the genera mentioned is greater than to others (see below), and although there are many Pleistocene European small mammal faunas, both older and younger than those with *Macroneomys*, its direct ancestor or descendant has not been found so far and its phylogenetic relationships remain unclear.

There are no data pointing to its immigration from Asia. On this continent only *Soriculus* and *Episoriculus* have been noted as fossil representatives of the tribe Neomyini (STORCH et al. in press). However, neither of them have been found in Europe and Western Asia. The European species previously included in *Episoriculus*, although probably related to the extant Asiatic *Episoriculus*, are not congeneric with this genus, and have been recently referred to the genus *Asoriculus* (HUTTERER 1994). *Macroneomys* developed in all probability in Europe and its forerunner is to be found among taxa recorded on this continent, such as *Neomyosorex*, *Asoriculus*, *Nesiotites* or *Neomys*.

The monospecific genus *Neomyosorex*, in some characters approaching *Asoriculus*, is a small and delicate form limited to the Early Pliocene (MN 14) of one or maybe two localities (RZEBIK-KOWALSKA 1981). Its only records are too old, and it is too different from *Macroneomys* to be a member of its evolutionary lineage.

Members of the genus *Nesiotites* populated exclusively Western Mediterranean islands (Corsica, Mallorca, Menorca, Sardinia) from the Early Pleistocene to the Holocene (REUMER 1997). Data on their presence in Italy (BARTOLOMEI 1966, 1977, BARTOLOMEI and PASA 1970) need revision. *Nesiotites* is clearly derived from *Asoriculus* (REUMER 1997) but developed then in insular conditions. Because of this biogeographical limitation it can be excluded from the ancestry of *Mac-*



*roneomys*. FEJFAR (1966) after studying morphological affinities of *Macroneomys* came to the conclusion that it resembles *Neomys* rather than *Nesiotites*.

*Neomys* appears in several parts of Europe in the Early Pleistocene (e.g. Monte Peglia in Italy – VAN DER MEULEN 1973, Zalesiaki 1/A in Poland – RZEBIK-KOWALSKA 1991; RZEBIK-KOWALSKA 1998). Its two records from the Late Pliocene of Uryv 2 (AGADZHANYAN 1977) and Rudnyj 3 (HOLMOVOJ 1992) in Russia need confirmation.

So far, the geologically oldest Neomyini in Europe are represented by *Asoriculus*. The genus ranged from the latest Miocene (MN 13) to the early Middle Pleistocene. Its oldest remains belong probably to *A. gibberodon* (PETÉNYI, 1864) [*Episoriculus* aff. *gibberodon* in MASINI and ROOK 1993 = *E. cf. gibberodon* in DE GIULI 1989, from Monticino Quarry (MN 13) near Brisighella in Italy]. The youngest records of this species were reported from the late Early Pleistocene ("*E.*" *gibberodon* from Les Valerots in France – JAMMOT 1977). Still younger remains of the genus come from Hohensülzen in Germany (cf. *Asoriculus* sp. 1 and 2 – STORCH et al. 1973) and from the early Middle Pleistocene locality of Montoussé 3 in France (CLOT et al. 1976). The latter were listed together with *M. brachygnathus* as a new unnamed species of *Asoriculus*, "*Soriculus*" n. sp.

One of the youngest *Asoriculus* species is *A. thenii* from Podumci 1 in Croatia (*Episoriculus thenii* MALEZ and RABEDER, 1984). Because of the similar evolutionary level of the *Microtus* finds from Podumci and from Untermassfeld (MAUL in press), it can be assumed that both localities may be of similar age close to the Jaramillo event. In their description, MALEZ and RABEDER (1984) stressed the less developed exoedaenodonty and the different shape of the coronoid process of *A. thenii* in comparison with *Macroneomys* and therefore excluded a close relationship of both taxa. The latter conclusion is, in our opinion, not strictly justified (see below).

From the stratigraphic aspect the Pliocene representatives of *Asoriculus gibberodon* should be ancestors of all other Pleistocene neomyin taxa in Europe. *Nesiotites* appeared as a form distinct from *Asoriculus* as early as the base of the Quaternary (REUMER 1997). *Neomys* and *Asoriculus thenii* should be also descendants but belonging each to different lineages because the earliest records of *Neomys* (see above) are older than the fauna of Podumci with *A. thenii*.

The question that remains is to which taxon *Macroneomys* was connected most closely? Did it derive from the line leading to *Neomys* or that leading to *A. thenii* (Fig. 11)? An independent origin of *Macroneomys* directly from *A. gibberodon* also cannot be excluded. Comparisons of absolute and relative sizes of some mandibular and dental measurements of recent *Neomys* and the Biharian *Asoriculus thenii* respectively with the *A. gibberodon* from the Pliocene localities of Csarnóta and Villány 3 (see Fig. 10) may contribute arguments to a possible phylogenetic relationship. It is evident that some features do not undergo remarkable changes, some trends develop (parallel) in the same direction and some go in different directions.

*Neomys fodiens* has larger dimensions but similar proportions to *Neomys anomalus* (Fig. 10). Comparing them with *Asoriculus gibberodon*, *A. thenii* and *Macroneomys* it is apparent that the relation of the length of  $M_1:M_2$  remains similar in all taxa. From *A. gibberodon* to *A. thenii* as well as to *Neomys* nearly all elements increase in absolute size. The width in relation to the length of  $M_3$  becomes larger in both lineages. The  $M_1$  and  $M_2$  become broader in relation to their length but more in the direction of *A. thenii* than to *Neomys*.

One difference lies in the relation of the  $M_3$  length to the  $M_2$  length. It is increasing from *Asoriculus gibberodon* to *Neomys* and decreasing in the direction to *A. thenii*. The relation  $M_1:M_1-M_3$  is decreasing to *Neomys* and slightly increasing to *A. thenii*. Moreover, the relation  $I_1:M_1-M_3$  is increasing in the direction to *A. thenii* and remains similar in the direction to *Neomys*.

When now comparing tooth proportions of *A. gibberodon*, *A. thenii* and *Neomys* with the situation in *Macroneomys* it appears that the proportions in *Macroneomys* show more of a continuation

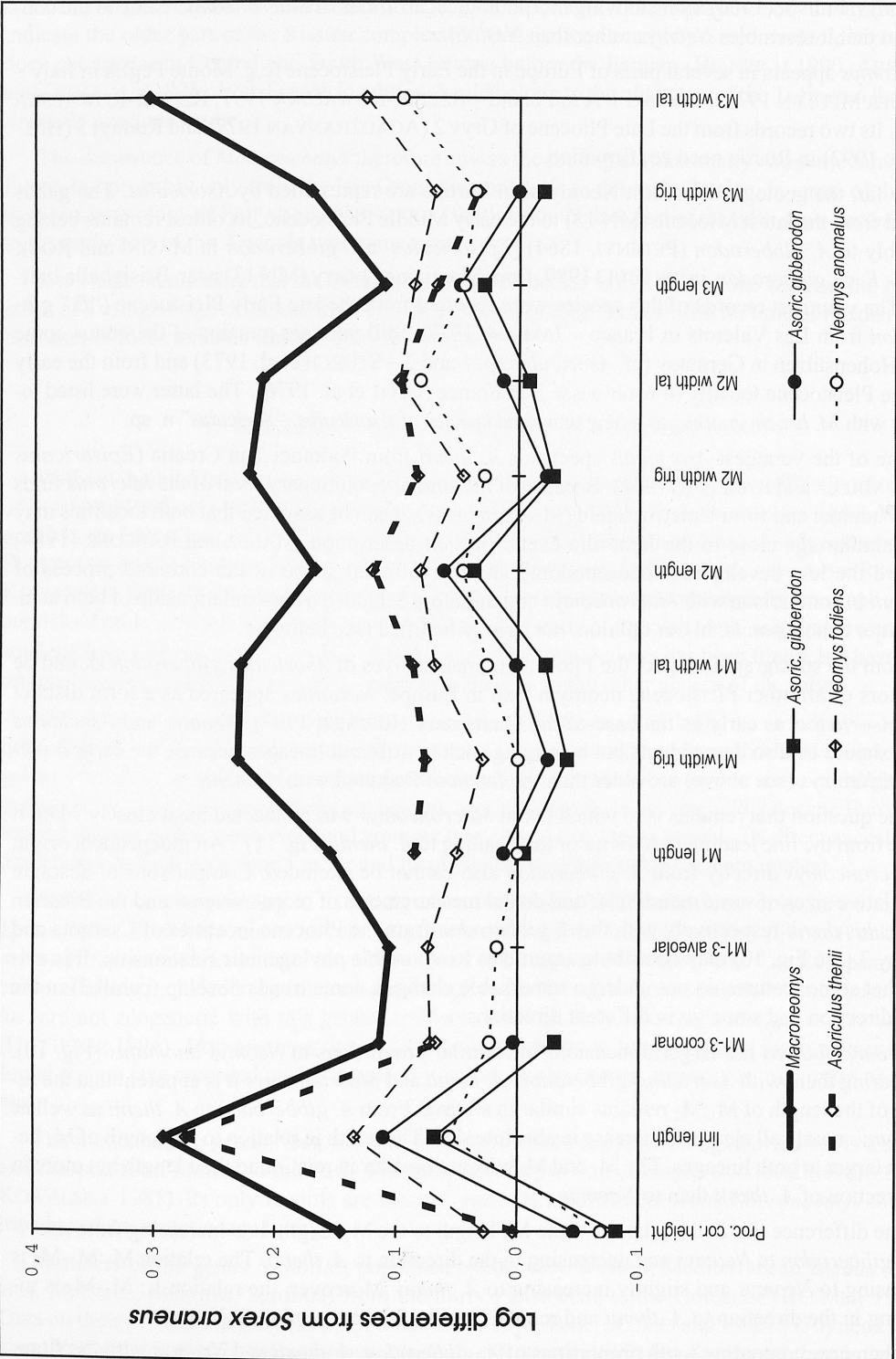


Fig. 10. Log diagram showing the absolute and relative sizes of the measured mandible and molar elements of various representatives of European Neomyini. Data for *Macroneomys brachygnathus* FEJFAR, 1966, are the mean values taken from Table I and II; for *Asoriculus gibberodon* (PETÉNYI, 1864) of Villány 3 and Csarnóta 2 from Reumer (1984), for *Asoriculus thenii* (MALEZ and RABEDER, 1984) of Podumci 1 from MALEZ and RABEDER (1984).

of the trend from *A. gibberodon* to *A. thenii* than from *A. gibberodon* to *Neomys*. That is, the  $M_1$  and  $M_2$  are still broader in relation to the length and the  $M_3$  length is still more reduced in relation to  $M_2$  length. This could be a reason to assume a phylogenetic connection *A. gibberodon* – *A. thenii* – *Macroneomys*. If *Macroneomys brachygnathus* did not appear before the late Cromerian (see chapter IV) and if the record of *Asoriculus thenii* dated to the Jaramillo event, then the time difference between both species would be sufficient (at least c. 300 ky) for the evolutionary change in morphology to occur.

However, this argument concerns only some characters of the mandible and lower teeth. Possible tendencies towards a reduction of the tooth pigmentation and the development of the upper teeth are still unclear. On the latter feature, FEJFAR (1966) only showed that the upper antemolars from the type locality are more rounded and stout in comparison with *Neomys*. According to RZEBIK-KOWALSKA (1988) these teeth in *Asoriculus* are short, sometimes broader than long, and stand very tightly side by side whereas in *Neomys* and *Nesiotites* they are more elongated and relatively spaced apart in the row.

Finally, it is worth mentioning that the anterior part (between the apex and main cusp) of the  $I_1$  is shorter in *Asoriculus* than in *Neomys*, *Nesiotites* and *Macroneomys*. The ratio of the overall length to its anterior part ranges in *Asoriculus* from 2.70 to 3.00 ( $n=10$ ), whereas the same ratio is 2.19 to 2.43 ( $n=10$ ) in *Neomys* and 2.50 ( $n=2$ ) in *Nesiotites* (RZEBIK-KOWALSKA 1988). The ratio for the unique complete lower incisor of *Macroneomys* from Koněprusy is c. 2.47 (measurements made on drawing). Because the short anterior part in *Asoriculus* represents the plesiomorph state and *Neomys* and *Nesiotites* belong to different lineages the elongation of this element developed independently at least two times - and a third parallel development in *Macroneomys* would not be unlikely.

In each case an independent development for many characters in different lineages of shrews as an adaptation for similar diet must be taken in account. More complete material of lower Pleisto-

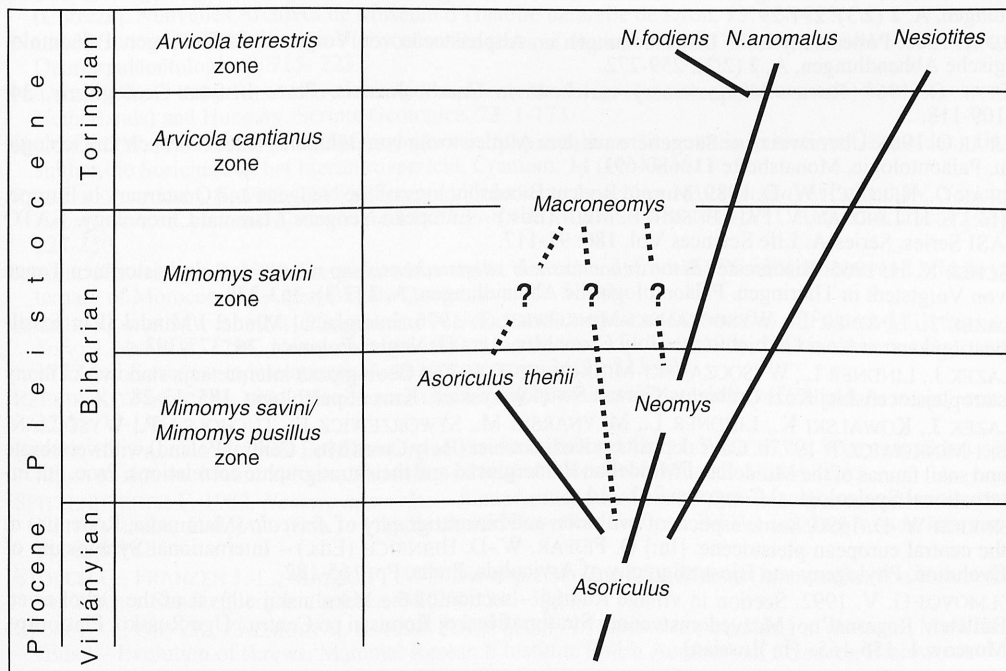


Fig. 11. Possible relationship between European members of Neomyini.



cene Neomyini, with more features available for analysis, is needed to confirm the relation and separation of these lineages.

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