

Voles of the Tegelen fauna

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Abstract

The rich small mammal assemblage of the Tegelen Egypte locality is revised. The following species are recognized (the frequency of remains is given in brackets): Mimomys pliocaenicus (10.9%), M. reidi (17.4%), M. tigliensis n. sp. (38.3%), M. pitymyoides (0.1%), Clethrionomys kretzoi (20.1%) and Ungaromys dehmi (13.2%). Mimomys pitymyoides is recognized in the fauna for the first time. The genus name, Pitymimomys, is proposed for the 'Mimomys pitymyoides' group. Mimomys tigliensis sp. nov. is considered to be the ancestral form of M. tornensis. The new species is less hypsodont and smaller than M. tornensis. The vole association is thought to represent humid forest and riparian biotopes of the late Tiglian. The Tegelen fauna is of late Villanyian age and predates the terminal Villanyian assemblage with Mimomys ostramosensis-Mimomys tornensis.

Introduction

The fossil voles from the Tiglian deposits of the Netherlands have been known for over 90 years. Throughout this period several important investigations of the fossil voles of the Tegelen have been published (Newton, 1907, Hinton, 1926, Schreuder, 1945, Van der Meulen, 1976, Van Kolfschoten, 1990 and others).

The importance of this fauna in the European context is further enhanced by the range of evidence for the development of the Tiglian environment obtained by Dutch workers (e.g. Zagwijn, 1960, 1985).

The successful field campaign in early 70s has produced a rich collection of small vertebrates from the famous Tegelen Egypte quarry (Freudenthal et al., 1976). The remains of Soricidae from this site were studied by Reumer (1984), the Desmaninae by Rümke (1985), the voles were reviewed by Van der Meulen (1976) and Van Kolfschoten (1990). This paper focuses on the arvicoline material in detail.

Material, methods and terminology

The collection described here is preserved in the Leiden Royal Geological Museum, The Netherlands; numbers RGM 423000 - 423999. In the text and figure captions specimens are referred to as follows: the specimen numbered RGM423001 is labelled Te001. Originally the Tegelen Egypte quarry material was collected in several independently numbered samples (Freudenthal et al., 1976). Close study of the material has shown that they can be regarded as integral parts of a single uniform sample. The original samples (e.g. Tegelen 1- 9/5) can be identified in Table 35 (Appendix).

Measurements of the occlusal surfaces were determined using a Leitz Ortholux Microscope, the elements of the crowns were measured using an ocular scale with the binocular microscope. The Leitz Ortholux measuring microscope constantly controlled ocular scale measurements. All measurements are given in millimetres.

Terminology of the occlusal surfaces follows A. van der Meulen (1973), Dentine tracts follow G. Rabeder (1981). Drawings of the material were made with the camera lucida equipped binocular microscope.

Description of the material

Family CRICETIDAE Fischer, 1817

Subfamily ARVICOLINAE Gray, 1821

Genus *Mimomys* F. Major, 1902

Comments

The generic taxonomy of Plio-Pleistocene voles is beyond the scope of this article. However, the brief diagnosis of *Mimomys*, as understood by the author, may clarify some of the points discussed below.

Medium sized and large voles. Molars with cement. Lower M/1 has an enamel islet, which may be reduced in hypsodont forms. The posterior lobe of the upper M3 is simplified with the formation of an enamel islet. The islet can be reduced in hypsodont forms. No anterior enamel islet is present in the upper M3.

In this definition the author follows V. Zazhigin (1980) in part. Certainly *Mimomys* is a grade of arvicoline evolution comparable to the modern *Microtus* group. Since the beginning of the century studies in the evolution of voles has demonstrated the independent origin (and parallel development) of several *Mimomys*-like arvicolines: *Borsodia*, *Cromeromys*, '*Mimomys pitymyoides*' group, etc. (Jánossy & Van der Meulen, 1975, Zazhigin, 1980, Tesakov, 1993b). Future research will probably lead to a further splitting of the genus as in the case of *Microtus*. The definition given above of *Mimomys* allows a closer association with the natural group, leaving outside the genus the variety of early Pliocene forms of the '*Promimomys-Cseria*' evolutionary grade.

Subgenus *Mimomys* F. Major, 1902

Mimomys pliocaenicus F. Major, 1902

Figures 1, 2A, 3- 11, Tables 1-7

1902 *Mimomys pliocaenicus*: F. Major, Exhibition on...: p.102-107, fig.13-15 (partim).

1926 *Mimomys pliocaenicus* F. Major F. Major, Monograph of ...: p. 357-363, fig. 99 - 100 (partim).

1976 *Mimomys pliocaenicus* F. Major: Van der Meulen, The smaller ...: p.17, fig. 2-3.

1981 ?*Mimomys* cf. *pliocaenicus* F. Major: G. Rabeder, Die Arvicoliden...: p. 227-228, Abb.140

1986 *Mimomys pliocaenicus* F. Major (partim): D. Mayhew & A. Stuart, Stratigraphic and ...: p.444-450, fig.22: 1-8, 23: 1- 6, 24: 1- 8, 25: 1- 15, 26: 1 - 16.

1988 *Mimomys pliocaenicus* F. Major: T. van Kolfschoten, The Pleistocene...: p. 73-86, fig. 1: 6.

1990 nec *Mimomys pliocaenicus* F. Major: D. Mayhew, Small mammal...: p.63-65, Pl.1: 8-9,12, Pl.2: 4-10, Pl.3: 4, 9-13, Pl.4: 7-10, Pl.5: 5-7.

1994 *Mimomys* cf. *pliocaenicus* F. Major: B. Sala et al., Villanyian ...: p. 6-8, Pl.2: fig. 8, 10-11, Pl.3: fig. 1-3.

Material studied

Tegelen, 12 M/1, 16 M/2, 14 M/3, 20 M1/, 20 M2/, 20 M3/.

Description

This is the largest vole in the Tegelen fauna (Tables 1-6, Figure 1). The dentine fields are moderately closed. The enamel band is of a well-developed '*Mimomys*'- type in older animals and is less differentiated in juveniles and

<i>Table 1</i> <i>Dimensions of Mimomys</i> <i>pliocaenicus, Tegelen, M/1</i>		Variable	n	Mean	Minimum	Maximum	Standard deviation	Standard error
		Length	9	3.33	3.00	3.71	0.20	0.07
		Width	12	1.57	1.35	1.74	0.11	0.03
		Anteroconid index (A/L)	9	46.22	43.57	48.96	1.85	0.62
		Anterosinuid	2		3.89	4.02		
		Hyposinuid	2		3.38	3.7		
		Hyposinulid	6	3.16	3.00	3.43	0.18	0.07
		HH-index	2		4.54	4.93		

<i>Table 2</i> <i>Dimensions of Mimomys</i> <i>pliocaenicus, Tegelen, M/2</i>		Variable	n	Mean	Minimum	Maximum	Standard deviation	Standard error
		Length	13	2.21	2.04	2.50	0.14	0.04
		Width	16	1.48	1.20	1.66	0.11	0.03
		Anterosinuid	3	3.67	3.04	4.18	0.58	0.34
		Hyposinuid	5	3.11	2.72	3.42	0.29	0.13
		Hyposinulid	5	3.01	2.61	3.53	0.40	0.18
		HH-index	5	4.33	3.77	4.92	0.48	0.21

<i>Table 3</i> <i>Dimensions of Mimomys</i> <i>pliocaenicus, Tegelen, M/3</i>		Variable	n	Mean	Minimum	Maximum	Standard deviation	Standard error
		Length	14	2.03	1.81	2.25	0.13	0.04
		Width	14	1.23	1.07	1.45	0.10	0.03
		Anterosinuid	4	2.83	2.39	3.09	0.30	0.15
		Hyposinuid	6	1.64	1.30	2.01	0.26	0.11
		Hyposinulid	6	1.69	1.14	2.01	0.31	0.13
		HH-index	6	2.35	1.81	2.81	0.37	0.15

<i>Table 4</i> <i>Dimensions of Mimomys</i> <i>pliocaenicus, Tegelen, M/1/</i>		Variable	n	Mean	Minimum	Maximum	Standard deviation	Standard error
		Length	19	3.08	2.88	3.28	0.11	0.03
		Width	20	1.74	1.37	1.91	0.15	0.03
		Anterosinus	3	3.6	3.30	4.00	0.35	0.20
		Anterosinulus	4	2.56	2.10	3.50	0.65	0.33
		Protosinus	3	4.47	4.15	5.00	0.47	0.27
		Distosinus	3	4.40	4.20	4.50	0.17	0.10
		PA-index	3	5.76	5.30	6.40	0.57	0.33

<i>Table 5</i> <i>Dimensions of Mimomys</i> <i>pliocaenicus, Tegelen, M2/</i>		Variable	n	Mean	Minimum	Maximum	Standard deviation	Standard error
		Length	17	2.27	2.08	2.47	0.11	0.03
		Width	20	1.46	1.20	1.81	0.14	0.03
		Anterosinus	3	4.09	3.90	4.34	0.23	0.13
		Protosinus	4	3.86	3.37	4.46	0.45	0.23
		Distosinus	3	3.69	3.53	3.85	0.16	0.09
		PA-index	3	5.73	5.45	6.22	0.43	0.25

<i>Table 6</i> <i>Dimensions of Mimomys</i> <i>pliocaenicus, Tegelen, M3/</i>		Variable	n	Mean	Minimum	Maximum	Standard deviation	Standard error
		Length	17	2.19	1.92	2.40	0.11	0.03
		Width	19	1.25	1.13	1.40	0.08	0.02
		Lp/L	16	51.26	45.66	56.94	2.98	0.75
		Anterosinus	6	3.07	2.85	3.35	0.23	0.09
		Protosinus	7	2.56	2.10	2.80	0.25	0.09
		Distosinus	6	2.03	1.95	2.25	0.11	0.04
		PA-index	6	4.01	3.54	4.37	0.30	0.12

younger specimens. The amount of crown cement increases from moderate in younger animals to abundant in older ones.

Root formation stages (Figure 2A)

This is a relatively brachyodont species. 83% of the specimens studied show well-developed roots, 11% are at the merorhiz stage and only 6% of the specimens are at the arhiz stage of root development.

The crown height distribution (Figure 3) shows no obvious pattern probably because of the limited material.

However, in most graphs the central depression is developed. This pattern resembles the attritional age frequency profile (Korth & Evander, 1986).

Dentine tracts

The tracts are rather low; most being interrupted by wear of the fully-formed roots stage. There is a trend towards an enlargement of additional tracts. The sinogram is shown in Figure 4.

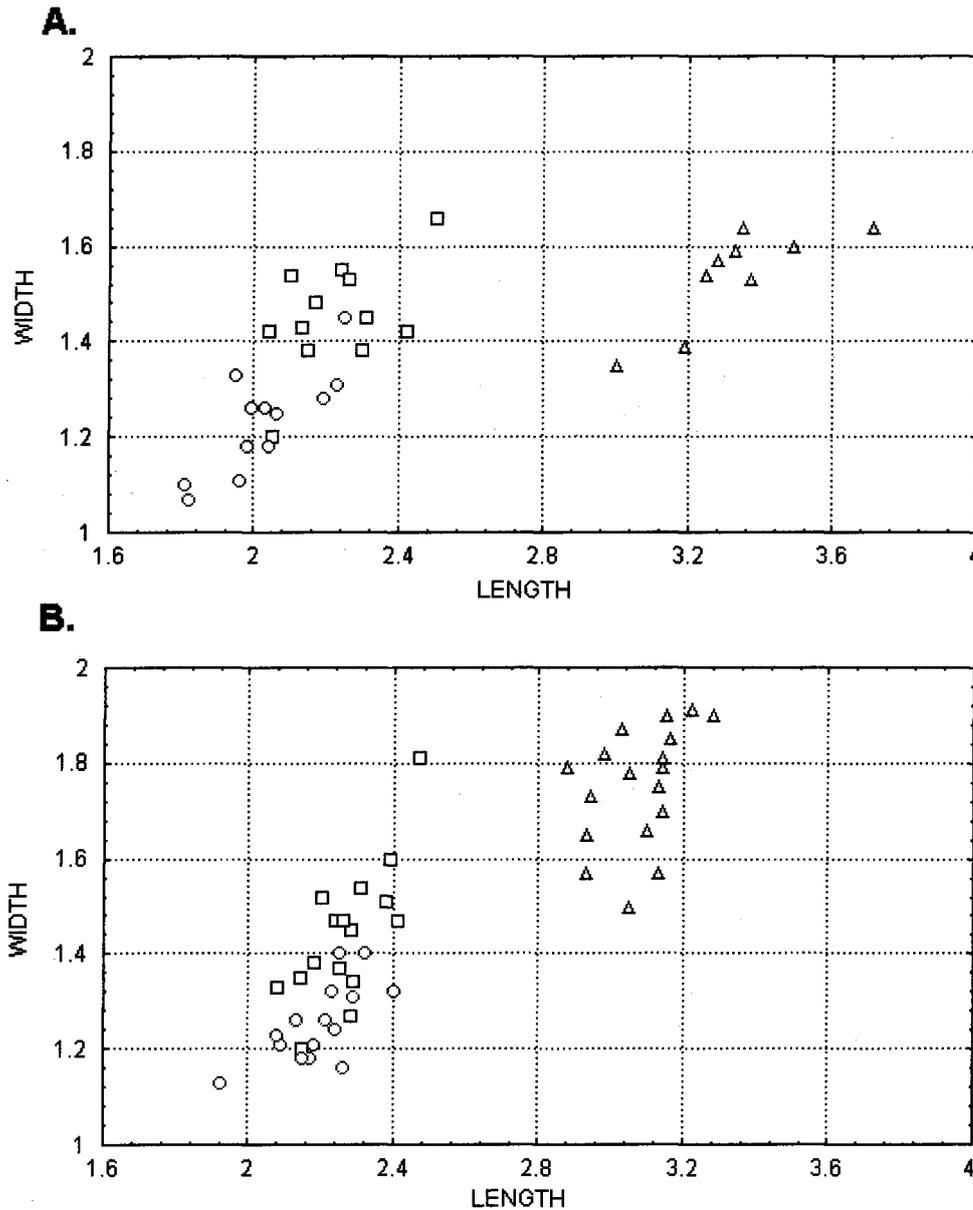


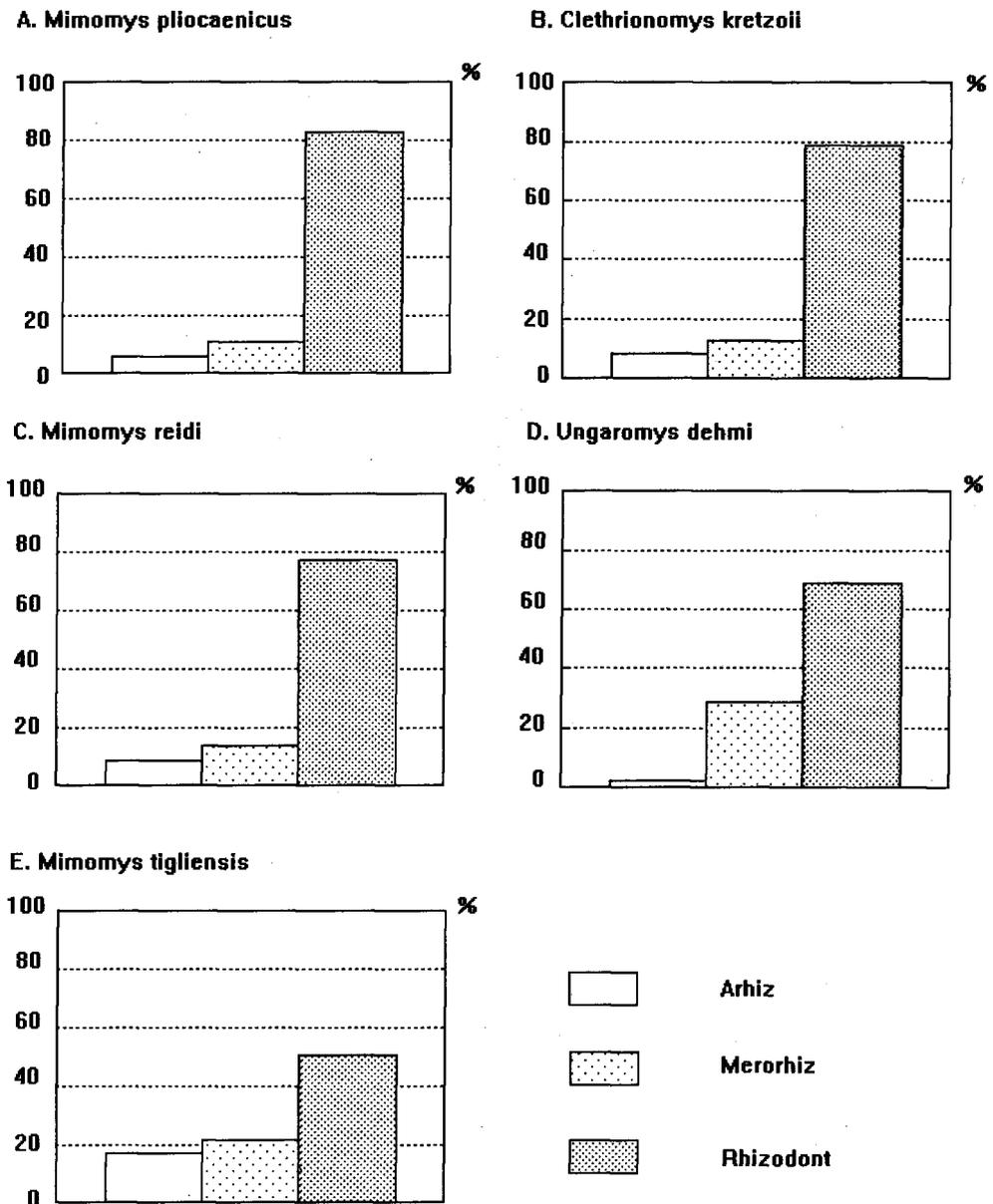
Figure 1
Mimomys pliocaenicus,
Tegelen. Scatter diagram of
length and width. A - Lower
molars, B - Upper molars.
Triangles - M1/1, squares -
M2/2, circles - M3/3.

M/1

The molar consists of the posterior loop, with three alternating triangles and the anteroconid complex. The relative length of the latter varies from about 44 to 49% (Table 1, Figure 5). In the youngest individuals, the BRA3 is very deep (Figure 6: 1). With continuing wear it becomes reduced with the formation of the enamel islet. In the single juvenile specimen (Te844) the isolation of the BRA3 occurs at the crown height of 3.48 mm. Figure 7 illustrates the islet formation in relation to crown height. It is evident that the insulation level is rather variable. The earliest

specimens with the closed islet have the crown height of about 3.5 mm. The lowest molars with an islet are about 3.0 mm high, though the primary dentine traces of the islet can still be seen in specimens with a crown height of about 1.2 mm. The *Mimomys*-ridge is well developed and deep. The elevation of the islet fold above the lower enamel boundary ranges from 1.00 to 2.12 mm, with the mean of 1.50 mm (n=10). Most of the specimens studied display a well-developed mimosinuid (Figure 6: 1-4) and slightly enlarged prismosinuid.

Figure 2
Root formation stages of the
Tegelen vole species
(%, all molars).



M/2

This molar has a typical arvicoline shape. Connections between T1 and T2, and between T3 and T4 tend to be closed. The posterior root of the molar has a clear acro-rhiz position (Figure 6: 7b)). The enamel-dentine boundary at the base of the basic triangles tends to form low dentine tracts (Figure 6: 6a-b).

M/3

This molar has a typical shape. The dentine fields of T1 and T2 are broadly confluent. BRA2 is more vergent than

BRA1 (Figure 6: 8-10). Thus the connection between T3 and T4 is narrower than that of the T1-T2. One specimen (Te318) displays a minute 'cingulum' cusplet at the base of the posterior loop.

M1/

All elements of the occlusal surface are well separated. BRA3 is almost not developed. LRA3 is very shallow. Most molars show three well-developed roots (n=17), although in some of them the anterior root and the protocone root are tightly connected (Figure 8: 3a). The single molar has

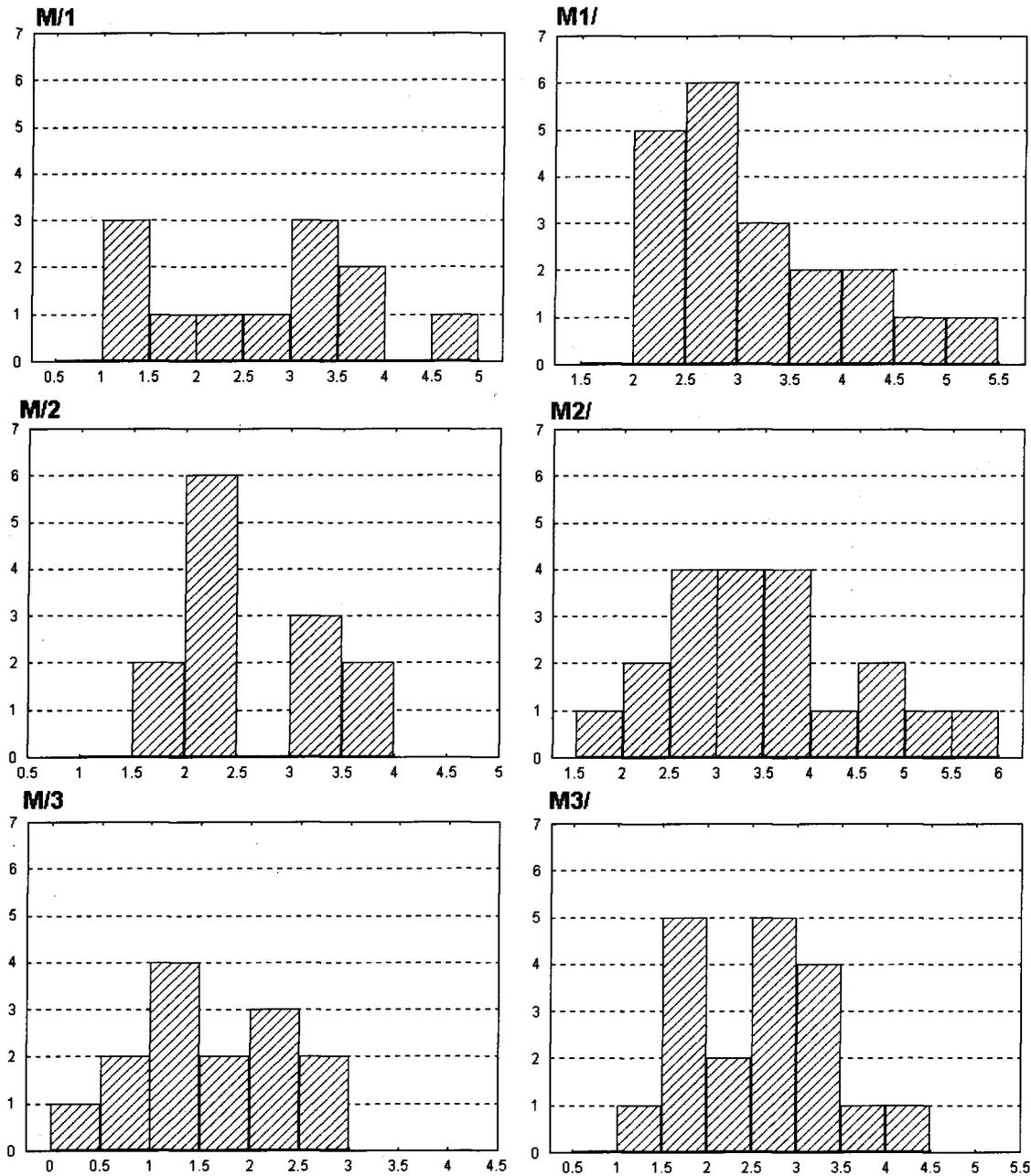


Figure 3
Mimomys pliocaenicus,
Tegelen. Frequency
histogram of crown height.

only two roots with the anterior and the protocone roots widely fused.

M2/

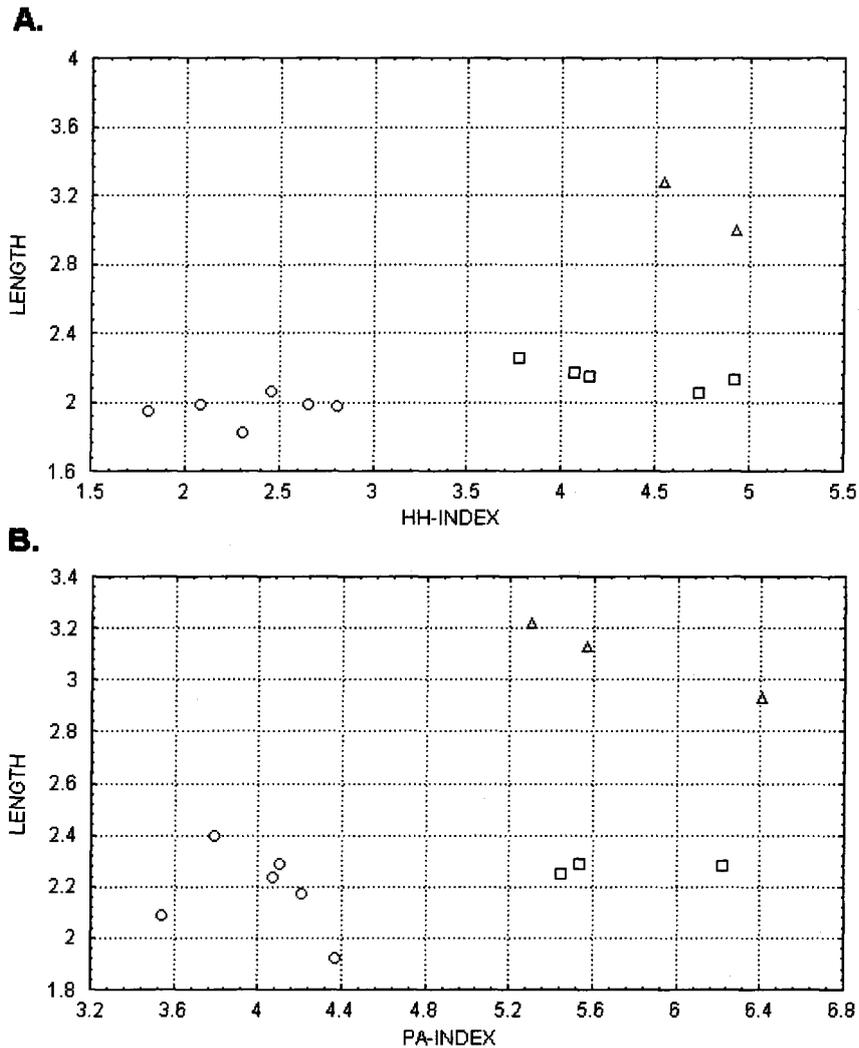
This molar has a typical arvicoline shape. BRA3 is extremely shallow in juvenile specimens or absent in later wear stages (Figure 8: 4-5). LRA2 is very shallow. The majority of the molars in the collection have two roots (n=9), though some specimens show a three-rooted condition (n=4). In many molars with two roots the anterior one is slightly compressed transversely (Figure 8: 5c). One spec-

imen (Te598) has an additional small root below the hypocone (T3), Figure 8: 5c. Additional tracts (parasinus, metasinus, and hyposinus) are well expressed. The height of the parasinus (the tract of T2) varies from 0.5 to 1.98, with the mean of 0.78 (n=18). The metasinus ranges from 0.3 to 1.98 mm, with a mean of 0.96 (n=16). The hyposinus varies from 0.15 to 2.0 with a mean of 0.7 (n=17).

M3/

The molar is composed of the anterior loop, two intermediate triangles (T2, T3) and the posterior lobe (T4 and +

Figure 4
Mimomys pliocaenicus,
Tegelen. Sinugram.
A - Lower molars, B - Upper
molars. Triangles - M1/1,
squares - M2/2, circles - M3/3.



posterior loop). The length of the posterior lobe decreases with wear (Figure 9). The posterior enamel islet is formed by reduction of the second lingual re-entrant (LRA2). As is the case with the first lower molar, the insulation is very variable in relation to the crown height (Figure 10). The hollow enamel pillar extends deep down the crown. Its maximum depth exceeds 2.0 mm. The osteodentine traces of the islet can be seen even in very worn specimens with a crown height about 1 mm. The enamel islet is elongated in younger stages and rounded in later stages of wear (Figure 11: 1-6). BRA3 is always present. LRA2 is preserved after the insulation and is normally filled with cement. In senile specimens the tips of LRA2 and BRA2 may get very close to each other (Figure 8: 5,6). Most molars have two roots. Only in four specimens the anterior root is subdivided into two separate roots (Figure 11: 6a). Additional dentine tracts (especially the hyposinus) are strongly pronounced. The height of hyposinus ranges from 0.5 to 1.62 mm, with a mean of 1.07 (n=16).

Comparison

M. pliocaenicus from Val d'Arno. Masini & Torre (1987) recently described the type specimen in detail. The illustrated M/1 (p. 130, fig. 3: 2a-b) shows the characteristic additional tracts. The rather high mimosinuid and prismosinuid demonstrate a broad similarity morphological and chronological between the type material and *Mimomys pliocaenicus* from Tegelen.

M. cf. pliocaenicus from Rivoli Veronese. The scanty material from the Italian fissure-filling locality is close in form to that from Tegelen in size and moderate development of additional tracts. One moderately worn specimen from Rivoli Veronese has a Hsd/L index >114 (L. Maul, personal comm., 1996). This probably falls within the range of the Tegelen form (103-123).

M. pliocaenicus from Eastern England. As noted by

Figure 6
Lower molars of *Mimomys pliocaenicus*, Tegelen.
1-4: M/1, 5-7: M/2, 8-10: M/3, occlusal surface;
1a-6a, 8a-10a: labial side;
1b-6b, 7a, 8b, 9b: lingual side;
7b: posterior side;
10b: anterior side.
1 - Te227, 2 - Te934,
3 - Te844, 4 - Te750,
5 - Te413, 6 - Te108,
7 - Te463, 8 - Te148,
9 - Te147, 10 - Te240.
Occlusal view 15x, lateral view 7.5x.

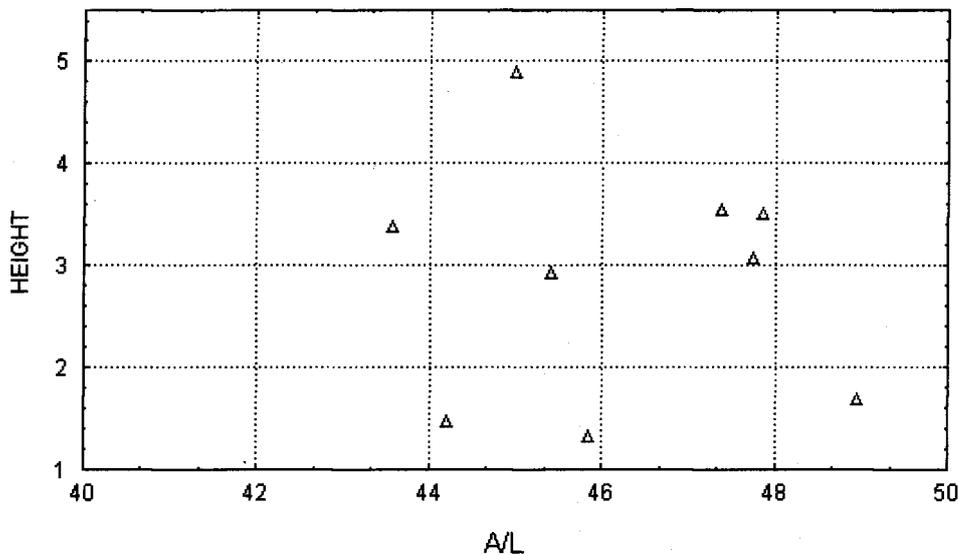


Figure 5
Mimomys pliocaenicus, Tegelen. Scatter diagram of relative length of the anteroconid of M/1 (A/L) and crown height.

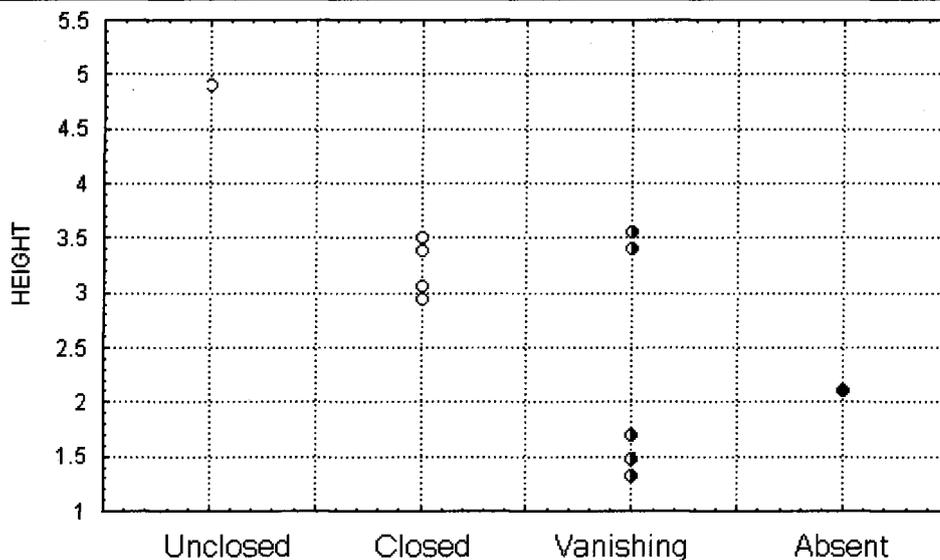
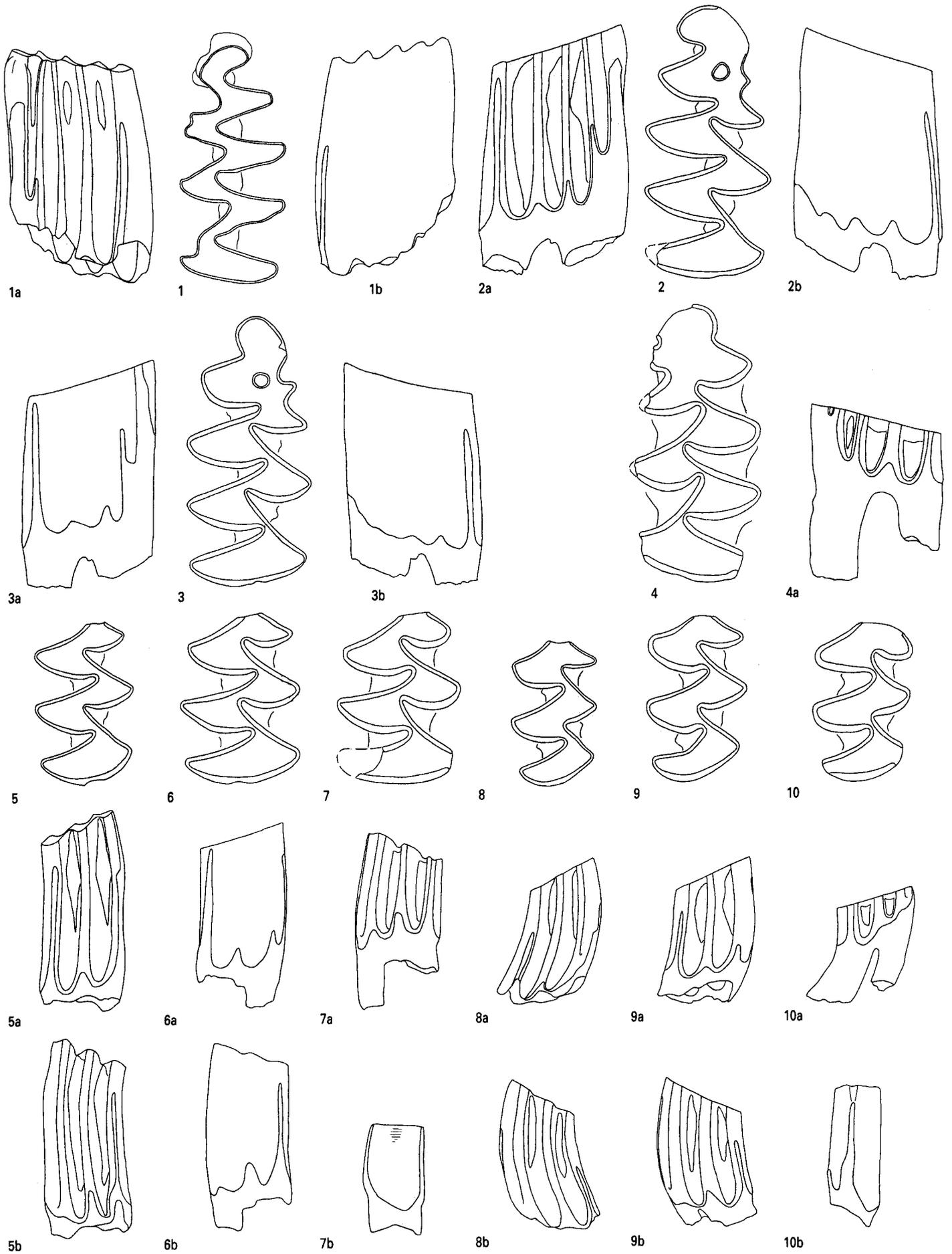


Figure 7
Mimomys pliocaenicus, Tegelen. M/1. Relationship of stages of the enamel islet development to crown height.



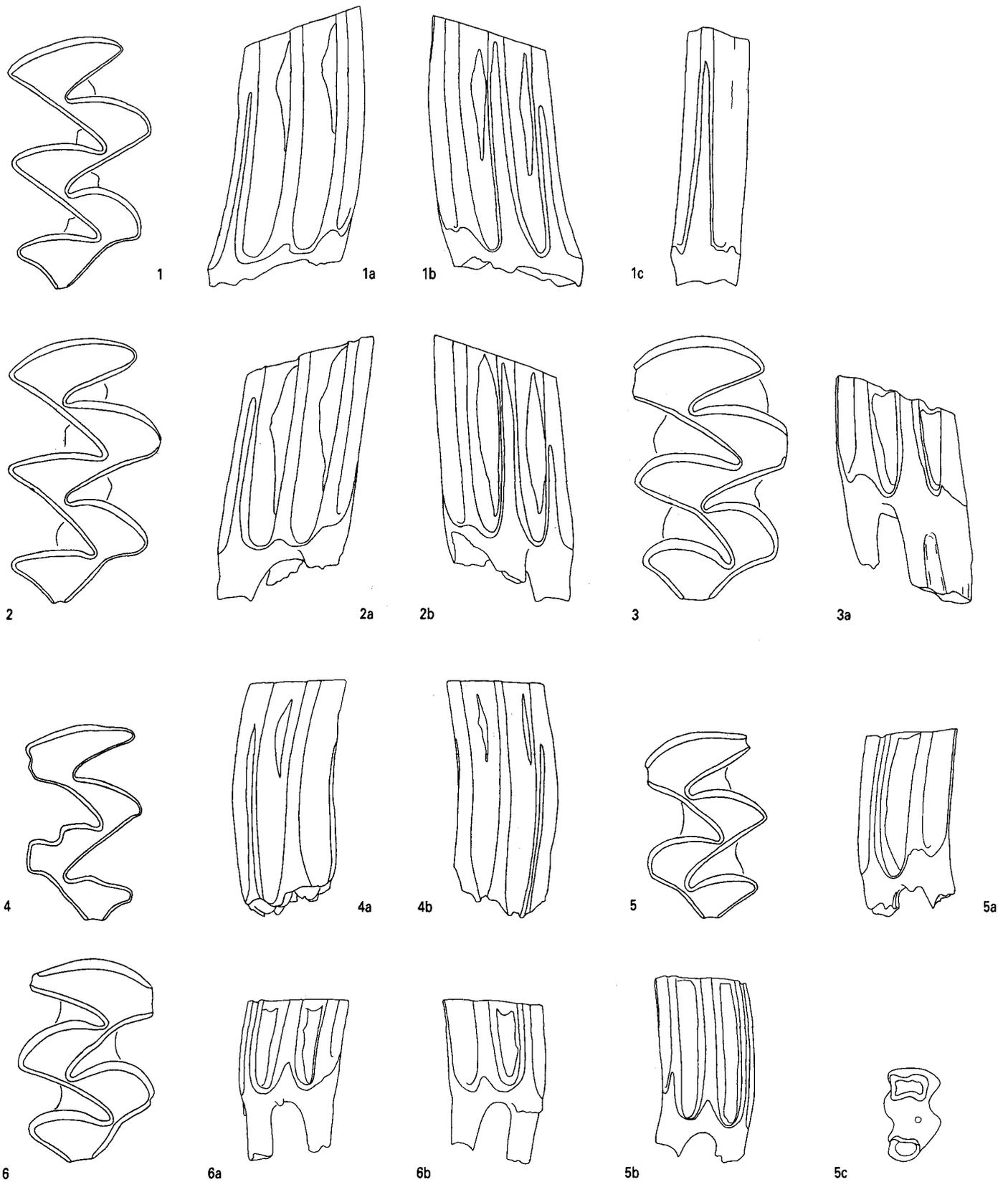


Figure 8

Upper molars (M1/ and M2/) of Tegelen *Mimomys pliocaenicus*, Tegelen.

1-3: M1/, 4-6: M2/: occlusal surface; 1a, 2a, 4b, 5b, 6a: labial side; 1b, 2b, 3a, 4a, 5a, 6b: lingual side; 1c: posterior side; 5c: root side.

- 1 - Te568, 2 - Te843, 3 - Te257, 4 - Te600, 5 - Te598, 6 - Te601. Occlusal view 15x, lateral view 7,5x.

Mayhew & Stuart (1986) and Mayhew (1990), there are two groups of *Mimomys pliocaenicus* in the East Anglian deposits.

These groups are distinct in hypsodonty. The molars from the deposits referred to the Bramertonian (Bramerton, Thorpe, Bulcamp) are considerably less hypsodont than those from the Pre-Pastonian/Pastonian deposits (East and West Runton, Sidestrand, Overstrand). In the author's opinion, the degree of hypsodonty of the Bramertonian large *Mimomys* (lower dentine tracts, higher number of roots in upper molars etc.) allows it to be classified as *Mimomys praepliocaenicus* Rabeder, rather than *M. pliocaenicus*. The latter name should therefore be restricted only to the Pre-Pastonian large *Mimomys*.

The Tegelen form is very close to *M. pliocaenicus* from East Anglian Pre-Pastonian/Pastonian localities in size, height of dentine tracts and occlusal morphology. Though some specimens demonstrate insulation of the islet re-entrant in M/1 in lower levels of the crown (cf. Figure 7 and Mayhew, 1990, fig.1). This character is probably very variable and has only general relations to systematics.

M. pliocaenicus from the Zuurland boring. The remarkable drilling by Mr. L. Hordijk has produced several superimposed small mammalian faunas broadly of Tiglian age (Hordijk, 1988, Van Kolfschoten, 1988, 1990). These finds have yielded abundant remains of large *Mimomys* from two main levels. The lower one, 91-96 m depth in Zuur-

Figure 9
Mimomys pliocaenicus,
Tegelen. M3/. Scatter
diagram of relative length of
posterior lobe (Lp/L) and
crown height.

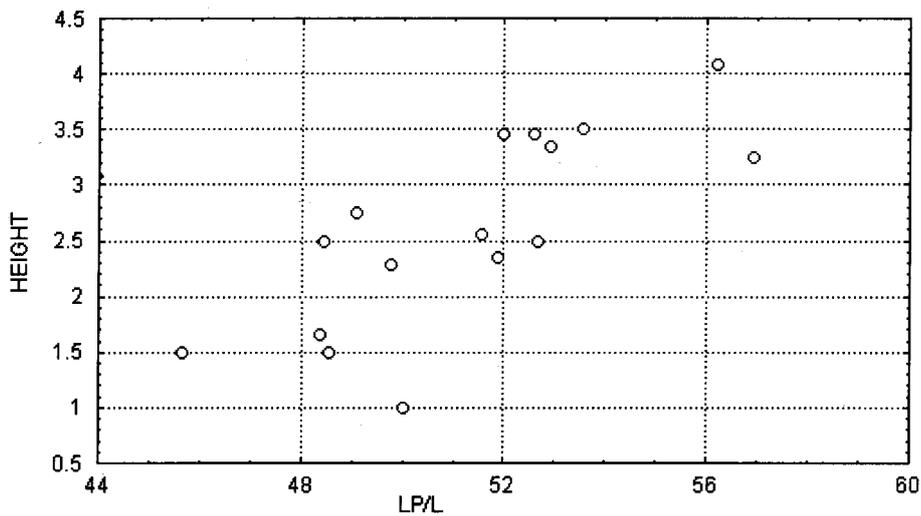
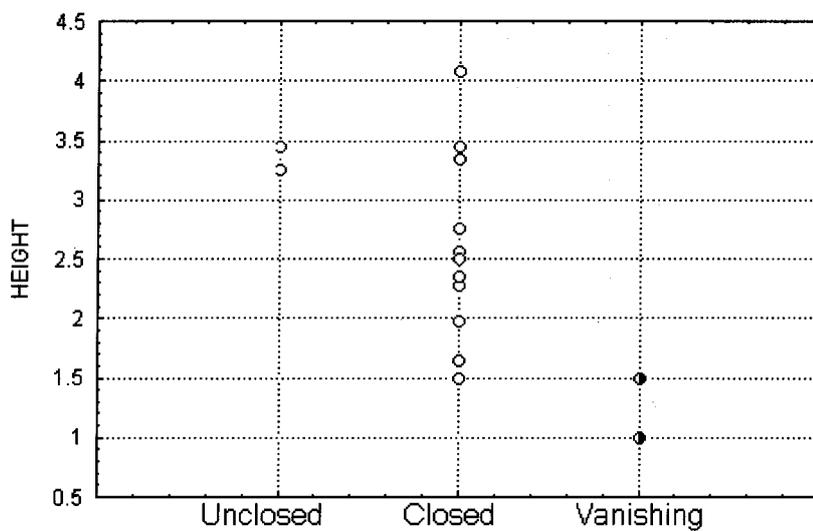


Figure 10
Mimomys pliocaenicus,
Tegelen. M3/. Relationship of
stages of the enamel islet
development to crown
height.



land-1 borehole, i.e. fauna 11 *sensu* Van Kolfschoten (1988), produced the form referable to *M. praepliocaenicus* Rabeder. This form is clearly more primitive than the Tegelen *M. pliocaenicus* in lower dentine tracts (Van Kolfschoten, 1988; Mayhew, 1990).

The upper Tiglian level of the Zuurland comprises, in the author's opinion, faunas 9 and 10 from the depth of 62 - 66 m (Van Kolfschoten, 1988). *Mimomys pliocaenicus* from this level is very close to the Tegelen form. Using *M. pliocaenicus* the author could not check the suggestion of the somewhat younger age for these faunas from Zuurland, in comparison to the Tegelen fauna (Van Kolfschoten, 1988). In fact the hypsodonty graphs for both faunas show a broad overlap of values. This probably indicates their very close chronological position.

M. ostramosensis from Osztramos 3 (Jánossy & Van der Meulen, 1975). The form of the large *Mimomys* lineage is clearly more advanced than *M. pliocaenicus*. As noted in the original description of *M. ostramosensis*, the disappearance of enamel islets of M1/ and M3/ occurs in younger ontogenetic stages and the dentine tracts are higher than in *M. pliocaenicus* from Tegelen.

M. ostramosensis from Schernfeld (Carls & Rabeder, 1988). This form is the best so far described *M. ostramosensis* sample. This material is distinctly different from the Tegelen *M. pliocaenicus* being larger in size and in higher main and additional dentine tracts (Table 7). It is evident that being only about 6-7% larger (similar size of third molars is apparently due to the selection of young specimens by Carls & Rabeder, 1988) *Mimomys ostramo-*

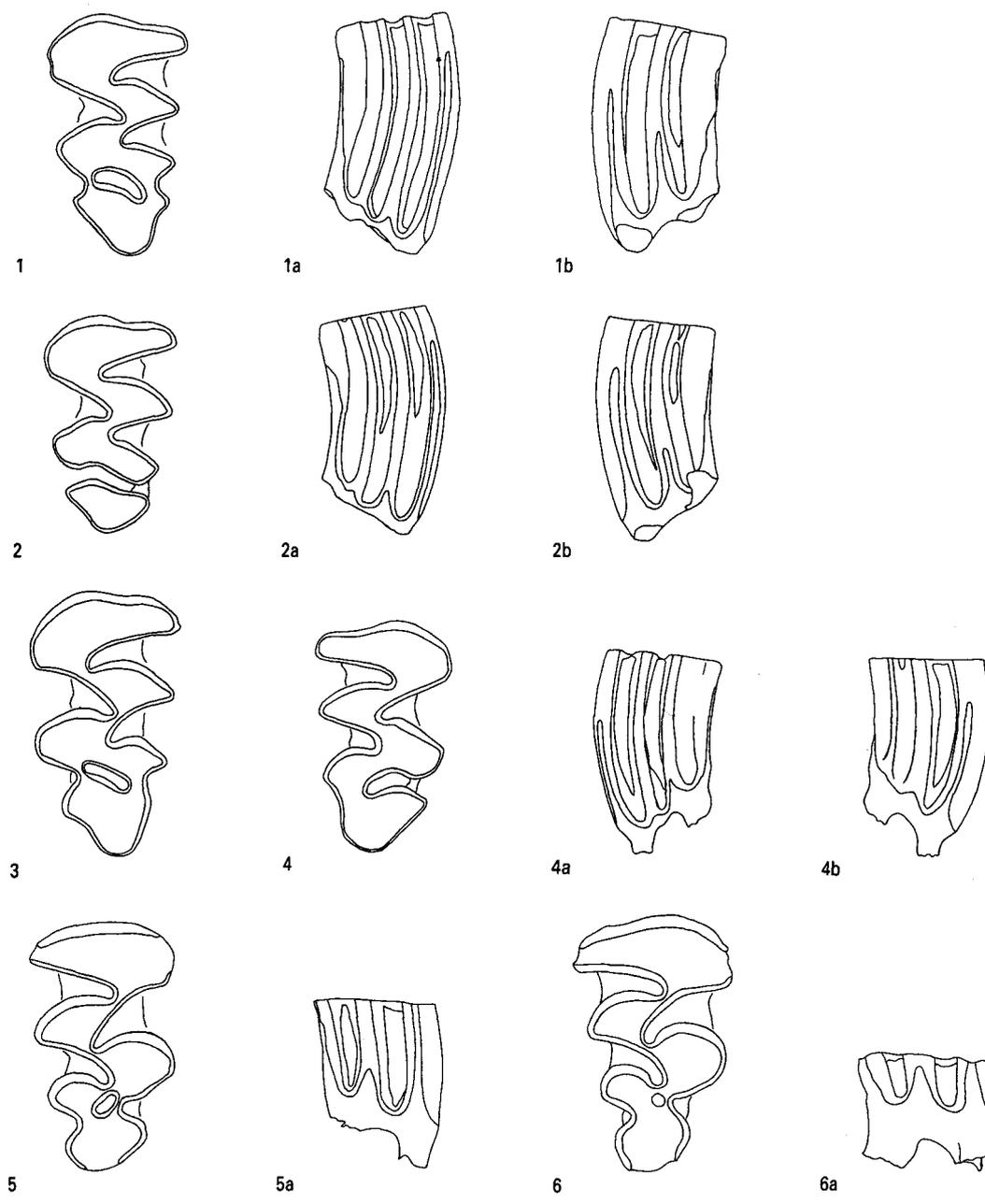


Figure 11
Upper molars (M3/) of
Mimomys pliocaenicus,
Tegelen.
1-6: M3/, occlusal surface,
1 - Te345,
2 - Te603,
3 - Te279,
4 - Te122,
5 - Te292,
6 - Te669,
1a - labial side,
1b - lingual side,
2a - labial side,
2b - lingual side,
4a - labial side,
4b - lingual side,
5a - lingual side,
6a - lingual side.
Occlusal view 15x,
lateral view 7.5x.

ensis from Schernfeld has about 20-30% higher tracts than *M. pliocaenicus* from Tegelen. Other differences are the clear trend to the separation of the T4 in M/1, the more shallow enamel islets in M3/ (the islet is closed at the crown height of about 4.0 mm and disappears at a height of 2.5 mm), higher cement concentration, later developed and fewer roots. Only 18% of M1/ have three roots in the *M. ostramosensis* form Schernfeld compared to about 90% three-rooted molars in the Tegelen material. The M1/ - M/1 ratio of *M. pliocaenicus* from Tegelen is 92.5 (nM1/=19, nM/1=9). This value is very close to that of the Schernfeld form (92.4).

M. praepliocaenicus Stranzendorf C, D, F (Rabeder, 1981). Based on scanty material from three superimposed fossiliferous levels at the Stranzendorf section, this form,

however, represents an intermediate unit in the chain between *M. polonicus* and *M. pliocaenicus*. The Tegelen large *Mimomys* has higher dentine tracts than the form from Stranzendorf, though the dimensions of both forms are very close.

M. polonicus from Rebielice Krolewskie (Kowalski, 1960). The species, described on the basis of the abundant material from fissure fillings, is widely recognized as the ancestral form for *M. pliocaenicus*. Chaline (1974) was the first to apply the measurements of the anterior dentine tract (=anterosinuid) to the compilation of the sequence of large *Mimomys* species. There are two localities at Rebielice Krolewskie, 1 and 2 (Kowalski & Nadachowski, 1990). The type locality is RK 1. On the basis of personal observations, the material from the second site, RK 2, is

Table 7
Size and dentine tracts
measurements of
M. pliocaenicus from
Tegelen and
M. ostramosensis from
Schernfeld.

	TEGELEN			SCHERNFELD			Difference in means (%)
	Mean	Range	n	Mean	Range	n	
M/1							
Length	3.33	3.00-3.71	9	3.55	3.27-4.19	60	-6.2
Anterosinuid		3.89, 4.02			5.22, 5.57		
Hyposinuid		3.38, 3.70		4.85	4.01-5.55	29	
Hyposinulid	3.16	3.00-3.43	6	4.61	3.72-4.96	40	-31.5
HH-index		4.54, 4.93		6.66	5.77-7.65	29	
M/2							
Length	2.21	2.04-2.50	13	2.33	2.21-2.44	30	-5.15
HH-index	4.33	3.77-4.92	5	5.60	5.01-6.15	30	-22.7
M/3							
Length	2.03	1.81-2.25	14	2.01	1.89-2.16	30	+1
HH-index	2.35	1.81-2.81	6	3.62	2.64-4.16	30	-35.1
M1/							
Length	3.08	2.88-3.28	19	3.28	3.04-3.50	30	-6.1
Protosinus	4.47	4.15-5.00	3	5.60	5.18-5.99	30	-20.2
Anterosinus	3.60	3.30-4.00	3	5.58	5.11-5.91	30	-35.5
Anterosinulus	2.56	2.10-3.50	4	4.47	3.80-5.18	30	-42.7
PA-index	5.76	5.30-6.40	3	7.87	6.92-8.54	30	-26.8
M2/							
Length	2.27	2.08-2.47	17	2.46	2.16-2.55	30	-7.7
Protosinus	3.86	3.37-4.46	4	4.89	3.72-5.77	30	-21.1
Anterosinus	4.09	3.90-4.34	3	5.42	4.45-5.91	30	-24.5
PA-index	5.73	5.45-6.22	3	7.30	5.95-7.91	30	-21.5
M3/							
Length	2.19	1.92-2.40	17	2.23	2.02-2.35	30	-1.79
Hyposinus	1.07	0.50-1.62	16	1.50	0.51-2.16	30	-28.7
PA-index	4.01	3.54-4.37	6	5.20	4.61-5.78	30	-22.9

markedly more primitive in hypsodonty than the type sample. *M. polonicus* is distinct from *M. pliocaenicus* from Tegelen in considerably less evolved hypsodonty, has less abundant cement, a somewhat smaller size and a higher frequency of three-rooted upper molars.

Comments

The large *Mimomys* lineage is well represented at numerous Late Pliocene localities throughout Europe. It became a classic example of phyletic evolution (Chaline, 1974, Viriot et al., 1990). The relevance of late Ruscinian '*Mimomys*' *occitanus* Thaler to this group was questioned by Zazhigin (1980) and Maul (1996). The lack of phyletic connection of large Late Pliocene *Mimomys* with the Pleistocene *Mimomys* (*Cromeromys*) *savini* - *Arvicola* lineage was pointed out by Zazhigin (1980), discussed by Van Kolfschoten (1993) and confirmed by Neraudeau et al. (1995). In the author's opinion the *Mimomys* (*Mimomys*) lineage may be considered as a sequence of the following species: *M. polonicus* Kowalski (MN16, HH-index of M/1 varying from 1.5 to 3.5), *M. praepliocaenicus* (MN17a, HH-index 3.5-4.5), *M. pliocaenicus* (MN17b, HH-index 4.5-5.5) and *M. ostramosensis* (MN17c, HH-index >5.5). The early MN16 forms such as *M. hajnackensis* and *M. hassiacus* should be revised in detail for further usage. It is possible that both these forms are in the range of variation of *M. polonicus* on the basis of their hypsodonty.

The relevant question is the genus *Kislangia*. It should be noted that in many cases the attribution of large *Mimomys* to this genus is only based on the size criterion. Thus *Kislangia* became a 'sack-term' for all specimens which authors considered to be too large for the *Mimomys pliocaenicus* group (e.g. several "*Kislangia*" species of Rabeder (1981), and *Mimomys* (*Kislangia*) *rex* from Bramerton (Mayhew & Stuart, 1986)). Zazhigin (1980, p. 85-56) questioned the validity of the subgenus *Kislangia*. However, the peculiar form of the anteroconid of the type material, unmatched in other large *Mimomys*, may serve as the characteristic feature for distinguishing *Mimomys* (*Mimomys*) from *Mimomys* (*Kislangia*). The group of large *Mimomys* species from southern Europe (*M. cappettai*, *M. ischus*, *M. gusii*) are certainly not connected with *Kislangia* and deserve a subgeneric status of their own.

***Mimomys* (? *Mimomys*) *reidi* Hinton, 1910**

Figures 2C, 12-23, Tables 8 - 13

Subgeneric assignment

The author considers that this species represents the primitive stage of the small *Mimomys* lineage leading to the Biharian *M. pusillus*. However, in the Tegelen level the lineage mostly shows primitive *Mimomys* characters, which closely resemble the situation in the nominative subgenus. The only major distinctive (derived?) condition is the broad antero-external confluence in M3/. There is

no data on the structure of the palatine area of *M. reidi*. The long palatine bridge is thought to be typical of *M. (Mimotomys) pusillus* (Von M hely, 1914; Gromov & Polyakov, 1977; Zazhigin, 1980). Therefore, *M. reidi* is tentatively placed in the nominative subgenus of *Mimomys* at present.

1926 *Mimomys reidi* Hinton: M. Hinton, Monograph of voles ...: p.363-364, fig. 99: 6.

1976 *Mimomys reidi* Hinton: Van der Meulen, The smaller ... : p.18, fig. 4, 6.

1986 *Mimomys reidi* Hinton (partim): D. Mayhew & A. Stuart, Stratigraphic and ... : p.458-460, fig.13: 5-9, 12-14, 14: 1-3, 5-11, 15: 23.

1990 nec *Mimomys reidi* Hinton: D. Mayhew, Small mammal... : p.65, Pl.1: 2-4, Pl.2: 2-3, Pl.3: 4, 6-8, Pl.4: 4-6, Pl.5: 1,9.

1990 *Mimomys reidi* Hinton: T. van Kolfschoten, Review... : fig. 4, 7.

Diagnosis (emend.)

A medium-size vole with moderate cement accumulation. Dentine fields of the occlusal surface tend to communicate. The re-entrants show weak vergence. The enamel islets in the M/1 and M3/ are present in younger wear stages. The posterior root of M/2 shows the semi-pleurohiz to acrorhiz position. The dentine tracts in anterior molars are interrupted by wear at the merorhiz stage of root formation.

Studied material

Tegelen, 31M/1, 31M/2, 23M/3, 23M1/, 28M2/, 27M3/

Description

A vole of medium size (Figure 12). Cement accumulations vary from sparse in younger individuals to moderate in older ones. Cement never fills more than half of a re-entrant. Dentine fields of the occlusal surface are never completely closed. In lower molars the labial re-entrants are nearly as deep as the lingual ones. In younger (and even in older) individuals the outlines of enamel triangles are distinctly angular. The thickness of enamel band is moderately differentiated according to the '*Mimomys*' (or negative) type.

Root formation stages

Comparatively hypsodont vole. The bulk of molars (77.2%, n=123) have well formed roots. Intermediate (merorhiz) stage is present in 13.8% (n=22) of molars. Only 8.8% (n=14) of the molars in the collection do not have roots (arhiz stage) (Figure 2C). The crown height distribution is illustrated in the Figure 13. One peak pattern is present in most of molars with the middle class (age) dominating the distribution. This can be interpreted as a combination of an attritional and catastrophic profile (Korth & Evander, 1986).

Dentine tracts

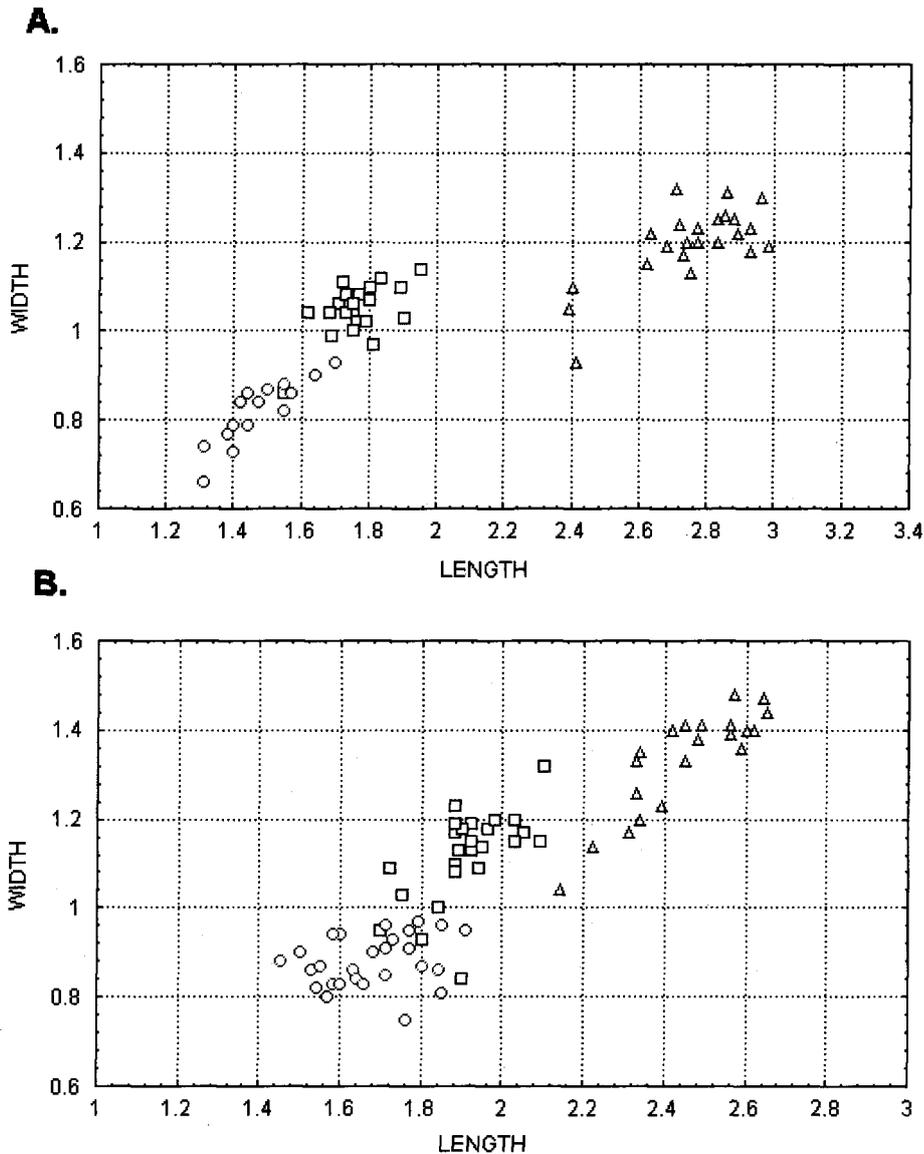
The tracts are relatively high (Tables 8-13). In anterior teeth major tracts are interrupted by wear at the merorhiz root formation stage. In all molars there are specimens with complete tracts and formed tooth base. Sinugram is given in the Figure 14.

M/1

The molar is composed of the posterior loop, three alternating triangles and an anteroconid complex. In young animals an enamel islet and a *Mimomys*-ridge is present. The enamel islet is formed by reduction of the BRA3 (the islet re-entrant) at the arhiz root formation stage with the

crown height about 2.7- 3.4 mm. The islet is still present in one molar at crown height of 2.17 mm. Thus the maximum depth of the islet enamel pillar is about 1.0 - 1.5 mm (Figure 15). It disappears during the rhizodont stage of root formation. Enamel islet is slightly oval in higher crowned molars, though it changes into a nearly round form with wear. The *Mimomys*-ridge is relatively deep. The depth of the islet-fold, expressed as an elevation of its lower point above the crown base, ranges from 0.8 to 2.3, with a mean of 1.63 mm, n=14. In molars of juvenile animals the anterior loop (cap) of anteroconid is delimited from T4-T5 by deep BRA3 and LRA4 (Figure 16:1). After the insulation the anteroconid becomes more compact,

Figure 12
Mimomys reidi, Tegelen.
Scatter diagram of length
and width.
A - Lower molars, B - Upper
molars. Triangles - M1/1,
squares - M2/2, circles - M3/3.



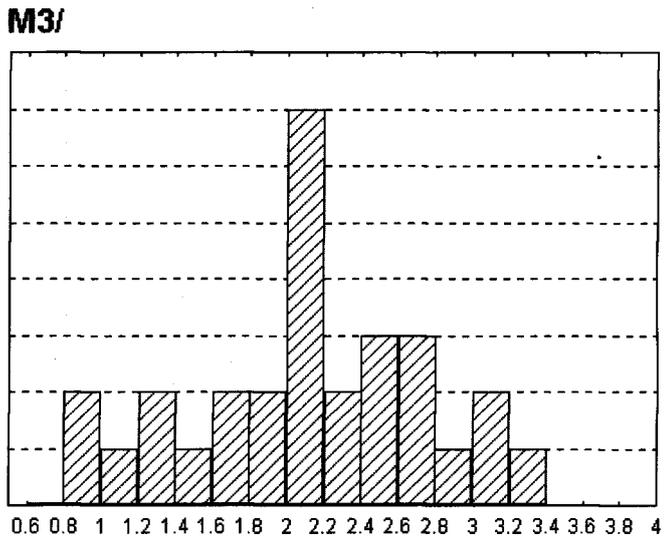
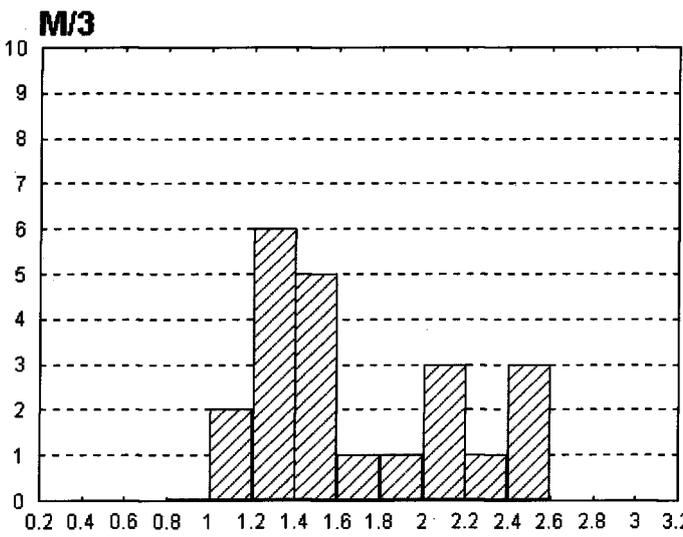
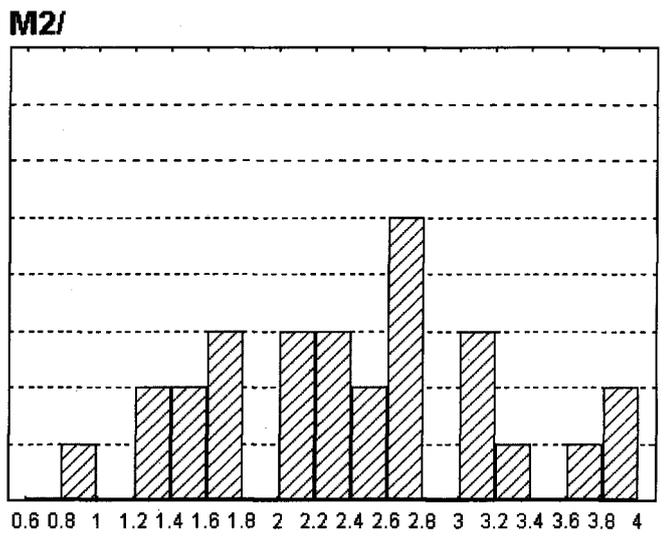
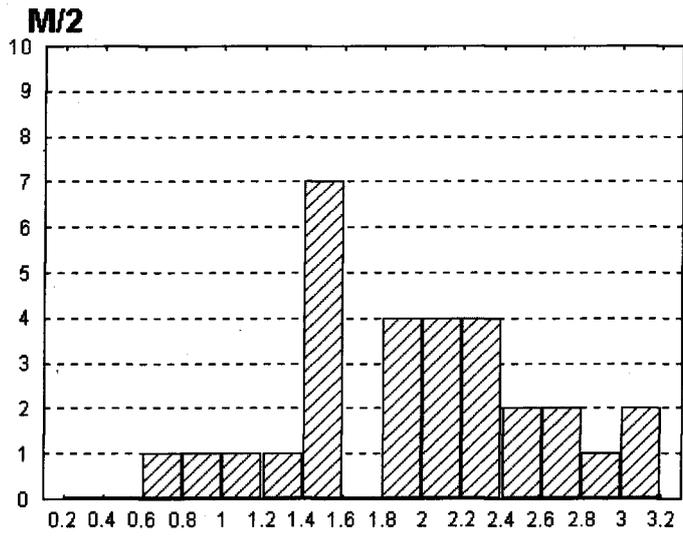
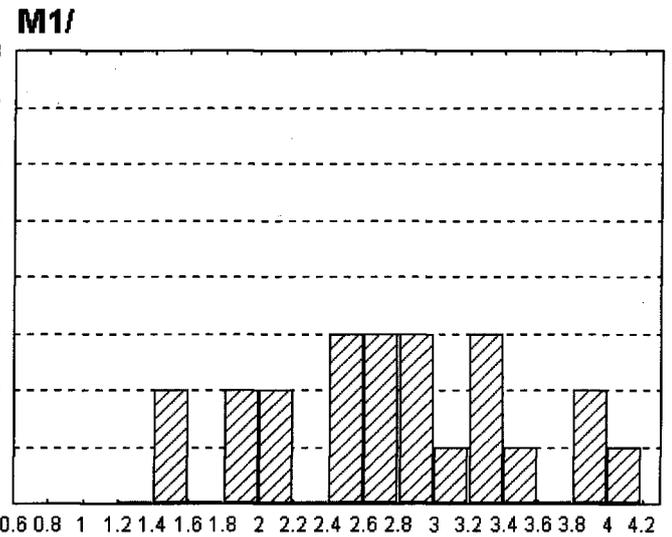
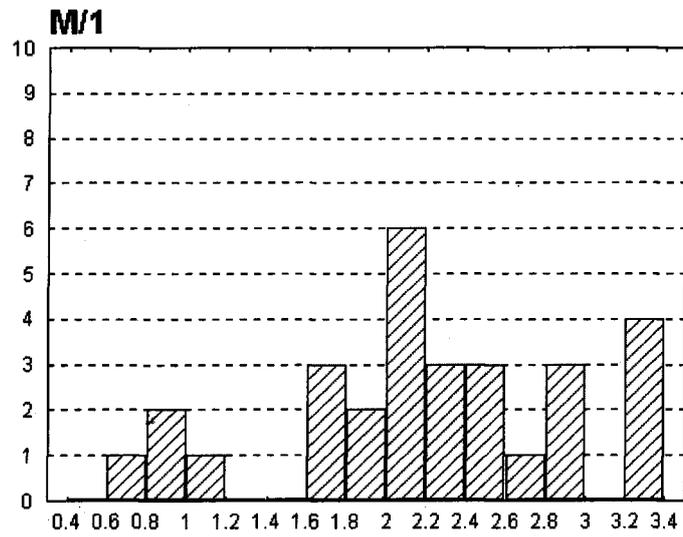


Figure 13
Mimomys reidi, Tegelen. Frequency histogram of crown height.

BRA3 and LRA4 get shallower. These re-entrants are not filled with cement. The anteroconid complex becomes shorter with wear (Figure 17). The anteroconid index (A/L) decrease from 45-47 in the most high-crowned specimens to 33-37 in worn molars (Figure 18). The mean value of A/L for the Tegelen sample of *Mimomys reidi* is 39.6, n=26 (Table 8).

The dentine fields of the occlusal surface are never perfectly closed. A well developed mimosinuid (dentine tract of the *Mimomys*-ridge) is present in some specimens (Figure 16: 1a, 2b).

M/2

A molar of typical morphology with posterior loop and two pairs of constantly widely confluent triangles. BRA3 is clearly developed in younger molars and becomes very shallow with wear. The posterior root is semi-pleurorhiz in younger individuals and acrorhiz in older animals (Figure 19: 2c, 3b). Tight contact of the posterior root with the incisor often leads to deformation of the lower part of the LRA1 making it somewhat shorter than LRA2 (Figure 19: 1c).

M/3

The molar of typical form. T1-T2 and T3-T4 are widely confluent.

M1/

The molar of a typical form. LRA3 is relatively deep even in worn specimens. The protocone root is shifted anteriorly. It is always clearly seen. In some cases the pulp cavity is fused with that of the anterior root: the 'two root' condition (n= 7). Less frequent are molars with a separate pulp cavity of the protocone root: the 'three root' condition (n=4).

Apart from four main tracts, the small hyposinus may be present (n=2).

M2/

The molar is of a typical form. LRA2 is present in all wear stages. Two roots. The anterior one is usually flattened transversely.

M3/

The molar has two dentine fields. One is formed by an anterior loop confluent with T2 and the other is the posterior lobe complex (Figure 20: 7-15). Re-entrants are typically poorly vergent. The confluence of the anterior lobe and T2 ('anterior confluence') is strongly dependent on wear stage, increasing in older individuals (Figure 21). Enamel islet is present in the posterior lobe. It has rounded outlines. It is formed by insulation of LRA2 at arhiz stage of root formation and may still be present in molars with well-developed roots. Maximum depth of enamel pillar of the islet is about 1.0 mm (Figure 22). The posterior lobe complex shows a general trend to be shorter with wear (Figure 23, triangles). LRA2 is always developed. BRA3

may be not expressed. The posterior loop is typically compact and broadly confluent with T3-T4. Only in some cases is the posterior loop elongated and slightly subdivided from T3-T4 by deepened LRA2 and BRA3 (Figure 20: 15). One of the molars with this morphology (Figure 20: 15, Te099) shows a very narrow anterior confluence (Figure 21) and vergent re-entrants. This molar is tentatively classified as *Mimomys reidi* because of the low amount of cement which is beyond the range of variation of *Mimomys tigliensis* of this ontogenetic stage. The posterior tract, the distosinus, is of simple blade-like form (Figure 20: 8b). Only rarely (n=1) may it have a small labial arm. The hyposinus and metasinus are typically developed. The hyposinus ranges from 0.7 to 1.84 mm, with a mean of 1.1 (n=7).

Comparison

Mimomys reidi, Weybourne Crag, Trimmingham (Hinton, 1910, 1926; Mayhew & Stuart, 1986). The Tegelen *Mimomys reidi* material closely resembles the morphology of the type specimen. The anterosinuid of the type is 2.7 mm (Mayhew & Stuart, 1986). This seems lower than in the Tegelen sample.

Mimomys reidi, East Anglia Crag, group 1 and 3 faunas (Mayhew & Stuart, 1986).

The *Mimomys reidi* material from West and East Runton and other relevant sites is very similar to *Mimomys reidi* from the Tegelen fauna. The anterosinus value of 3.02 mm for a specimen from West Runton (Mayhew & Stuart, 1986) is lower than the single available value from Tegelen (3.4 mm). The T1 in the East Anglian material is more developed and more blunt than in the Tegelen form.

Mimomys reidi, The East Anglian Crag, group 2 faunas: Bramerton, Thorpe, and Bulcamp (Mayhew & Stuart, 1986; Mayhew, 1990). This vole differs from the Tegelen *Mimomys reidi* by having markedly lower hypsodonty. It is probably a different, though ancestral to *M. reidi*, species resembling *M. hintoni* Fejfar.

Mimomys* cf. *reidi (W. v. Koenigswald, 1977). This form was described from the latest Villanyian fauna of Schambach. The form is similar to the Tegelen species. The German form is different in having higher dentine tracts (hyposinuid up to 4.0 mm), a more shallow enamel islet (disappears at the arhiz or merorhiz stage of root formation), a shallower *Mimomys*-ridge (the average elevation of the islet re-entrant above the crown base is about 2.5 mm, n=12, compared to 1.63, n=14, of the Tegelen species). In the framework of the concept of detailed subdivision of phyletic lineages into chronospecies the forms like that from Schambach deserve a separate specific status. This is probably an intermediate link in the chain between the late Villanyian *M. reidi* and Early Biharian *M. pusillus*.

Variable	n	Mean	Minimum	Maximum	Standard deviation	Standard error
Length	26	2.76	2.39	2.98	0.16	0.03
Width	30	1.19	0.93	1.32	0.10	0.02
Anteroconid index (A/L)	26	39.60	33.90	46.89	3.05	0.60
Anterosinuid	1			3.4		
Hyposinuid	5		>2.5	>2.9		
Hyposinulid	5		2.9	3.1		
HH-index	5		>3.68	>4.24		

Table 8
Dimensions of Mimomys reidi, Tegelen, M/1

Variable	n	Mean	Minimum	Maximum	Standard deviation	Standard error
Length	25	1.76	1.55	1.95	0.08	0.02
Width	31	1.04	0.70	1.14	0.09	0.02
Anterosinuid	2		2.99	3.37		
Hyposinuid	3	2.90	2.70	3.02	0.18	0.10
Hyposinulid	4	2.79	2.50	3.04	0.25	0.12
HH-index	3	4.06	3.68	4.29	0.33	0.19

Table 9
Dimensions of Mimomys reidi, Tegelen, M/2

Variable	n	Mean	Minimum	Maximum	Standard deviation	Standard error
Length	20	1.48	1.31	1.70	0.10	0.02
Width	22	0.83	0.66	0.93	0.06	0.01
Anterosinuid	6	2.34	1.96	2.72	0.27	0.11
Hyposinuid	8	1.74	1.40	2.23	0.24	0.09
Hyposinulid	10	1.51	1.11	1.90	0.26	0.08
HH-index	8	2.34	2.04	2.75	0.27	0.09

Table 10
Dimensions of Mimomys reidi, Tegelen, M/3

Variable	n	Mean	Minimum	Maximum	Standard deviation	Standard error
Length	23	2.46	2.14	2.65	0.14	0.03
Width	23	1.34	1.04	1.48	0.11	0.02
Anterosinus	3	3.62	3.53	3.75	0.11	0.07
Anterosinulus	3	3.17	2.99	3.26	0.16	0.09
Protosinus	1			3.70		
Distosinus	1			4.18		
PA-index				5.27		

Table 11
Dimensions of Mimomys reidi, Tegelen, M1/

Variable	n	Mean	Minimum	Maximum	Standard deviation	Standard error
Length	27	1.91	1.70	2.10	0.10	0.02
Width	28	1.12	0.84	1.32	0.10	0.02
Anterosinus	3	3.41	3.23	3.60	0.19	0.11
Protosinus	4	3.12	2.96	3.30	0.17	0.17
Distosinus	2		2.90	3.26		
PA-index	3	4.60	4.40	4.74	0.18	0.10

Table 12
Dimensions of Mimomys reidi, Tegelen, M2/

Variable	n	Mean	Minimum	Maximum	Standard deviation	Standard error
Length	29	1.68	1.4500	1.91	0.12	0.02
Width	29	0.88	0.75	0.97	0.06	0.01
Lp/L	29	54.37	49.03	58.48	2.61	0.49
Anterosinus	10	2.45	2.15	2.69	0.18	0.06
Protosinus	12	2.21	2.01	2.50	0.15	0.04
Distosinus	13	1.53	1.31	1.90	0.16	0.04
PA-index	10	3.31	3.00	3.65	0.21	0.07

Table 13
Dimensions of Mimomys reidi, Tegelen, M3/

Mimomys pusillus, Püspökfürdo (Von Mähely, 1914, Van der Meulen, 1973). The widely distributed phylogenetically advanced species of small *Mimomys*. It is recognized in Early Pleistocene faunas throughout Europe and West Siberia. This species is distinct from *M. reidi* from Tegelen in higher hypsodonty and related features, like strong reduction of enamel islets, development of pleuro-rhiz M/2 and higher HH-index.

Mimomys blanci, Monte Peglia (Van der Meulen, 1973). This species differs from the Tegelen *M. reidi* by having much higher hypsodonty: higher dentine tracts, more abundant cement, pleuro-rhiz M/2 and complete reduction of enamel islet in lower M/1.

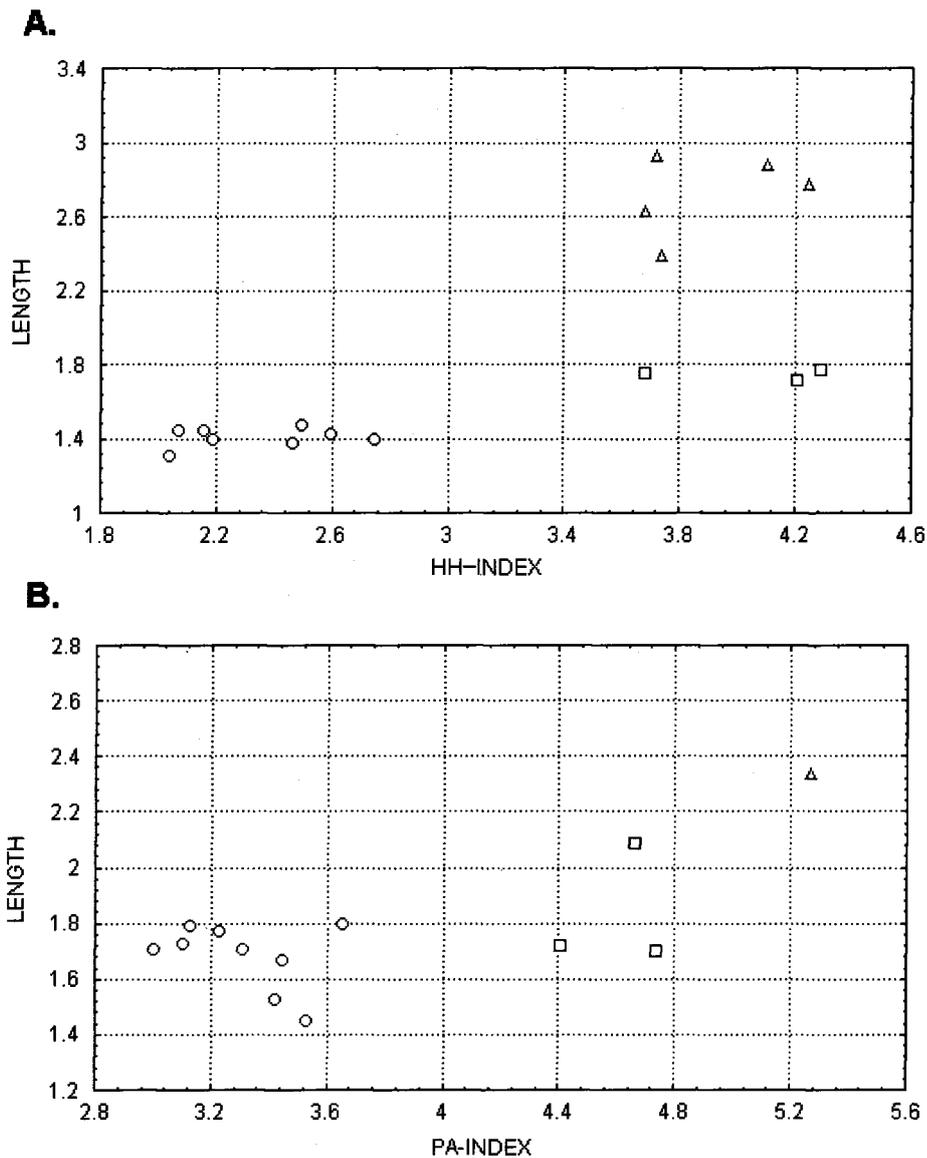
Mimomys tigliensis sp. nov., Tegelen. The comparison is given below, in the section devoted to *Mimomys tigliensis* sp. nov..

Comments

On the basis of the material described from the Tegelen fauna, *Mimomys reidi* Hinton is a very characteristic form of medium-sized *Mimomys*. The species has enamel islets in early wear stages of M/1 and M3/, acrorhiz position of the posterior root of M/2 and a very typical simplified M3/ with the constantly broad confluence of the anterior loop and T2, strongly resembling the morphology of Early Pleistocene *M. pusillus*. The material described suggests a phylogenetic link age of the *M. reidi* and the *M. pusillus* - *M. blanci* group.

The name *M. reidi* has been widely misused in the literature. The combination of the well-developed *Mimomys*-ridge with the absence of the enamel islet in M/1 in the original description led to a misunderstanding of this form. The name have been applied to the species of the *M. pitymyoides* group (Kowalski, 1958), or to older specimens of various species of small *Mimomys* with the worn enamel islet in M/1 (Alexandrova, 1976, Zazhigin, 1980). Mayhew &

Figure 14
Mimomys reidi, Tegelen.
Sinogram.
A - Lower molars,
B - Upper molars.
Triangles - M1/1, squares -
M2/2, circles - M3/3.



Stuart (1986) demonstrated the presence of an enamel islet in the M/1 and gave a clear diagnosis of the species.

Species content

Mimomys tornensis Jánossy et Van der Meulen, 1975,
Mimomys haplodentatus Savinov et Tutkova, 1987, *Mimomys tigliensis* nov. sp.

**Subgenus *Tcharinomys*,
 Savinov et Tutkova, 1987**

Diagnosis (emend.)

The group of hypsodont species with abundant crown cement. The average length of lower M/1 not more than 3 mm. Anteroconid of M/1 without an enamel islet and with an extremely reduced *Mimomys*-ridge. M3/ with shallow posterior enamel islet. Median sloping septum of the palate is short and broad.

Type species

Mimomys haplodentatus Savinov et Tutkova, 1987.

Comments

The hypsodont lineage of Euro-Asian smaller *Mimomys* is clearly distinct at the subgenus level. Surprisingly no appropriate name has been given to this species until recently. The names *Microtomys* (and its younger synonym *Pusillomimus*) (Rabeder, 1981, 1983), *Cseria* (Fejfar & Horáček, 1983) are inapplicable for the group, because they were based on considerably less hypsodont (*Microtomys pusillus*) and were unrelated to the *Mimomys* (*Cseria gracilis*) species. Carls & Rabeder (1988) designated the group of *M. tornensis* as 'subgenus n.'. The subgenus *Tcharinomys* was recently described for the small *Mimomys* species with hypsodont molars and abundant crown

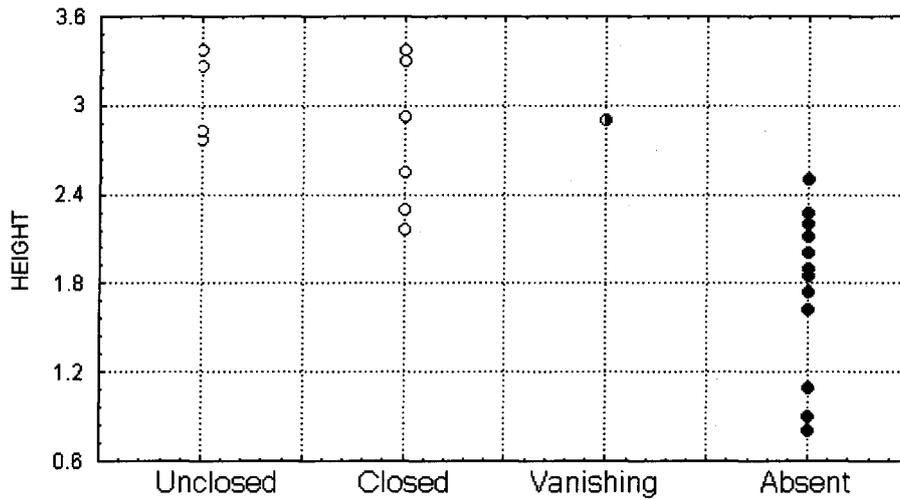


Figure 15
Mimomys reidi, Tegelen. M/1.
 Relationship of stages of the enamel islet development to crown height.

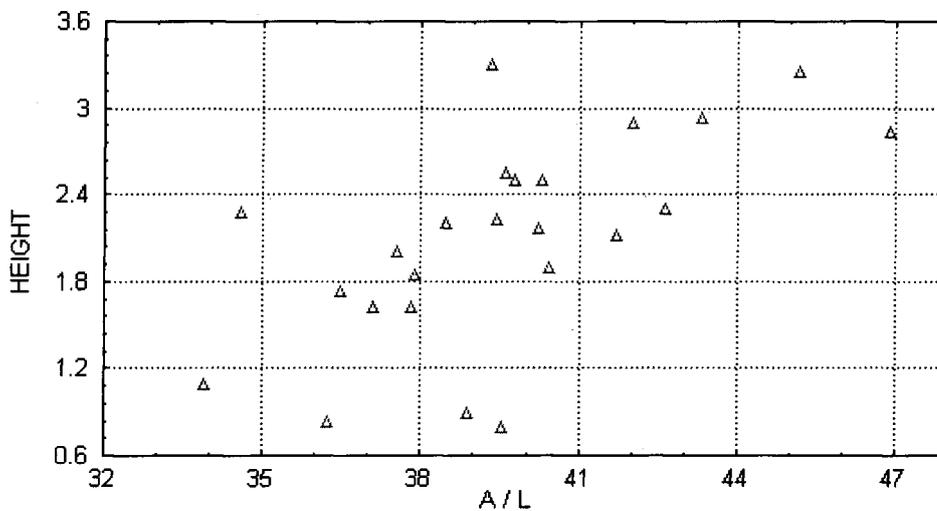
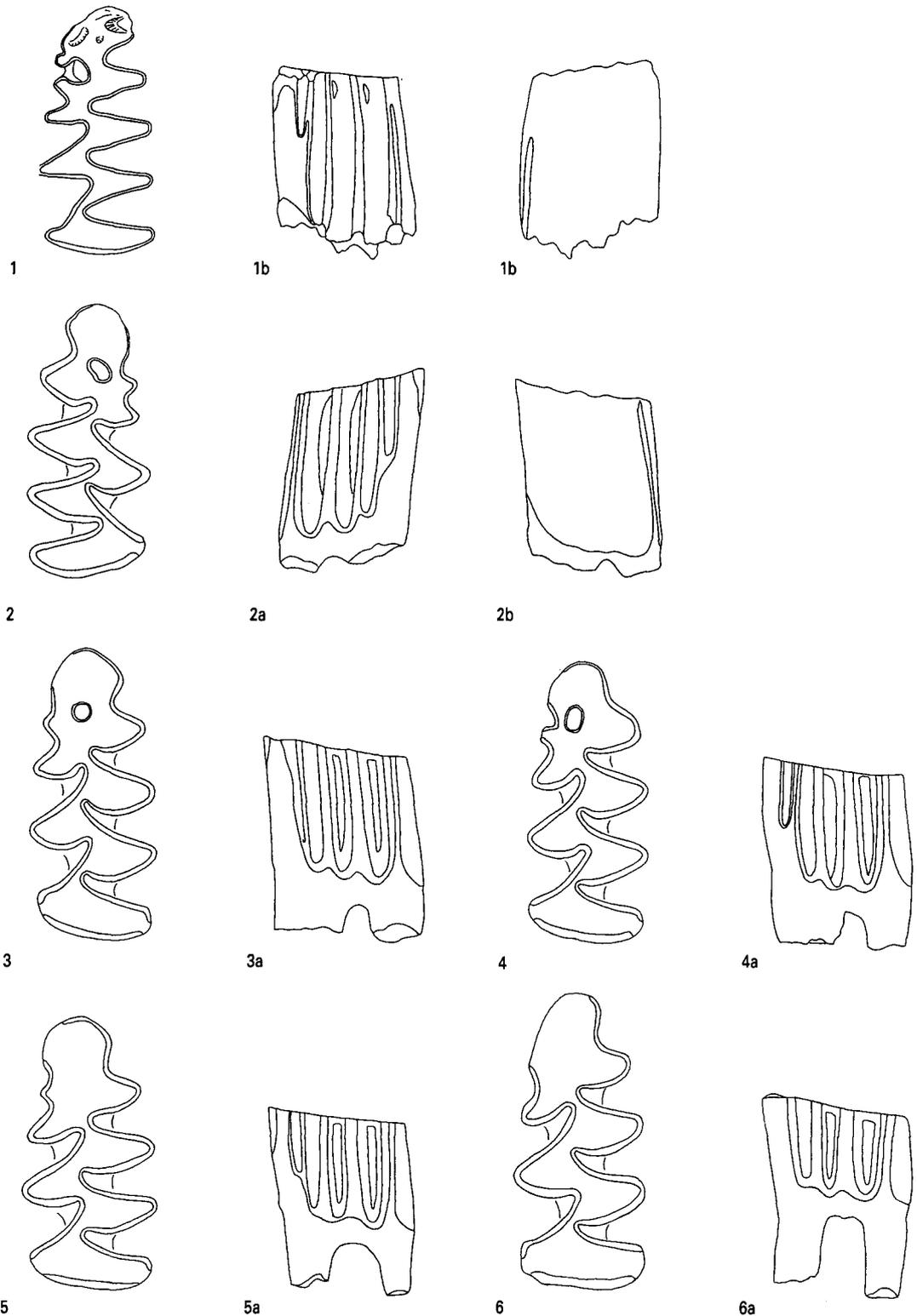


Figure 17
Mimomys reidi, Tegelen.
 Scatter diagram of relative length of anteroconid of M/1 (A/L) and crown height.

cement. The species *M. haplodentatus* is reported from the south-east Kazakhstan locality Aktogay (Kopaly section). The beds with *Mimomys* is thought to be of Late Pliocene - Early Pleistocene age (Kojamkulova et al., 1988; Tutkova, 1989). Like European *M. tornensis* and *M. tigliensis* n. sp., the Kazakhstan form combines M/1 without an enamel islet, and M3/ with the islet in the younger wear

stages. In fact the species is morphologically so close to the European *M. tornensis* (see discussion below) that it may well be its younger synonym; although, additional studies are required. The early history of the subgenus may be represented by the form described as *Cromeromys irtyschensis* Zazhigin, 1980 from the south of the west Siberian Plain (Zazhigin, 1980). If it is really so, then Cro-

Figure 16
Lower molars (M/1) of
Mimomys reidi, Tegelen.
1-6: M/1, occlusal surface;
1a-6a: labial side;
1b, 2b: lingual side. -
1 - Te604,
2 - Te191,
3 - Te634,
4 - Te845,
5 - Te221,
6 - Te495.
Occlusal view 15x,
lateral view 7,5x.



meromys is the earliest valid name for the group, because *C. irtyschensis* is the type species of the taxon. However, *Cromeromys* was intended to include *Mimomys*-like voles with primarily complex structure of upper M3/LRA2 is unreduced by the formation of an islet (Zazhigin, 1980). *Cromeromys* species are well known in Siberia and North America (Zazhigin, 1980, Sher et al., 1979, Reppening & Grady, 1988). The relationship of *Cromeromys* to *Mimomys savini* was discussed by Van Kolfshoten (1993). Until new data is published on the structure and history of the *Cromeromys* group it is too early to use this name for hypsodont smaller *Mimomys* species of the *tornensis* group. It is also obvious that the *Tcharinomys* subgenus diagnosed as it is here may include unrelated hypsodont forms. These forms may be similar only in their advanced characters associated with the progressing hypsodonty. The indirect indication of this is markedly heterogeneous supergenus *Microtus* s.l., which is most likely related to *Tcharinomys* s.l. On the other hand, the fact that numerous *Mimomys* lineage's can be traced through time by peculiar combinations of advanced and primitive characters suggests to the author that the typical *Tcharinomys* morphology accounts for a rather natural group of species.

***Mimomys (Tcharinomys) tigliensis* sp. nov.**

Figures 2E, 23-27, Tables 14 - 20.

- 1902 *Mimomys newtoni* sp. n.: F. Major, p. 106, fig. 23.
- 1926 *Mimomys newtoni* F. Major: M. Hinton, Monograph of voles ...: p.375 - 378, fig. 99: 18,19, 23, ?27; 103.
- 1958 ?*Mimomys newtoni* F. Major (partim): K. Kowalski, An Early Pleistocene...: p. 36- 37, Fig. 21, a-c, e.

- 1976 *Mimomys newtoni*; Van der Meulen., The smaller ... : p.17, fig. 7.
- 1986 *Mimomys blanci* Van der Meulen: D. Mayhew & A.J. Stuart, Stratigraphic and ... : p. 451-453, fig. 4, 5, 9, 15, 16.
- 1990 *Mimomys blanci* Van der Meulen: T. van Kolfshoten, Review ... : fig. 4, 4.
- 1994 ?*Mimomys tornensis* Jánossy et Van der Meulen: B. Sala et al., Villanyian ... : p.8, Pl.2, fig. 4-7, ?9.
- 1996b, *Mimomys tigliensis* sp. nov.: Tesakov, Voles of the ..., p. 95 (nom. provis.).

Derivatio nominis

The species name is derived from the Tiglian, the chronostratigraphical stage to which the Tegelen fauna belongs.

Locality and age

Tegelen Egypte quarry, Late Pliocene (Late Villanyian, MN17).

Diagnosis

Medium-sized hypsodont *Mimomys* species with abundant cement in the re-entrants, lacking an enamel islet, prominent *Mimomys*-ridge in younger stages of wear and rounded anterior loop of the anteroconid of lower M/1 and with a shallow enamel islet in the compact posterior lobe of upper M3/.

Differential diagnosis

The new species differs from the closely related *Mimomys tornensis* in smaller size, less advanced hypsodonty (HH-index is less than 5.9), higher percentage the *Mimomys*-ridge occurrence, better developed roots.

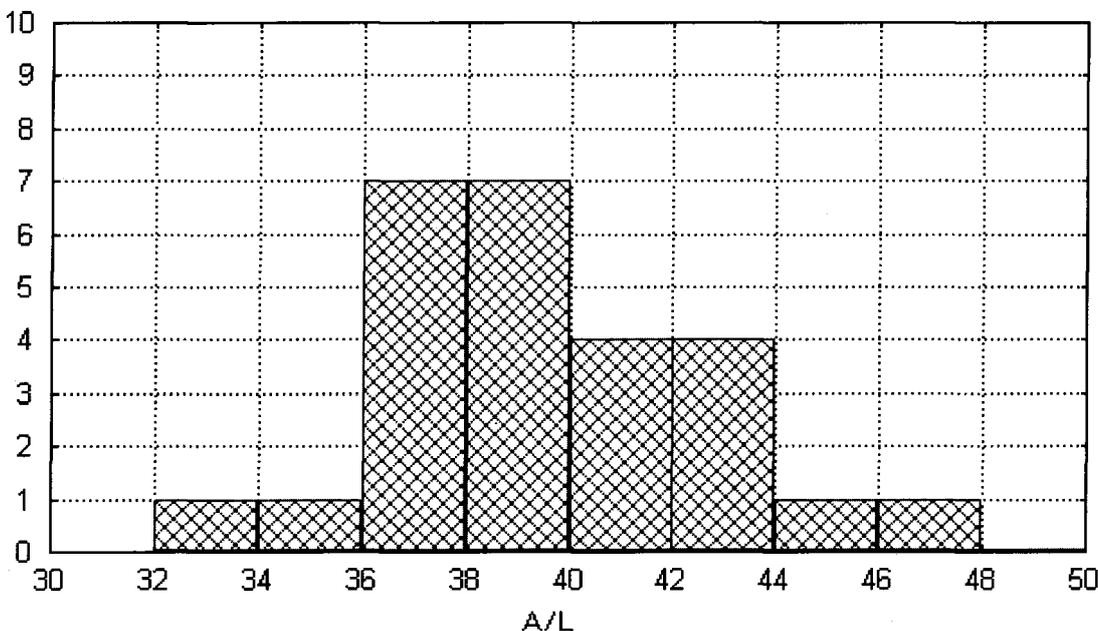


Figure 18
Mimomys reidi, Tegelen. M/1.
Histogram of the relative length of anteroconid (A/L).

Holotype

Right first lower molar, collection of the Royal Geological Museum, Leiden, number RGM 423798 (Figure 16: 4, Figure 17: 6,7).

Studied material

Tegelen, 71 M/1, 62 M/2, 55 M/3, 55 M1/, 58 M2/, 58 M3/; 1 fragment of the palatal area of the skull.

Description

Vole of medium size (see Tables 14 - 19, Figure 18). Cement accumulations are from moderate in younger individuals to abundant in older ones. Dentine fields of the occlusal surface are fairly well subdivided. Enamel band of the typical 'Mimomys' (or negative) differentiation.

Root formation stages (Figure 2E)

The most hypsodont vole of the Tegelen fauna. The well rooted molars constitute only 50.6% (n=277) of the collection. The intermediate (merorhiz) stage is displayed by 21.2% of the teeth (n=95). The young individuals with no crown base formed (arhiz stage) account for 17.2% (n=77) of the total material.

The crown height distribution is presented in the Figure 19. Most molars show a uniform one-peak pattern with a slightly longer left parts (low crowned teeth) of diagrams. Taking into consideration the high percentage of young arhiz individuals with a still unformed crown base, the actual age distribution would show a much higher right peak and less common middle age classes. For example, the histogram of A/L index may better represent the age

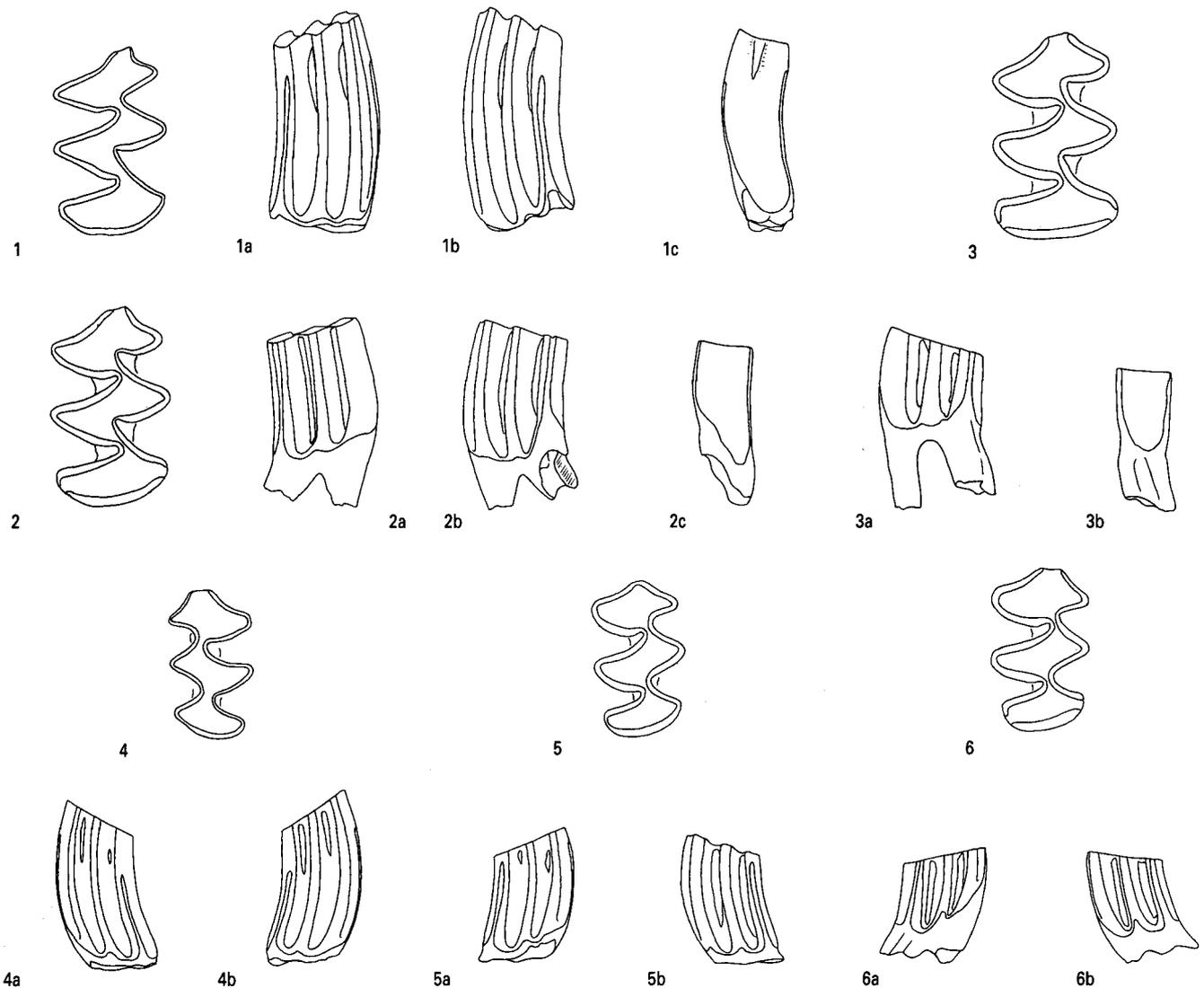


Figure 19

Lower molars (M/2 and M/3) of *Mimomys reidi*, Tegelen.

1-3: M/2, 4-6: M/3, occlusal surface:

1a, 2a, 4a-6a: labial side; 1b, 2b, 3a, 4b-6b: lingual side; 1c, 2c, 3b: posterior side. - 1 - Te264, 2 - Te545, 3 - Te806, 4 - Te809, 5 - Te575, 6 - Te701. Occlusal view 15x, lateral view 7,5x.

Figure 20
Upper molars (M1, M2/
and M3) of *Mimomys reidi*,
Tegelen.

1-3: M1, 4-6: M2, 7-15: M3/
occlusal surface: 1a, 2a, 4a-
8a, 10a, 12a, 13a: labial side;
3a, 4b, 5b, 7b, 8c, 12b, 14a,
15a: lingual side;
8b: posterior side.

1 - Te437, 2 - Te052,
3 - Te201, 4 - Te039,
5 - Te008, 6 - Te231,
7 - Te674, 8 - Te477,
9 - Te290; 10 - Te775,
11 - Te810, 12 - Te339,
13 - Te130,
14 - Te299 (*Mimomys reidi*?),
15 - Te670 (*Mimomys reidi*?).
Occlusal view 15x,
lateral view 7.5x.

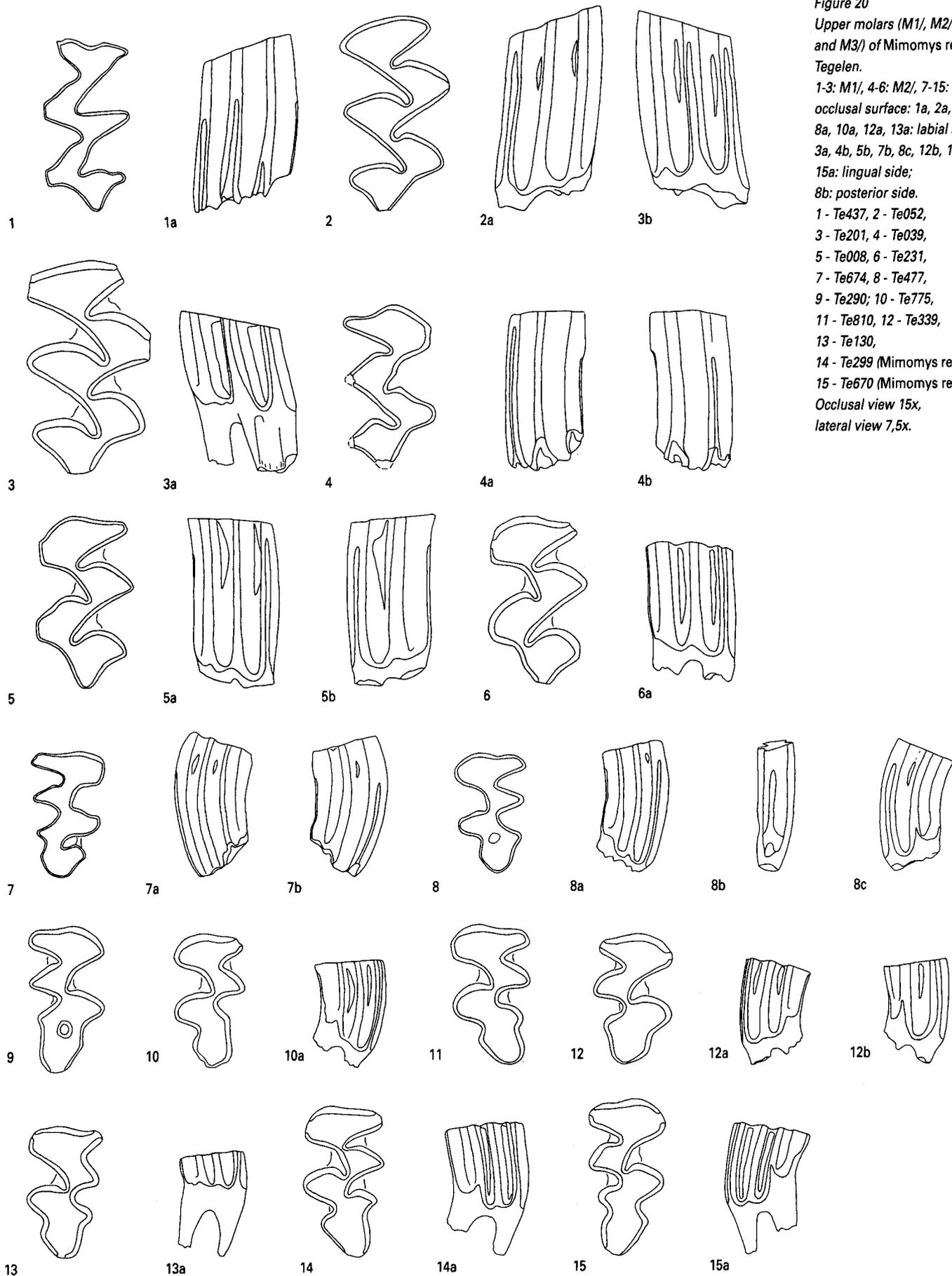


Figure 21
Mimomys reidi, Tegelen. M3/
 Scatter diagram of the
 anterior confluence (depth of
 BRA1) and crown height.

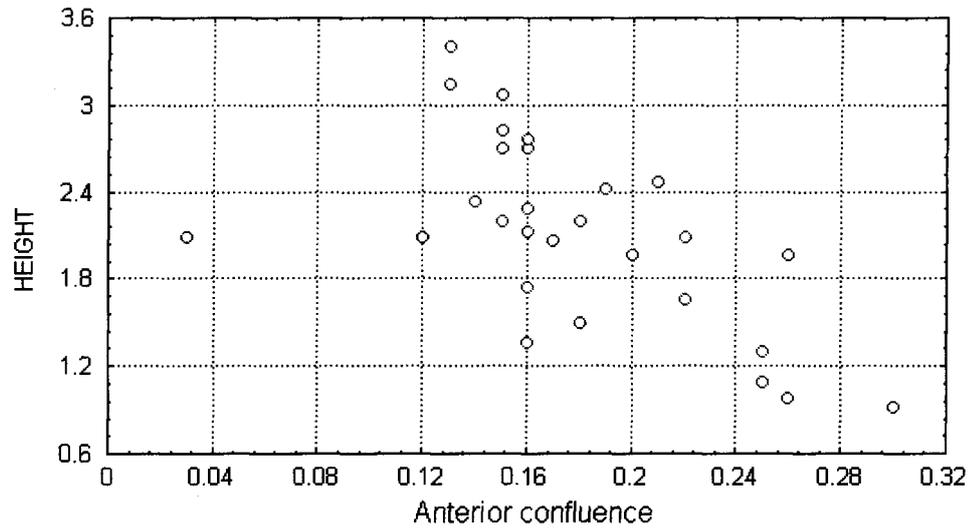


Figure 22
Mimomys reidi, Tegelen. M3/
 Relationship of stages of the
 enamel islet development to
 crown height.

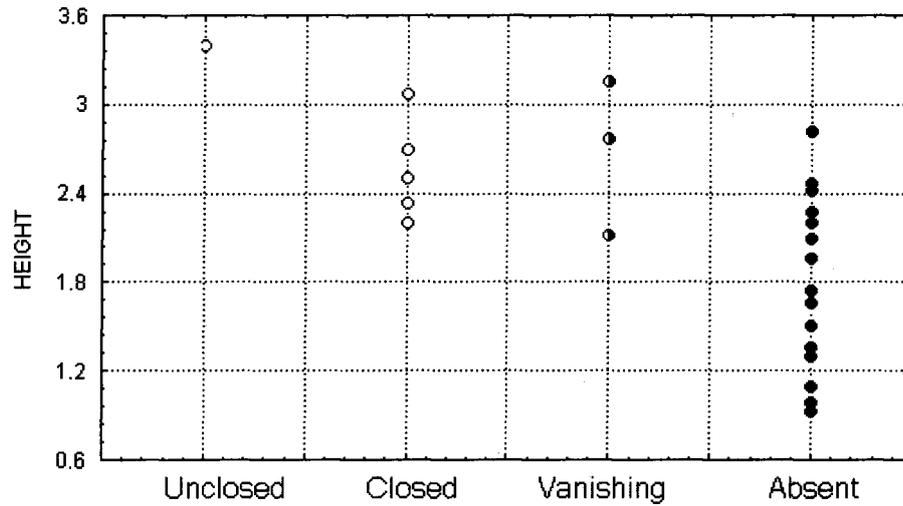
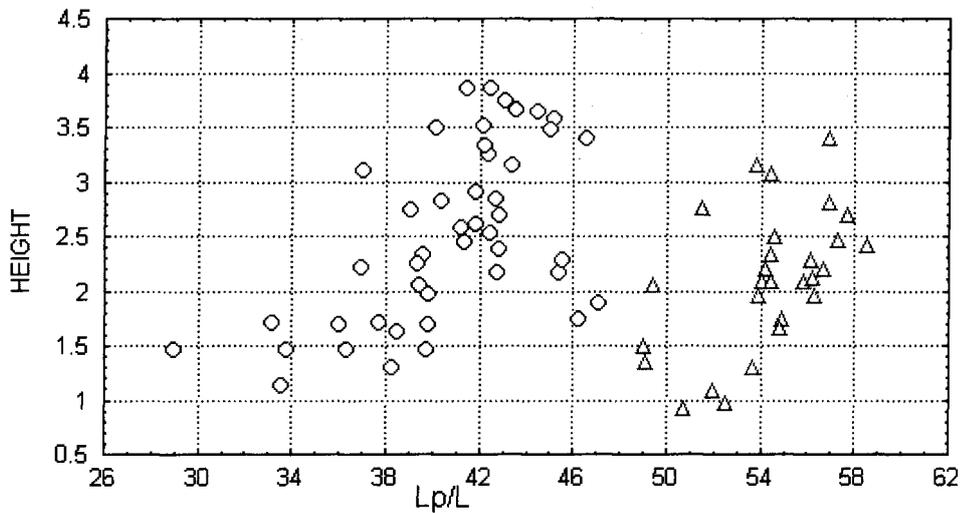


Figure 23
 Scatter diagram of relative
 length of the posterior lobe
 of M3/ and crown height.
 Circles - *Mimomys tigliensis*
 sp. nov, triangles - *Mimomys*
reidi.



frequency distribution (Figure 30). Thus the age profile of *Mimomys tigliensis* may be considered as a true attritional one (Korth & Evander, 1986).

Dentine tracts

Being a very hypsodont vole, *Mimomys tigliensis* has already reached the stage when in most of molars the tips of dentine tracts are interrupted by wear while crown base is not yet formed. However, occasionally specimens do occur with the complete dentine tracts and the formed crown base. In lower M1/ and M2/ these are typically hypsinulids, in the upper M1/ and M2/ these are respectively anterosinus and anterosinulus, and protosinus. It should be noted that these complete dentine tracts are obviously the rare lowest possible variants, because there are much higher tracts which are already interrupted by wear. In M3/3 there are numerous examples of complete tracts of posterior and anterior lobes, and also of the distosinus of M3/. The distribution areas of minimum values of HH and PA indexes are illustrated in Figure 28.

Cranial morphology

The Tegelen material includes one fragment of the palatal portion of the skull with M1/-M2/ and the postero-palatal region preserved. Judging from abundant cement filling the re-entrants of the molars, the specimen belongs to *Mimomys tigliensis* sp. nov. (Figure 29). The posterior edges of the anterior palatal foramens (=foramina incisiva) are situated anteriorly from the anterior loops of M1/. The maxillo-palatine suture projects to the M1/ - M2/ contact. The posterior palatine pits (foramen palatinum posterior) are at the level of LRA1 of M2/. The postero-medial sloping septum (=protuberantia marginalis descendens, = palatine bridge) is short and relatively broad. The post-palatine pits (fossa palatina lateralis) are shallow and perforated with two or three medium sized foramens. The anterior edge of post-palatine pits is at the level of the posterior wall of T3 of M2/.

Hinton (1926) was first who emphasized the importance of the postero-palatine morphology for vole systematics. He described the palatal structure of *Mimomys*, "Palate of normal Arvicoline type with postero-lateral bridges and pits, and with postero-medial sloping septum clearly defined although short and broad" (Hinton, 1926, p.16). He also described the main arvicoline palate morphologies. Ognev (1948) gave detailed terminology of the palate elements. Later Zazhigin (1980) classified palates of the extant arvicolines into three distinct types: *Clethrionomys-Alticola*, *Microtus-Arvicola*, and *Dinaromys*. He pointed out that the fossil rooted voles of the *Mimomys* group resemble the *Microtus*-type group and show two types of morphology. Most forms have short and broad postero-medial spine between the postero-palatine pits (this group obviously corresponds to Hinton's *Mimomys* definition). The other group of fossil voles is represented only by *Microtomys pusillus* Von M hely,

1914. This form shows a very long postero-medial spine which is typical of many species of modern *Microtus* and *Arvicola* (Von M hely, 1914, Hinton, 1926, Zazhigin, 1980). The morphometric approach to the study of the palate morphology was proposed by Recovets (1994). He introduced the W/L index for the postero-medial sloping septum. Its length is measured from the anterior edge of post-palatine pits to the anterior edge of the fossa mesopterygoidea, and width - in the middle of the septum. The other useful index is the tooth row divergence index (Recovets, 1994). It is measured as the ratio of the width between the alveolas of the protocones of M1/ and the width between the alveolas of anterior loop of M3/. The W/L index for the Tegelen specimen is about 100. The divergence index is 76.

M1

The molar consists of the posterior loop, three alternating triangles, and the anteroconid complex which integrates the anterior loop and the anteroconid triangles (T4-T5). The relative length of anteroconid, A (A/L) (Van der Meulen, 1973) shows a clear relationship with the crown height / individual age (Figure 27). The range of variation is illustrated by histogram in Figure 30. The mean value of A / L is 39.28, n=63 (Table 14). The anterior loop is of rounded form. The B/W index (Van der Meulen, 1973), which characterizes the confluence between the anterior loop and the anteroconid triangles, shows an inverse correlation with the A/L index (Figure 31). This means generally that the longer the anteroconid complex (= the younger the animal), the narrower the connection between the anterior loop and anteroconid triangles. The mean value of B/W index is 37.67, n=68 (Figure 32A, Table 14). The C/W index (Van der Meulen, 1973) is used to evaluate the degree of confluence between the anteroconid triangles (T4-T5). The index, like the previous one, is inversely correlated with the A/L index (Figure 31). This means that the confluence between T4 and T5 increases with the increase of the relative anteroconid length (=individual age). The mean value of the C/W index is 21.60, n=68 (Figure 32B, Table 14). The *Mimomys*-ridge is frequently present in young individuals at the arhiz and merorhiz stage of root formation (n=7), but rarely at the rhizodont stage (n=1). Typically the *Mimomys*-ridge is very short and obliquely directed into the proximal direction (Figure 24: 4, 6). This means that it shifts anteriorly with wear. However, the *Mimomys*-ridge may be not developed even at the juvenile stage (Figure 24: 1).

Because of the great influence of the wear stage on the morphology of the anteroconid complex, the morphotype system, as it is used for rootless voles, is inapplicable for the hypsodont form, like *Mimomys tigliensis*. The actually existing individual variability is strongly modified and disguised by the individual age / wear stage. This is clearly shown by the attempted application of the morphotype system of Rabeder (1986). Therefore, if there is an evolu-

tionary shift in morphotypes, to compare two samples using the morphotype system would require the evaluation of the hypsodonty and the detailed age groups analysis. Generally, four types of the anteroconid morphotypes can be distinguished in the Tegelen material: A. - with *Mimomys*-ridge ("*Mimomys*" of Rabeder, 1986), B. - with broadly confluent anteroconid elements and shallow LRA4 ("*laguroides*" of Rabeder, 1986), C. - with broadly confluent anteroconid elements and deep LRA4 ("*pliocae-nicus*" of Rabeder, 1986), and D. - with slightly more disconnected, mushroom-like anterior loop ("*protonivalis*" + "*eonivalis*" of Rabeder, 1986). The morphotypes with separated T4 ("*praeratticeps*", "*ratticepoides*" etc. of Rabeder, 1986) have no independent significance. The more subdivided anteroconid triangles may modify other morphotypes. These 'morphotypes' account for 12.5% (A.), 34.7% (B.), 48.6% (C.), and 4.2% (D.) of the variability. In young and medium-aged individuals cement may fill the BRA3 and LRA4.

The complete tip of anterosinuid in young specimens shows typical splitting into two parts. The distal branch corresponds to the mimosinuid. It may be present even when the *Mimomys*-ridge is not manifest.

M/2

The typical *Mimomys* form (Figure 33: 1 - 3). The basic triangles T1 and T2 tend to be disconnected. The broad confluence of T1-T2 is demonstrated only by 9% (n=5), the bulk of the molars, 79% (n=46) shows intermediate condition with rather narrow connection (Figure 33: 2, Te113). And about 12% of the material (n=7) demonstrate complete disconnection.

The anterior pair of triangles (T3-T4) also show fairly high percentage of markedly subdivided variants, though less than for the T1-T2 pair.

The posterior root of the molar is situated completely labially from the incisor (pleurorhiz condition) (Figure 33: 3c). The depth of the LRA1 is not reduced.

M/3

The molar shows the typical form (Figure 33: 4 - 7). The T1-T2 and T3-T4 are widely confluent. However the BRA1 and BRA2 display the anterior vergence marking the initial stage of closing of the respective connections.

M1/

The molar shows a characteristic *Mimomys* shape with the anterior loop and four alternating separated triangles (Figure 34). LRA3 is blunt. BRA3 is only slightly developed or absent. All the molars at the rhizodont stage of root formation have two roots. However, the middle root can still be seen as a lingual appendix of the anterior root (Figure 34: 3b).

M2/

The molar consists of the anterior loop and three alternat-

ing separated triangles (Figure 34). LRA2 is developed and sometimes filled with cement. BRA3 is blunt or absent. In some young specimens the T4 may be slightly elongated posteriorly. Occasionally the hyposinus may be enlarged.

M3/

The molar consists of the anterior loop, the T2, T3, and the posterior lobe complex, which integrates T4 and the posterior loop. The relative length of the posterior lobe (Lp/L) shows decrease with wear (Figure 23, circles). The mean value of index of the posterior lobe is 40.73, n=51 (Table 19, Figure 35). The confluence between the anterior loop and T2 ranges from 0.04 to 0.25, with the mean 0.13 mm (n=58). There is no clear age dependent changes of the anterior confluence (Figure 36). On one hand, the large group of specimens shows increasing confluence with progressing tooth wear. On the other hand, a group of low crowned senile molars in the left low corner of the diagram demonstrates very low values of the confluence. Most probably this is an intraspecific variability.

In young animals the enamel islet is present in the posterior lobe (Figure 34: 8-11). The islet closes at the rootless stage. It may be well expressed during the arhiz and merorhiz stages of root formation. The islet starts to disappear during the merorhiz stage. There are no fully rooted molars with enamel islet. The relation of the crown height and the stages of islet formation is shown in the Figure 37. The maximum depth of the enamel islet apparently does not exceed 2 mm.

The variability of the posterior lobe can be expressed in a morphotype system (Rabeder, 1986; Carls & Rabeder, 1988). The approach meets the same criticism as was discussed above in association with M/1 morphotypes. Generally four 'morphotypes' can be distinguished in the material. A. ("*mit insel*" of Rabeder, 1986) - 23.2%, n=13; B. ("*eosimplex*" of Rabeder, 1986) - 71.4%, n=40; C. ("*praesimplex*" of Rabeder, 1986) - 3.6%, n=2; D. ("*protosimplex*" of Rabeder, 1986) - 1.8%, n=1.

The dental tract of the posterior lobe, the distosinus, is often trident-shaped (Figure 34: 7c). Hyposinus is fairly well developed. It varies from 0.43 to 2.17, with a mean of 1.04 mm, n=22.

Comparison

Mimomys tornensis, Osztromos 3. According to Jánosy & Van der Meulen (1975), this species is larger and has more abundant cement in the re-entrant angles than *Mimomys tigliensis* from Tegelen. The Tegelen form seems to have more variants with the *Mimomys*-ridge.

Mimomys tornensis, Deutsch Altenburg. This form (only M/1 are illustrated) from several localities in Deutsch Altenburg: 3, 10, 2C1, 4B shows larger dimensions than *Mimomys tigliensis* from Tegelen (Rabeder, 1981). One specimen illustrated (Rabeder, 1981, Abb.108,

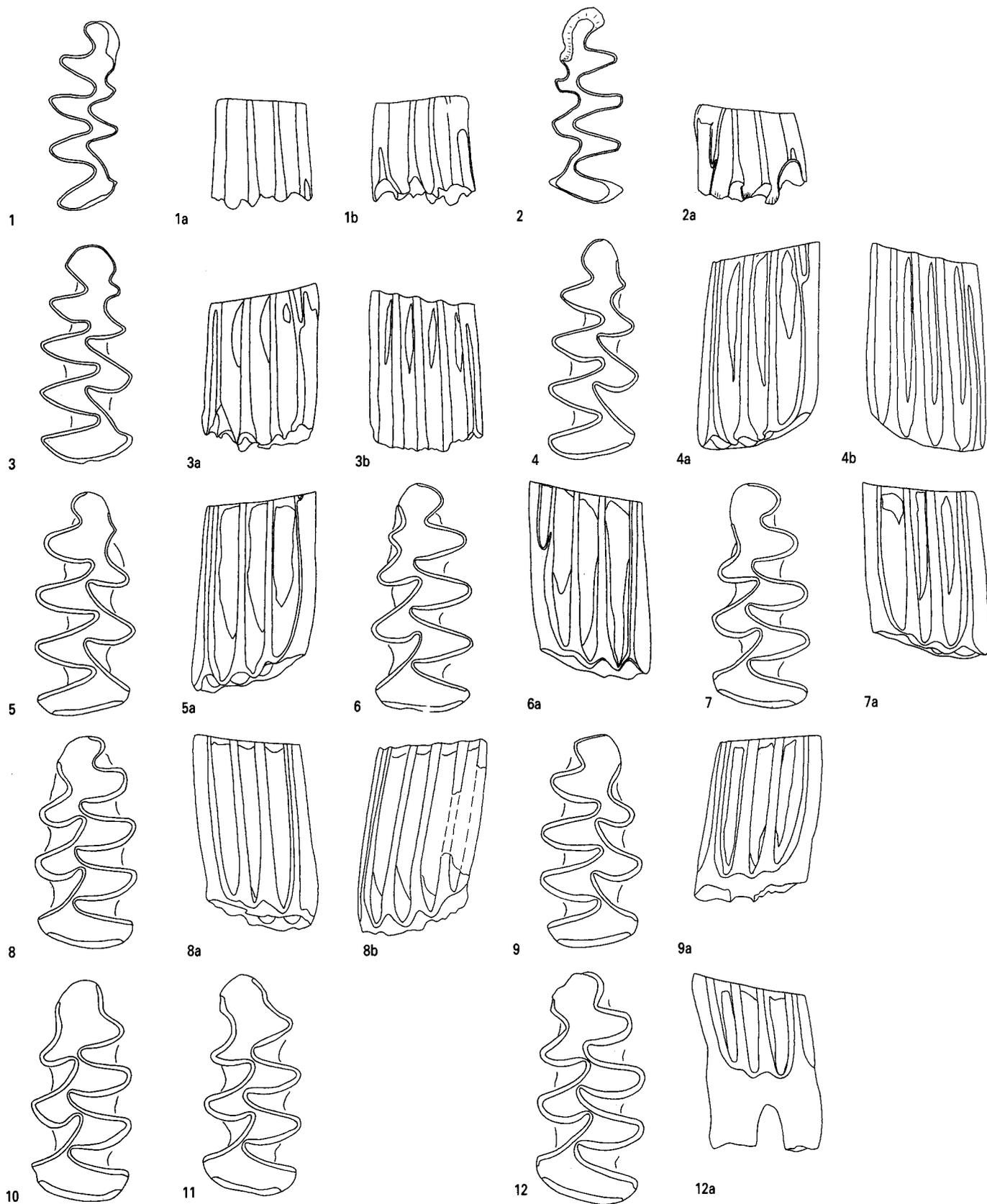


Figure 24

Lower molars (M/1) of *Mimomys tigliensis* sp. nov., Tegelen.

1-12: M/1, occlusal surface; 1b, 2a-9a, 12a: labial side; 1a, 3b, 4b, 8b: lingual side. - 1 - Te745, 2 - Te195, 3 - Te299, 4 - Te798 (holotype), 5 - Te303, 6 - Te494, 7 - Te220, 8 - Te778, 9 - Te142, 10 - Te360, 11 - Te492, 12 - Te822. Occlusal view 15x, lateral view 7.5x.

<i>Table 14</i> <i>Dimensions of Mimomys</i> <i>tigliensis, Tegelen, M/1</i>		Variable	n	Mean	Minimum	Maximum	Standard deviation	Standard error
		Length	63	2.59		2.22	2.92	0.15
		Width	71	1.10		0.78	1.29	0.11
		Anteroconid index (A/L)	63	39.28	28.90		44.40	2.99
		B/W	68	37.67	14.10	56.10		1.17
		C/W	68	21.60	9.47	38.82	6.05	0.73
		Anterosinuid				>4.5		
		Hyposinuid				>4.46		
		Hyposinulid			4.02	>4.6		
		HH-index	8	>6.00	>5.76	>6.41		

<i>Table 15</i> <i>Dimensions of Mimomys</i> <i>tigliensis, Tegelen, M/2</i>		Variable	n	Mean	Minimum	Maximum	Standard deviation	Standard error
		Length	56	1.71	1.53	1.89	0.08	0.01
		Width	61	1.02	0.86	1.14	0.10	0.01
		Anterosinuid				>4.1		
		Hyposinuid				>3.75		
		Hyposinulid			4.08	>4.2		
		HH-index	14	>5.14	>4.42	>5.63		

<i>Table 16</i> <i>Dimensions of Mimomys</i> <i>tigliensis, Tegelen, M/3</i>		Variable	n	Mean	Minimum	Maximum	Standard deviation	Standard error
		Length	51	1.48	1.22	1.65	0.09	0.01
		Width	55	0.81	0.59	0.92	0.07	0.01
		Anterosinuid				>3.15		
		Hyposinuid	6	2.45	2.12	2.61	0.19	0.08
		Hyposinulid	8	2.29	2.01	2.45	0.14	0.05
		HH-index	5	3.42	3.19	3.58	0.15	0.07

<i>Table 17</i> <i>Dimensions of Mimomys</i> <i>tigliensis, Tegelen, M/1</i>		Variable	n	Mean	Minimum	Maximum	Standard deviation	Standard error
		Length	50	2.36	1.97	2.6	0.14	0.02
		Width	55	1.28	0.93	1.43	0.09	0.01
		Anterosinus	2		4.08	4.73		
		Anterosinulus	5	4.26	3.91	4.50	0.22	0.10
		Protosinus				>5.43		
		Distosinus				>5.40		
		PA-index				>6.80		

<i>Table 18</i> <i>Dimensions of Mimomys</i> <i>tigliensis, Tegelen, M/2</i>		Variable	n	Mean	Minimum	Maximum	Standard deviation	Standard error
		Length	56	1.80	1.57	2.00	0.08	0.01
		Width	58	1.03	0.84	1.20	0.07	0.01
		Anterosinus				>5.27		
		Protosinus			2.99	>5.00		
		Distosinus				>4.60		
		PA-index				>7.27		

<i>Table 19</i> <i>Dimensions of Mimomys</i> <i>tigliensis, Tegelen, M/3</i>		Variable	n	Mean	Minimum	Maximum	Standard deviation	Standard error
		Length	51	1.61	1.34	1.82	0.10	0.02
		Width	58	0.87	0.74	1.03	0.07	0.01
		Lp/L	51	40.73	28.97	47.06	3.67	0.51
		Anterosinus			3.32	>3.86		
		Protosinus			3.02	>3.64		
		Distosinus	10	1.71	1.40	2.12	0.21	0.07
		PA-index			4.52	>5.31		

6c) demonstrates both posterior loop tracts complete (hyposinuid - 4.23, hyposinulid - 4.23, HH-index - 6.45). There are no specimens with both tracts complete in the Tegelen material, although the tracts values and HH-index of the Austrian form falls within the variation range of *Mimomys tigliensis* from Tegelen. In Deutsch Altenburg 2C1 and 4B *Mimomys tornensis* is accompanied by abundant *Allophaiomys* (Rabeder, 1981).

***Mimomys tornensis*, Schernfeld.** The detailed description of this form (Rabeder, 1986; Carls & Rabeder, 1988) enables the close comparison with the Tegelen vole.

Dimensions

The Tegelen and Schernfeld samples show very similar dimensions. However, the Tegelen material exhibits lower minimum values of length in all molars (except M3/). In most of Tegelen molars the mean values of length are also lower than those of the Schernfeld form.

Dentine tracts

In both forms the tracts height and HH-index are mostly minimum values. Most of the maximum, minimum, and mean (when known) values are higher in Schernfeld. Therefore the *Mimomys tornensis* from Schernfeld is more hypsodont than *Mimomys tigliensis* from Tegelen.

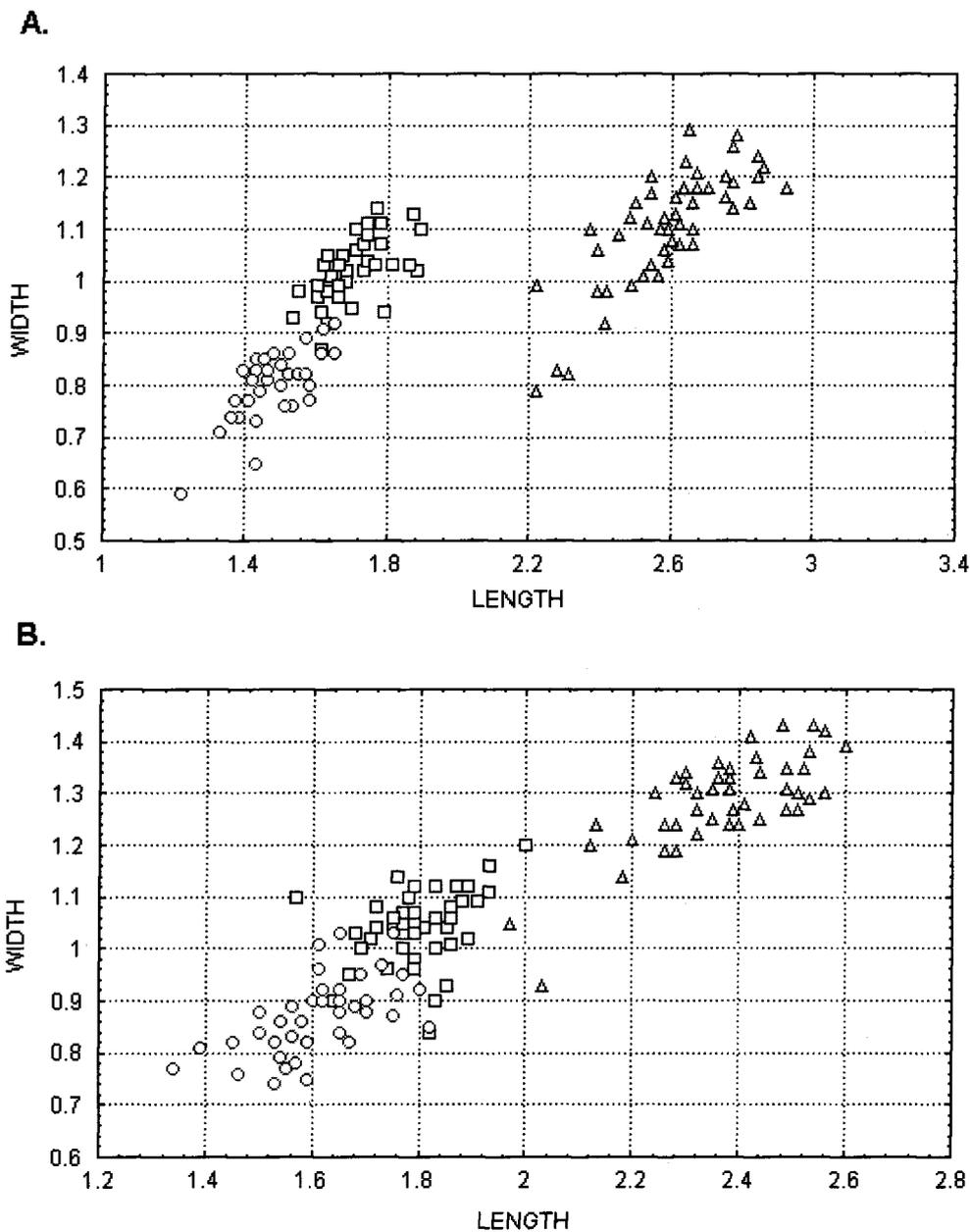


Figure 25
Mimomys tigliensis sp. nov., Tegelen. Scatter diagram of length and width. A - Lower molars, B - Upper molars. Triangles - M1/1, squares - M2/2, circles - M3/3.

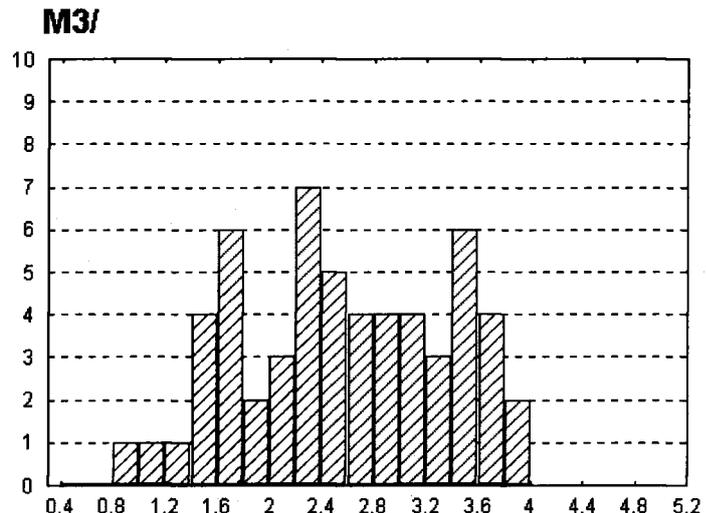
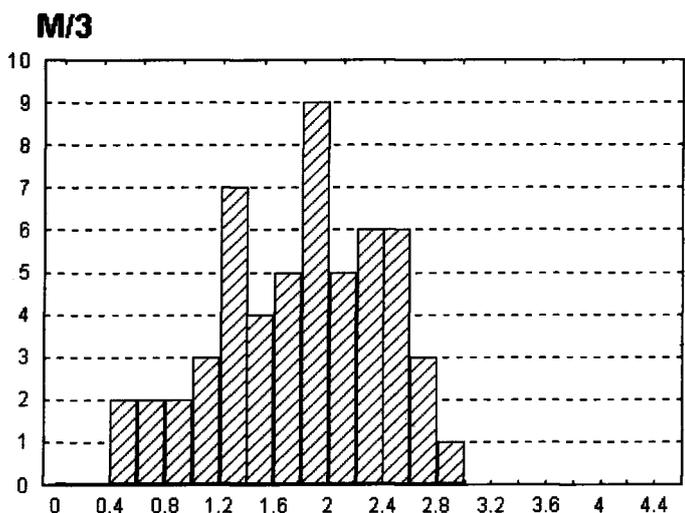
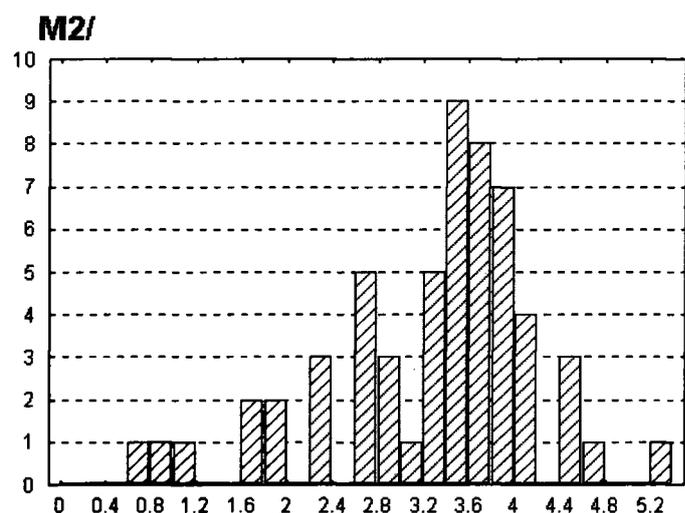
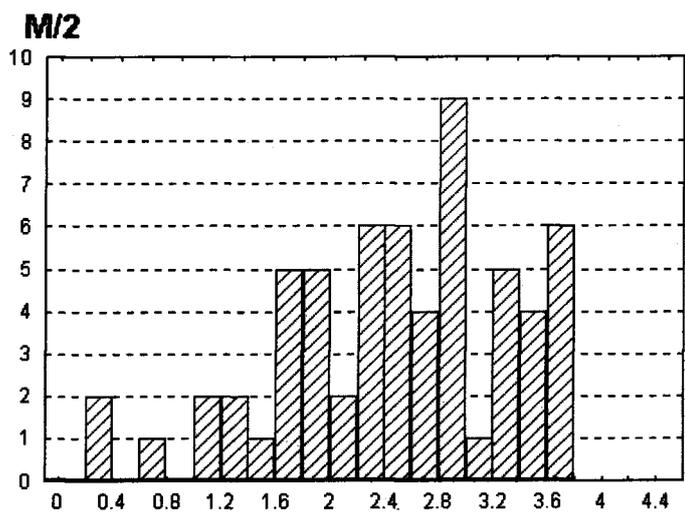
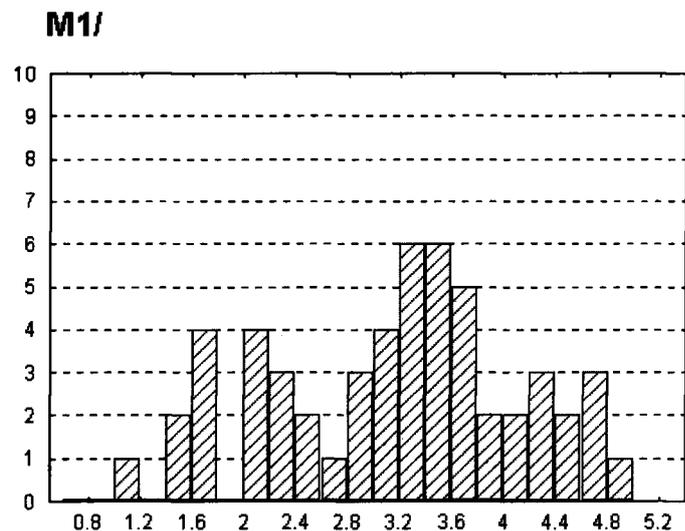
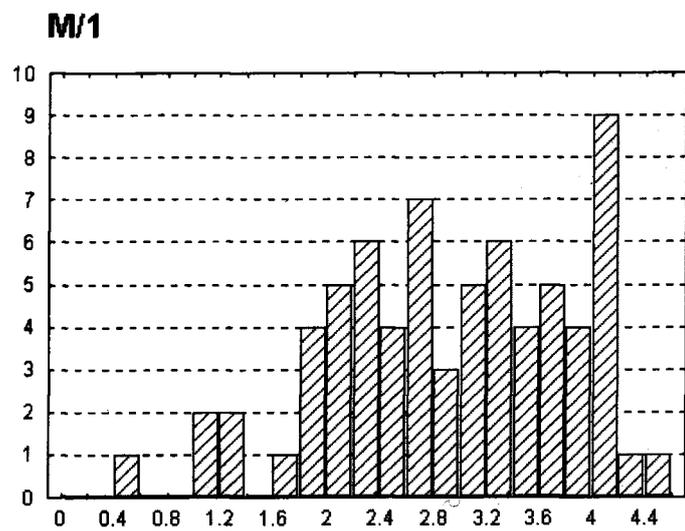


Figure 26
Mimomys tigliensis sp. nov., Tegelen. Frequency histogram of crown height.

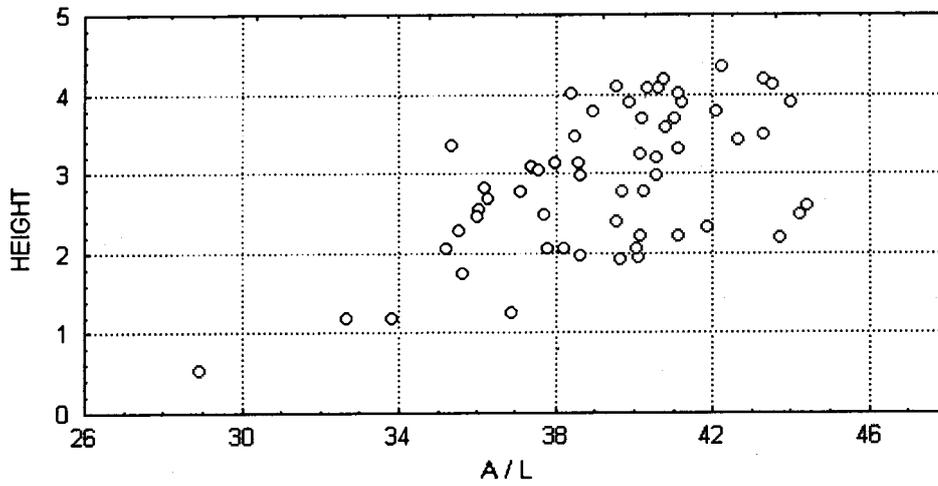


Figure 27
Mimomys tigliensis sp. nov.,
 Tegelen. Scatter diagram of
 relative length of anteroconid
 of M/1 (A/L) and crown
 height.

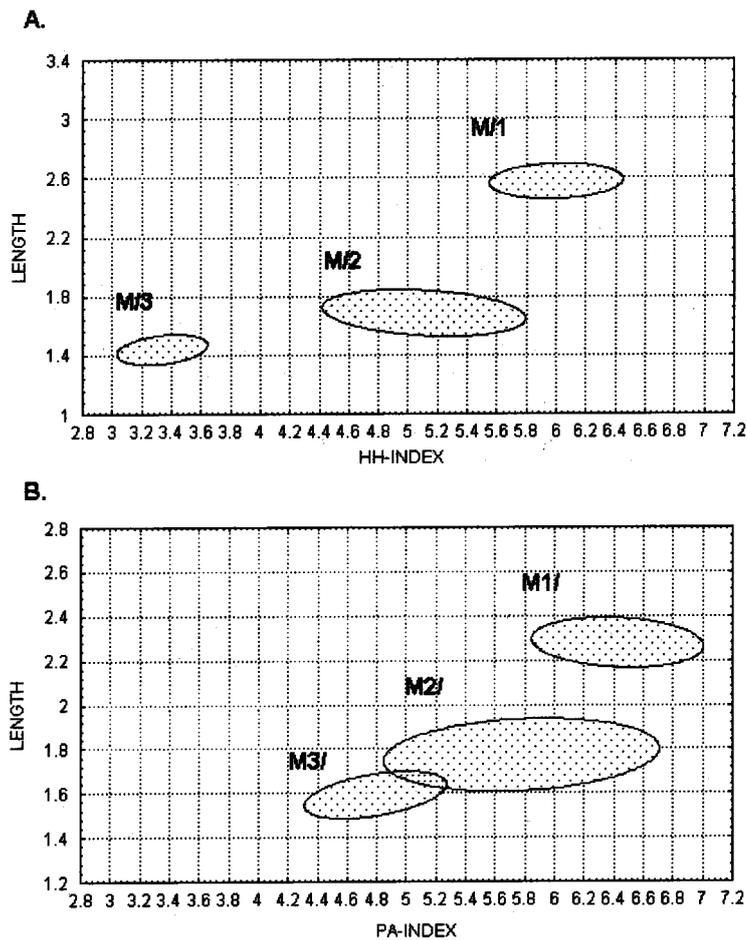


Figure 28
Mimomys tigliensis sp. nov.,
 Tegelen. Sinugram.
 A - Lower molars, B - Upper
 molars. Minimum values.

Anteroconid index

The relative length of anteroconid is almost equal in both forms. The mean values of A/L index is only 0.2% higher in the Tegelen form (Table 20). However the range of the Schernfeld form is distinctly shifted towards higher values.

Morphotypes of M/1

Bearing in mind all the reservations discussed above, the Tegelen material presents an higher overall frequency of primitive morphotypes. Thus, the '*Mimomys*' morphotype reaches 12.5% of the variability (compared to 2% at Schernfeld), the '*laguroides*' morphotype is 34.7% (12% at Schernfeld), the '*pliocaenicus*' morphotype is 48.6% (60% in Schernfeld). Advanced morphotypes of the 'nivaloid' type are less frequent in Tegelen - 4.2% , compared to over 20% at Schernfeld.

Morphotypes of M3/

Of the two main morphotypes known from Schernfeld, the Tegelen form has less numerous 'young' morphotype with enamel islet: 23.2% (compared to 44% at Schernfeld), and more frequent 'eosimplex' morphotype: 71.4% (44% at Schernfeld). It is also worth noting the equally

negligible percentage of the complicated 'praesimplex' morphotype: 3.6% (1.3% at Schernfeld).

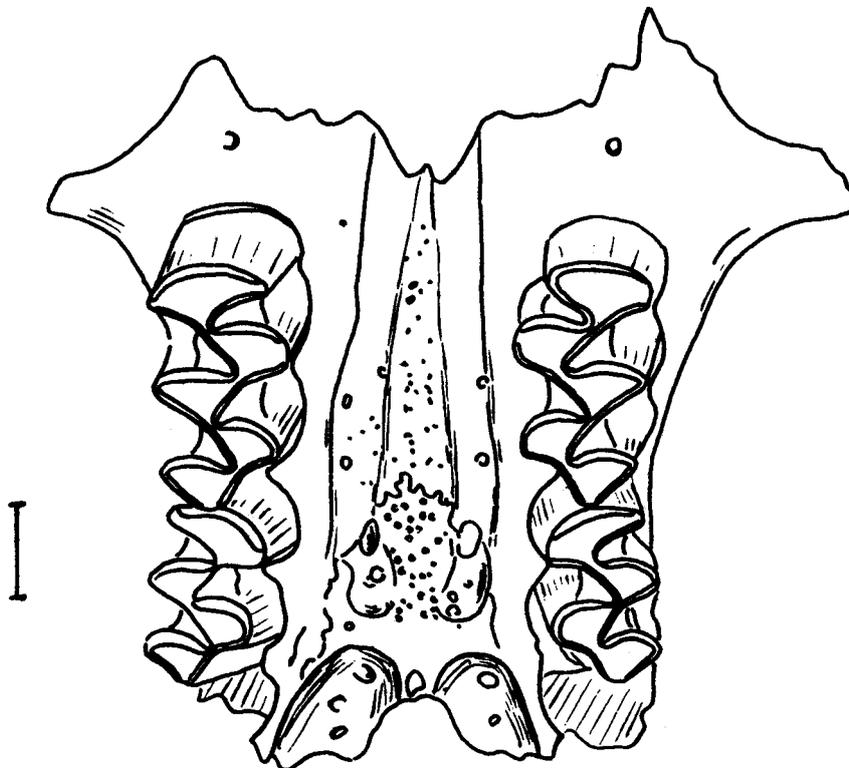
Root formation stages.

Mimomys tigliensis from Tegelen show less advanced ratio of root formation stages as compared to *Mimomys tornensis* from Schernfeld. In lower M/1 the arhiz stage (juvenile + arhiz *sensu* Rabeder, 1986) is recorded in 32.9% (n=23) of molars (28.7% at Schernfeld), the merorhiz (intermediate) stage is known in 20% (n=14) of molars (61.3% at Schernfeld), and finally the rhizodont stage is known in 47.1% (n=33) of teeth in Tegelen (only 10% at Schernfeld). Statement of Carls & Rabeder (1988) of much more frequent occurrence of rhizodont stages in third molars is not confirmed by the Tegelen material (Kazantseva & Tesakov, 1997).

Conclusions. The comparison presented shows the generally less advanced stage of hypsodonty of *Mimomys tigliensis* from Tegelen expressed in various sets of characters.

***Mimomys tornensis*, Rivoli Veronese (Sala et al., 1994).** This form follows *tornensis* - *tigliensis* morphology. It is slightly larger: the mean length of M/1 is 2.75 (n=6)

Figure 29
Mimomys tigliensis sp. nov.
Palatal region of the skull,
Te939.



contrary to 2.59 mm in Tegelen. The limited material does not allow the hypsodonty comparison. Indirect observations enable to assume conspecific relationships of the two forms.

Mimomys blanci, from East Anglia (Mayhew & Stuart, 1986). The material described from East and West Runton, Sidestrand-Overstrand, and Easton Bavents closely follows the morphology of *Mimomys tigliensis* from Tegelen. The smaller dimensions both in means and maximum values are noteworthy. For example, in the largest sample described (East Runton) the mean value of length of M/1 is 2.41 (n=7) with a range of 2.26 - 2.68. The English form is probably conspecific with *Mimomys tigliensis* from Tegelen. Therefore, the author does not follow the usage for the Late Villanyian *Tcharinomy*s of the name *M. blanci*, which represents a different taxon approximately 1 million years younger (see below).

Mimomys tornensis, Casablanca 1 (Esteban & Lopez Martinez, 1987). This form differs from the Tegelen *Mimomys tigliensis* in large dimensions (mean length of M/1 is 3.08, n=25), with a deeper and more developed *Mimomys*-ridge, the presence of traces of enamel islet in the anteroconid of juvenile M/1 (never seen in *Mimomys tigliensis*), the presence of three separate roots in upper M1/ (never seen in *Mimomys tigliensis* sp. nov.). The form from Casablanca 1 is similar to *Mimomys tigliensis* in advanced hypsodonty, abundant crown cement, and overall similarity of occlusal pattern. The Spanish vole probably represents an independent (?endemic) lineage of advanced *Mimomys* distinct from the *tigliensis-tornensis* lineage.

Mimomys tornensis, Kamyk. Originally the medium-sized vole, with characteristic abundant cement and advance hypsodonty, was described as *Mimomys* sp. (Kowalski, 1960). Kowalski noted the similarity of the Polish

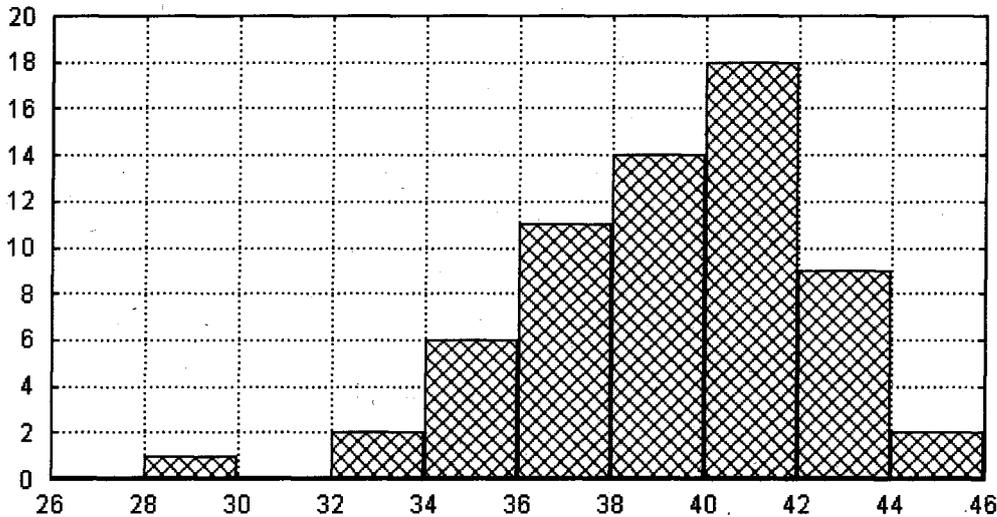


Figure 30
Mimomys tigliensis sp. nov., Tegelen. Histogram of the relative length of anteroconid (A/L).

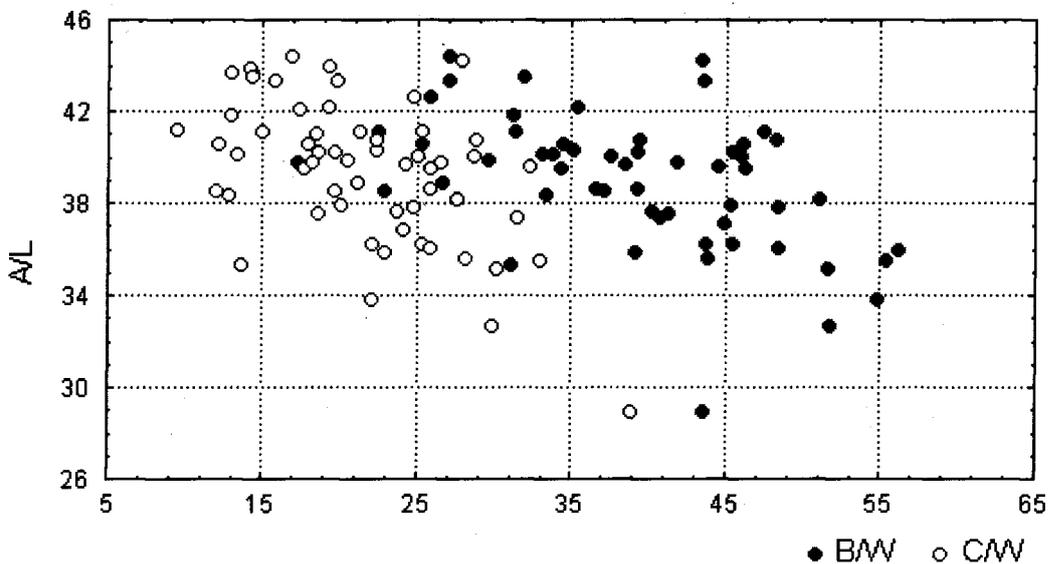


Figure 31
Mimomys tigliensis sp. nov., Tegelen. M/1. Scatter diagram of the B/W (black circles) and C/W (white circles) indexes and relative length of anteroconid (A/L).

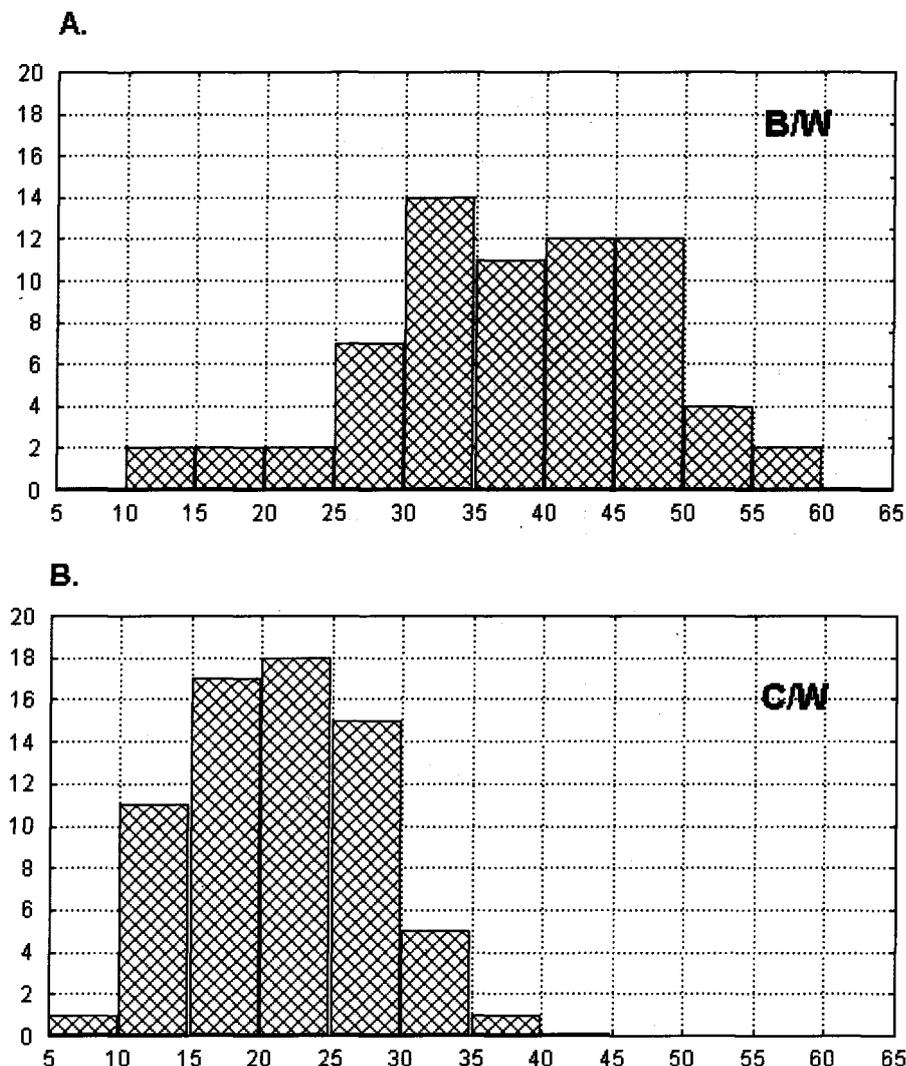
form to *M. newtoni*. The species was cited as *M. tornensis* by Kowalski & Nadachowski (1990). Recently the species was considered by Garapich & Nadachowski (1996) in accordance with the detailed comparison with co-occurring *Allophaiomys*. *Mimomys tornensis* from Kamyk differs from the Tegelen form its larger dimensions: mean value of length of M/1 is 2.69, n=51, range is 2.4 - 3.08 (The 17 specimens measured by Kowalski (1960) gave a mean value equal to 2.8); somewhat shorter anteroconid: A/L of Kamyk's *Mimomys* ranges from 26.2 to 40.4, with a mean of 37, n=51; presumably more abundant cement occurs in old individuals.

Mimomys haplodentatus, Aktogay, Kopaly section (Kojamkulova et al., 1988). The species from Late Villanyian - Earliest Biharian of Kazakhstan differs from *Mimomys tigliensis* sp. nov. in its larger dimensions (mean 2.85, range 2.7 - 3.1, n=12), in more abundant cement filling of re-entrants, and in shorter posterior lobe of M3/. There is a possible hypsodonty difference between the two main

levels with *M. haplodentatus* in Kopaly section. At least the upper bed (with *Allophaiomys*) material has markedly more advance stage of hypsodonty (HH-index of M/1 is more than 6.5 -7.0, personal observations) compared to *Mimomys tigliensis* from Tegelen (the maximum HH-index value is >6.41).

Mimomys blanci, Monte Peglia (Van der Meulen, 1973). This form is clearly different from *Mimomys tigliensis* in its somewhat smaller dimensions, less abundant cement, more gracile outlines of the occlusal surface, less oblique *Mimomys*-ridge in juvenile and young M/1, much less frequent morphotypes of M/1 with closed T4, more confluent T1-T2 and T3-T4 in M/2-M/3, more developed pleuro-rhiz position of the posterior root of M/2 (no difference in the depth of LRA1 and LRA2), less vergent re-entrants in M3/3 and less reduced labial re-entrants of M/3. *Mimomys blanci* is a late early Biharian derivative of the *Mimomys pusillus* lineage. The form is distinct from the *M. tigliensis - tornensis* group and shows some morphological

Figure 32
Mimomys tigliensis sp. nov.,
Tegelen. M/1. Frequency
histogram of B/W index (A),
and C/W index (B).



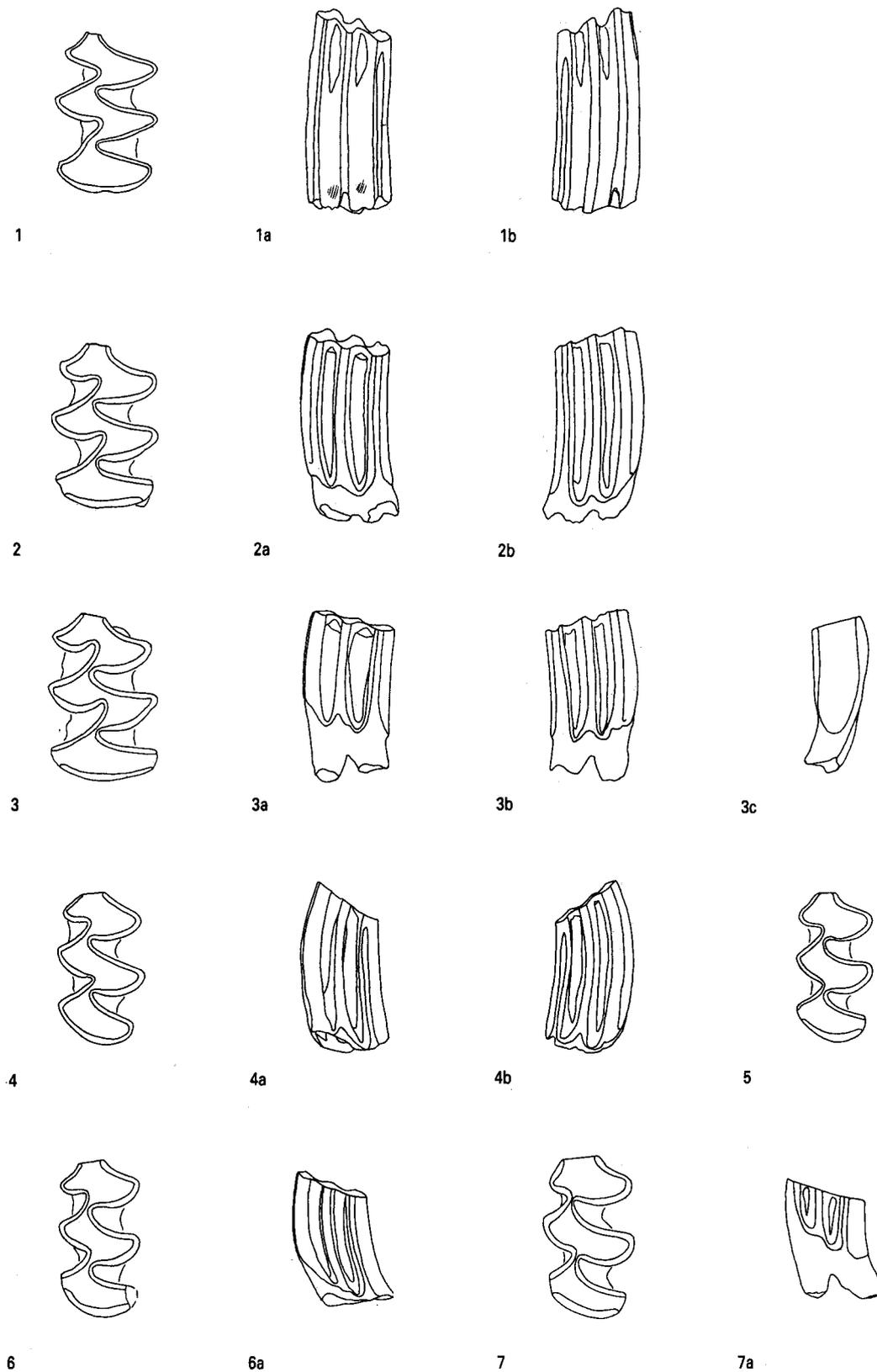


Figure 33

Lower molars (M/2 and M/3) of *Mimomys tigliensis* sp. nov., Tegelen.

1-3: M/2, 4-7: M/3, occlusal surface; 1a-4a, 6a, 7a: labial side; 1b-4b: lingual side; 3c: posterior side. - 1 - Te403, 2 - Te113, 3 - Te398, 4 - Te690, 5 - Te079, 6 - Te310, 7 - Te018. Occlusal view 15x, lateral view 7,5x.

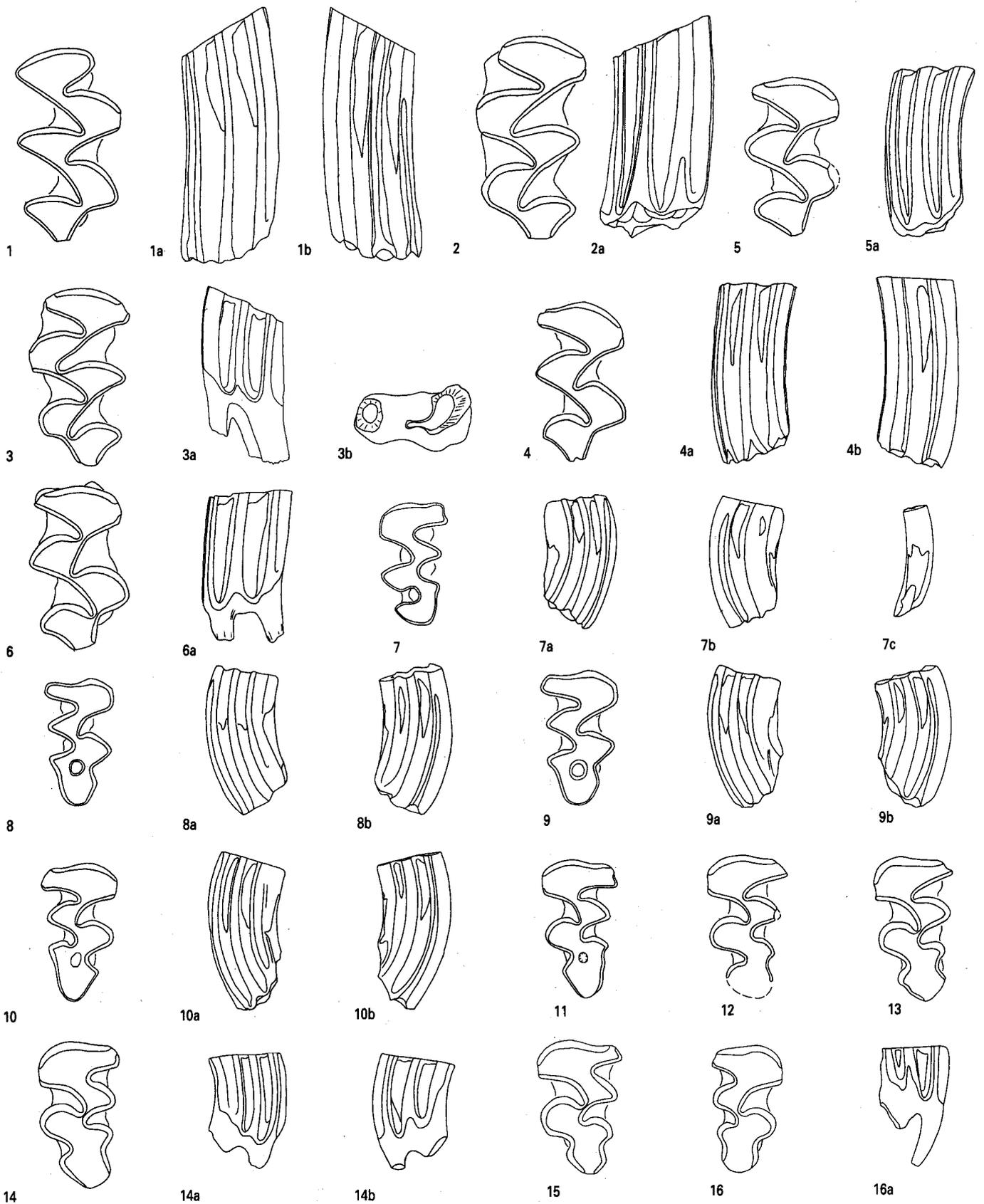


Figure 34

Upper molars (M1, M2/ and M3) of *Mimomys tigliensis* sp. nov., Tegelen.

1-3: M1, 4-6: M2, 7-16: M3; occlusal surface; 1a, 3a-10a, 14a: labial side; 1b, 2a, 4b, 7b-10b, 14b, 16a: lingual side; 7c: posterior side.

1 - Te607, 2 - Te457, 3 - Te155, 4 - Te389, 5 - Te427, 6 - Te507, 7 - Te336, 8 - Te332, 9 - Te334, 10 - Te124, 11 - Te126, 12 - Te476, 13 - Te572, 14 - Te020, 15 - Te351, 16 - Te296. Occlusal view 15x, lateral view 7,5x.

similarity resulting from parallel evolution in the direction of hypsodonty. In the geological record *Mimomys tigliensis* and *Mimomys blanci* are separated by a time interval of almost 1 million years.

Mimomys oswaldoreigi, Gilena 2 (Agusti et al., 1993). This form is different from the *Mimomys tigliensis* of Tegelen in its slightly larger size (mean - 2.71, range 2.61 - 2.82, n=11), slightly shorter anteroconid (A/L ranges from 36 to 41, mean 38, n=11) and mostly rootless M/1. The species is thought to represent a particular stage of an early Biharian endemic Spanish *Mimomys* lineage with rootless M/1 and still rooted M/3. In the author's opinion more material is needed to exclude combination of *Allophaiomys* first lower molars with *Mimomys* M/3.

Mimomys malezi, Tatinja Draga, Razvodje (Rabeder, 1983). This Early Biharian form from the Balkans is distinct from *Mimomys tigliensis* sp. nov. in its more abundant crown cement, less advanced stage of hypsodonty, different structure of anteroconid with prominent *Mimomys*-ridge and almost disconnected dentine field of the anterior loop, different structure of posterior lobe of M3/ without enamel islet and the almost disconnected posterior loop. The species is a very interesting endemic form from the Balkans. It has no direct relation with the lineage of *Mimomys tigliensis* - *Mimomys tornensis*.

Mimomys reidi, Tegelen. Co-occurrence of two species of small *Mimomys* from the Tegelen fauna makes it necessary to outline major distinctive features of both forms.

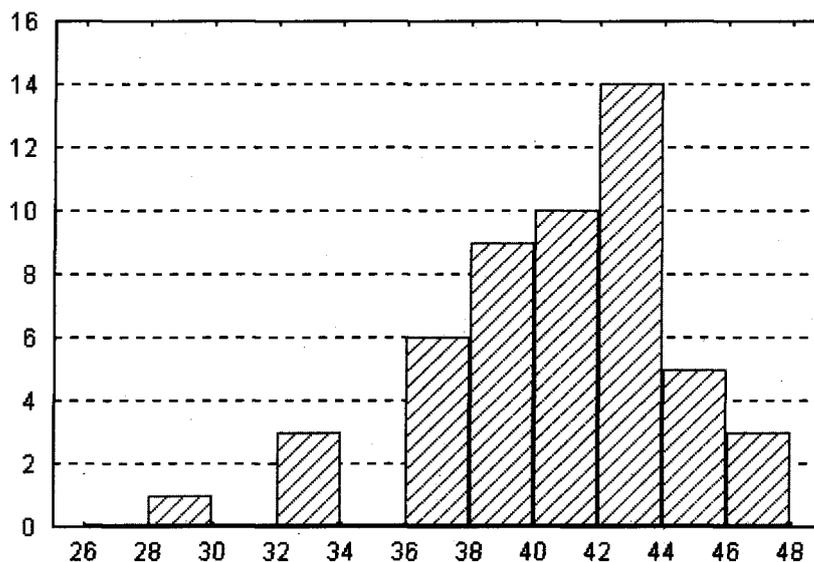


Figure 35
Mimomys tigliensis sp. nov., Tegelen. M3/. Histogram of the relative length of posterior lobe (Lp/L).

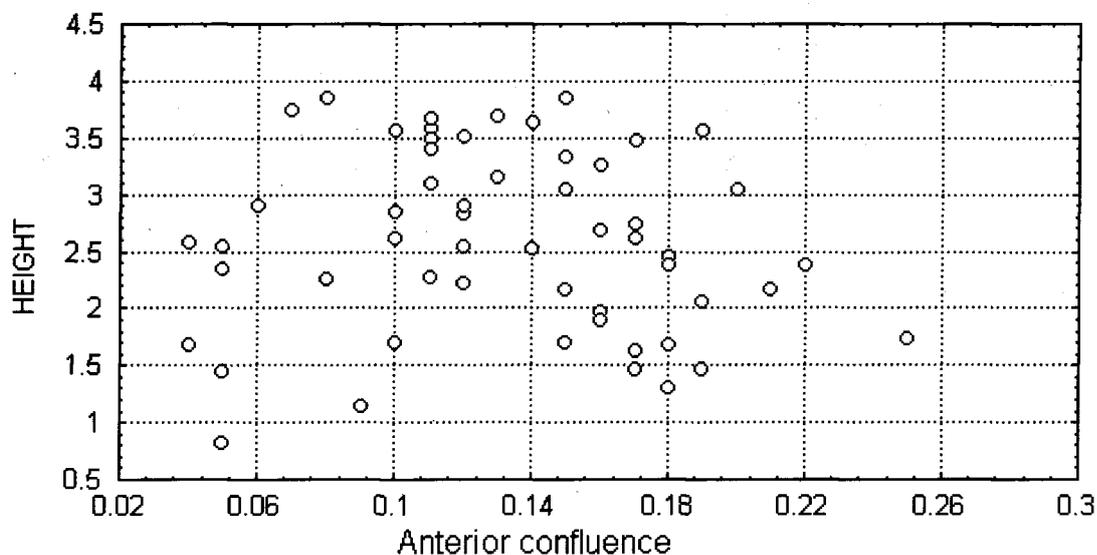


Figure 36
Mimomys tigliensis sp. nov., Tegelen. M3/. Scatter diagram of the anterior confluence (depth of BRA1) and crown height.

Figure 37
Mimomys tigliensis sp. nov.,
 Tegelen. M3/. Relationship of
 stages of the enamel islet
 development to crown
 height.

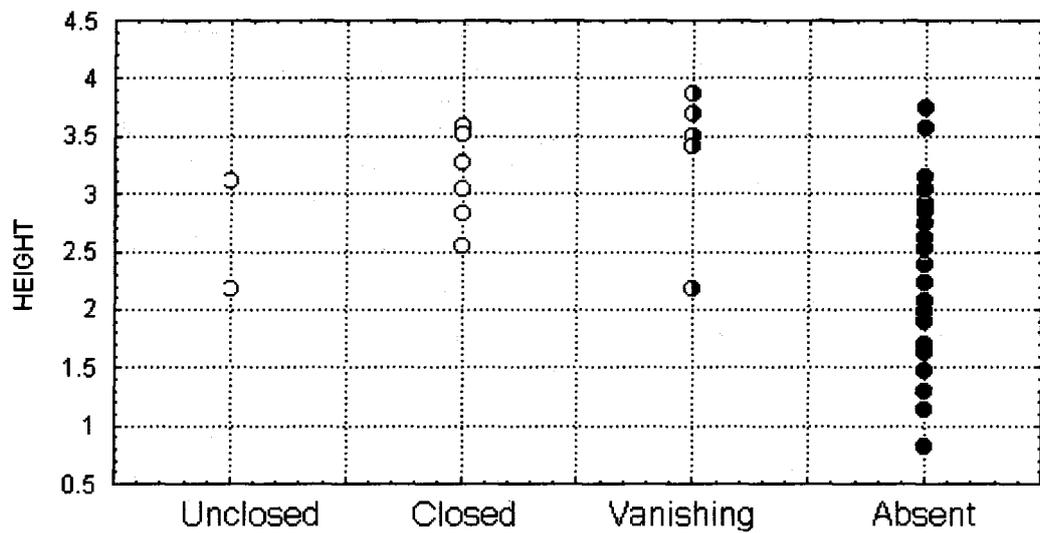


Table 20
 Size and dentine tracts
 measurements of
M. tigliensis nov. sp. from
 Tegelen and *M. tornensis*
 from Schernfeld.

	TEGELEN			SCHERNFELD			Difference in means (%)
	Mean	Range	n	Mean	Range	n	
M/1							
Length	2.59	2.22 - 2.92	63	2.66	2.33 - 3.04	214	- 2.6
A/L	39.28	28.90-44.40	63	39.22	34.5 - 44.8	214	+ 0.2
Hyposinulid		4.02->4.6		>4.49	3.77 - >4.95	10	
HH-index	>5.63	>4.42->5.63	56	>5.90		10	
M/2							
Length	1.71	1.53-1.89	56	1.73	1.56 - 1.93	50	- 1.2
HH-index	>5.14	>4.42->5.63	14	>5.47		14	
M/3							
Length	1.48	1.22 - 1.65	51	1.47	1.33 - 1.66	40	+ 0.7
HH-index	3.42	3.19 - 3.58	5	>3.60	2.90 ->4.35	14	
M1/							
Length	2.36	1.97 - 2.6	50	2.32	2.12 - 2.67	40	+ 1.7
Anterosinulus	4.26	3.91 - 4.50	5	>4.67	4.23 - >5.10	13	
PA-index		>6.80			>7.30	13	
M2/							
Length	1.80	1.57 - 2.00	56	1.88	1.72 - 2.02	40	- 4.3
PA-index		>7.27			>7.00	14	
M3/							
Length	1.61	1.34 - 1.82	51	1.67	1.33 - 1.79	100	- 3.6
PA-index		4.52 ->5.31		>5.26	4.86 - >5.7	15	

M. tigliensis differs from *M. reidi* in its much more abundant cement, much higher hypsodonty (in most specimens of *M. tigliensis* dentine tracts are interrupted by wear at early stages of root formation), in the absence of enamel islets in the anteroconid of M/1, two-rooted M1/ (mostly three-rooted in *M. reidi*), much more vergent re-entrants and thus more separated dentine fields of the occlusal surface. The higher vergence of the re-entrants leads to an artificially shorter posterior lobe of M3/ (measured from the tip of BRA2 to the posterior edge of the molar) in *M. tigliensis* compared with *M. reidi* (Figure 17). This measurement allows the differentiation of most of the M3/ of the two species.

Comments

Mimomys tigliensis is the most abundant species in the Tegelen fauna. The need to describe this species arises from the fact that the earlier names given to this form either designate the species of the other genus (*Borsodia newtoni*, see discussion in Mayhew & Stuart, 1986) or unrelated and geologically younger species (*Mimomys blanci*, Van der Meulen, 1973).

According to the view adopted here, *Mimomys tigliensis* represents the Late Villanyian vole ancestral to the Latest Villanyian *Mimomys tornensis*. In this opinion the writer follows Jánossy and Van der Meulen (1975). *Mimomys tigliensis* is less hypsodont than *Mimomys tornensis* which is detectable in the measurements of dentine tracts, frequencies of the occlusal morphotypes and the less abundant crown cement. *Mimomys tigliensis* is also slightly smaller than its presumed descendant. Those systematists who prefer to unite all stages of a phyletic lineage by a single species name would inevitably consider *Mimomys tigliensis* as at most a subspecies of *Mimomys tornensis*. However, the author thinks that the obvious morphological differences in phyletic lineages deserve a taxonomic reflection in order to increase the precision of studies.

As is evident from the comparison, it is difficult to evaluate differences between most relevant populations and/or samples because of the lack of data on hypsodonty of these forms. In some cases the taxonomic assignment of a certain sample to *M. tigliensis* or to *M. tornensis* was done on the basis of the biochronological position of a fauna assemblage. This is a limitation of the present state of knowledge.

Rabeder (1986) and Carls & Rabeder (1988) postulated the origin of the rootless *Allophaiomys* from *Mimomys tornensis* in the course of autochthonous phyletic evolution in Central Europe. The hypothesis is substantiated by numerous morphological similarities in the dentition of *Mimomys tornensis* and early *Allophaiomys*. No major objectives can be raised against this idea in general. It is likely that one or several stems of rootless forms of *Microtus s.l.* originated from a species of *Tcharinomys* somewhere in the middle latitudes of Eurasia. However, in Central Europe the first primitive *Allophaiomys* co-occur with

Mimomys tornensis in a number of Latest Villanyian faunas (Villany 5, Neulingen, Kamyk, Vceláre 5, etc.). Carls & Rabeder (1988) assumed that in these assemblages the single transitional form is present with a high percentage of individuals lacking signs of root formation. In this context it should be noted that the first *Allophaiomys* do not conform to hypsodont *Tcharinomys* among other features in having less abundant cement, a disconnected anterior loop and a T2 in M3/ and a different frequency of M3/ morphotypes. In all the presumably transitional populations of *Mimomys tornensis*, the morphotype of M3/ with the deep LRA2 is very rare. On the contrary in the first *Allophaiomys* this morphotype is common or predominant. Special study of one of these 'transitional' faunas (Kamyk, in Poland) rejected this hypothesis and confirmed co-occurrence of *Mimomys* and *Allophaiomys* (Garapich & Nadachowski, 1996). Furthermore, in the well studied Late Villanyian - Early Biharian faunal transition in the south-eastern Europe (Topachevsky et al., 1987, Tesakov, 1993a, Recovets, 1994) the first *Allophaiomys* appear migratorially and no hypsodont *Mimomys* ex gr. *tornensis* are present in the preceding faunas.

Further detailed studies of transitional faunas and forms like *M. haplodentatus* from Kazakhstan will most probably elucidate the problem of the origin of *Microtus s.l.*

Genus *Pitymimomys* nov. gen.

Derivatio nominis

The name combines two roots: *Pitymys* and *Mimomys*, indicating the *Pitymys*-like confluences of the occlusal surface.

Diagnosis

The genus of medium sized voles, having characteristically broadly confluent triangles T2 - T3 (proto- and metaconids) in the first lower molars, T1 - T2 (proto- and paracones) in the first upper molars, and T2 - T3 (para- and hypocones) in the second and the third upper molars and moderate cement accumulation. In less advanced species the BRA3 in M/1, and BRA1 and LRA2 in M3/ are reduced with the formation of an enamel islet.

Differential diagnosis

Pitymimomys differs from all genera of the *Mimomys* group in its characteristic confluence pattern. *Pitymimomys* differs from *Mimomys* by the presence of the anterior enamel islet in M3/ in phylogenesis, by sparse cement and by the less developed *Mimomys* differentiation of enamel; from *Cseria* and *Borsodia* by the presence of crown cement; from *Borsodia* also by the presence of the enamel islet in the anteroconid of M/1 in phylogenesis and from *Cromeromys* in the persistent reduction of LRA2 in M3/ through insulation.

Type species

Mimomys pitymyoides Jánossy and Van der Meulen, 1975; Late Villanyian, Osztramos 3, Hungary.

Species content

P. altenburgensis (Rabeder, 1981), *P. baschkiricus* (Suchov, 1970), *P. stranzendorfensis* (Rabeder, 1981), *P. stenokorys* (Rabeder, 1981), *P. jota* (Rabeder, 1981), *P. pitymyoides* (Jánossy et Van der Meulen, 1975).

Comments

The subgenus *Pusillomimus* erected by G. Rabeder (1981) for this group, was based on *Mimomys (Microtomys) pusillus* Von M  hely, 1914, the type species of *Microtomys* Von M  hely. Therefore, *Pusillomimus* is a younger synonym of *Microtomys*. As is evident from the geological record, *M. pusillus* have been derived from *M. reidi* and is unrelated to the *P. pitymyoides* group. Two lineages developed in parallel during the Late Pliocene. In this situation a new name for the 'pitymyoide' group is required. The genus was apparently derived from a species related to *Cseria* at the end of the Ruscinian to the beginning of the Villanyian.

A further complication of the taxonomic situation with the 'pitymyoides' group is the genus *Laguropsis* Kretzoi. Originally described as *Lagurus pannonicus* from the Gundersheim locality by Heller (1936), the single rootless specimen then served as a basis for the new species of steppe lemmings, *Lagurodon helleri* (Kretzoi, 1956). Then Kretzoi simply listed this species as *Laguropsis helleri* (Kretzoi, 1962). He noted the confluent triangles of the type specimen and compared it with *L. arankae* (Kretzoi, 1956). The Villanyian appearance of the accompanying fauna allowed Gromov & Polyakov (1977) to question the validity of this lagurine genus; the occlusal morphology of the type specimen resembles juvenile *P. pitymyoides* (see Heller, 1936, 1968). According to Storch & Fejfar (1990), the *P. pitymyoides* group is present in the Late Villanyian part of the material from this taphonomically-mixed locality. Therefore, there is a possibility that the specimen mentioned as *Laguropsis helleri* is in fact a juvenile molar of *P. pitymyoides*. No description and any other formal actions accompanied

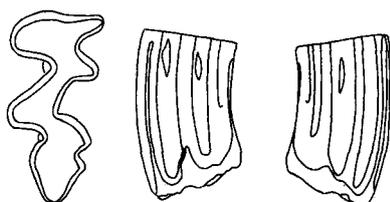


Figure 38

Pitymimomys pitymyoides, Tegelen.

M3/1 - 1 - occlusal surface, 2 - labial side, 3 - lingual side. - Te094.

Occlusal view 15x, lateral view 7,5x.

the mentioning of '*Laguropsis*'. Bearing in mind the taphonomic situation at the locality and the juvenile appearance of the type, the name *Laguropsis* should be regarded as *nomen nudum* and *nomen dubius* belonging only to the type specimen.

Pitymimomys pitymyoides

(Jánossy et Van der Meulen, 1975) Figure 38.

Studied material

Tegelen, 1 M3/, Te094.

Description

The single M3/ present is characterized by distinct confluence of all elements of the occlusal surface (Figure 38: 1). The cement accumulations are very sparse. The molar is at the beginning of the rhizodont stage of root formation. Length 1.36, width - 0.82, the length of posterior lobe 0.79, the crown height 2.69, the height of roots 0.25, the height of distosinus >2.07, the height of anterosinus \geq 2.69, the height of protosinus 2.5 and the PA-index \geq 3.67 (all measurements in mm).

Comparison

The occlusal surface of the M3/ from Tegelen closely fits the morphology of the type material from Osztramos 3 (Jánossy & Van der Meulen, 1975), although measurements of dentine tracts have been published. The dentine tracts of the specimen from the Tegelen fauna are distinctly higher than those known for *P. jota* from Stranzendorf I (Rabeder, 1981).

Comments

This species is extremely rare in the fauna ($n=1$). It is fairly frequent in the European faunas of the Late Villanyian. This form is first encountered in the Dutch fossil record in the Zuurland borehole (Van Kolfschoten & Van der Meulen, 1986, Hordijk, 1993). Van Kolfschoten (1988) suggested that the presence of *Mimomys pitymyoides* in the late Tiglian of the Zuurland borehole may indicate a slightly younger age of these faunas compared to the Tegelen fauna, where no *P. pitymyoides* was known at that time. The recognition of the species in the Tegelen fauna indicates that the rarity of the group in the Dutch Tiglian faunas is apparently due to ecological rather than stratigraphical reasons.

Recently the known geographical range of the species was significantly broaden. Apart from the dense Central European record, it has been recognized in the Villanyian faunas of the East Anglian Crags (Mayhew & Stuart, 1986), North Italy (Sala et al., 1994), Greece (Van der Meulen & Van Kolfschoten, 1986), Romania (Radulesco & Samson, 1986), Moldavia (Mikhaillesku & Markova, 1992) and North Caucasus (Tesakov, 1994). In 1967 Kretzoi described a new species, *Mimomys valeriani* for two teeth from the Bzhe-dukhovskaya locality in the North Caucasus. The locality

is only about 30 km east of the well known Psekups locality which has yielded remains of true *P. pitymyoides* (Vangengeim et al., 1990; Tesakov, 1994). Both localities have very similar geological situations (Lebedeva, 1963). The juvenile specimen of the lower M/1, described by Kretzoi, closely fits the morphology of *M. pitymyoides*. However, no illustrations were given. As both the type materials and type locality of this species have not been revised since their original description, it is proposed that the name *P. pitymyoides*, which is widely used among European palaeontologists, is preserved.

Genus *Clethrionomys* Tilesius, 1850

Clethrionomys kretzoi (Kowalski, 1958)

Figures 2B, 39-46, Tables 21 - 27.

1958 *Dolomys kretzoi* n. sp.; K. Kowalski, An Early Pleistocene...: p. 27-29, Fig. 14-15.

1976 *Pliomys kretzoi*; L. Alexandrova, Rodents of Anthropogene...: p. 44-45, Fig. 19, partim.

1988 *Clethrionomys kretzoi*; N. Carls & G. Rabeder, Die Arvicoliden ...: p. 148-157, Abb. 15-22.

1989 *Clethrionomys* sp.; V.A. Topachevsky & V.A. Nesin, Rodents of the Moldavian and ...: p. 71-73, Fig. 27.

1996 *Clethrionomys kretzoi*; A.S. Tesakov, Evolution of bank voles...: p. 2-6, Fig. 1-2.

Studied material

Tegelen, 45 M/1, 35 M/2, 23 M/3, 34 M1/, 25 M2/, 26 M3/.

Description

Vole of small dimensions (see Tables 21-26, Figure 39). Cement accumulations are moderate, usually not more than half of the re-entrants. The enamel band is thin in younger specimens, becoming thicker with wear. It is slightly thicker on the trailing edges of the triangles (so-called *Miomys* or negative type). Dentine fields of occlusal surface are commonly connected by spaces, which are wider than the width of the enamel band.

Age distribution

Root formation stages. Most of molars show the well rooted (rhizodont) condition (Figure 2B). On average for all molars, the first unrooted (arhiz) stage is represented by 8.1% of molars (n=15), the intermediate (merorhiz) stage - by 13% (n=24), and the rhizodont situation is observed in 78.9% (n=146) of molars.

The crown height distribution is presented in Figure 40. In most molars the situation is close to the classical attritional profile (Korth & Evander, 1986). Attritional mortality profile implies two peaks: one for the vulnerable group of young individuals, and the second corresponding to higher senility mortality. The only clear exception in this

material is the second upper molar. However, this molar type is poorly represented in the collection.

Dentine tracts

The information on dentine tracts is summarized in the sinogram (Figure 41).

M/1

The anteroconid complex consists of a broadly confluent anterior cap and anteroconid triangle (T4 and T5). The anterior cap is of variable form. In young specimens incipient re-entrants (BRA4 and LRA5) may occur (Figure 24: 1 - 3). They are, however, very shallow and soon disappear with wear. In juvenile animals the anterior cap may have a mushroom-like form, n=2, (Figure 42: 1). The relative length of anteroconid (A/L) shows a gradual decrease with wear (Figure 43). The mean value of the A/L index is 43.41, n=37. The confluence of the anterior cap (B) and the anteroconid triangles (C) slowly increases with individual age; This is particularly obvious when plotted against A/L (Figure 44). The dentine fields of the basic triangles (T1-T2-T3) are broadly connected. The confluence of T1 and T2 is often the widest. The dentine tracts are relatively low. They are interrupted by wear when the root shafts are well developed. Sometimes the anterosinuid may have a slightly bifurcated form.

M/2

The molar is of typical form. It consists of the posterior lobe and two pairs of widely confluent triangles (T1-T2 and T3-T4). The confluences between the posterior lobe and T1, and between T2 and T3 are more narrow (Figure 42: 9 - 11). The posterior root is distinctly placed on the upper face of the lower incisor, with the tendency to the labial shift: acrorhiz or semipleurorhiz condition (Figure 42: 10d, 11d). Because of the tight connection of the lingual part of the posterior root and the incisor, the LRA1 may be slightly (0.1 - 0.2 mm) more shallow than LRA2 when viewed from the lingual side.

M/3

The molar is composed of the posterior lobe and 4 triangles. T1-T2 and T3-T4 are broadly confluent (Figure 42: 12 - 14). In very young specimens the LRA3 is present. It disappears with wear. After the formation of the root shafts, they normally show no signs of fusion.

M1/

The occlusal surface is composed of the anterior loop and four alternating triangles (Figure 45). LRA3 is developed in more than half of the studied molars. The dentine fields of the occlusal surface are broadly fused in juvenile molars (Figure 45: 1) and moderately separated in older ontogenetic stages. One molar demonstrates an aberrant additional loop on the anterior loop (Figure 45: 3). This structure has its own dentine tract running along its fron-

tal face. Most of the molars (n=26) have three roots. The middle (protocone) root is typically situated at an equal distance from both the anterior and posterior roots (Figure 45: 3b, 4b). Rarely (n=5) the middle root is closer to the anterior root. In one case the anterior and the middle roots are fused and have a common pulp cavity.

M2/

The occlusal surface is formed by the anterior lobe and three alternating triangles. LRA2 is well developed and BRA3 is only present in very young specimens (Figure 45: 5). The dentine fields are strongly confluent in the juvenile condition (Figure 45: 5) and more separated with subsequent wear. The connection between T2 and T3 is normally the broadest. Two roots. The anterior root is typically rounded in cross-section. In one case it is distinctly transversely flattened and has an inner groove.

M3/

The molar is formed by the anterior lobe, two alternating triangles, and the posterior loop of variable form. The posterior lobe consists of T4 and the posterior loop. Though all the occlusal elements are distinctly confluent, the connections between the dentine fields of the anterior lobe and T2, and between T3-T4 are the broadest. The anterior confluence (anterior loop-T2) is increasing with wear. In one case the BRA1 is reduced with the formation of the enamel islet (Figure 45: 9).

The connection between T3 and T4 is constantly broad with a slight tendency to increase with the ontogenetic age. The length of the posterior lobe (or talon complex) slightly increase in older animals (Figure 46). The average relative length of the posterior lobe (Lp/L) is 53.5 (n=24).

The variable shape of the posterior loop enables to distinguish three morphotypes. They partly follow the system of Carls & Rabeder (1988, see 'comparison'):

1. simplex (Figure 27: 1, 3). LRA3 and BSA4 are undeveloped or incipient (n=7, 26.9%).
2. praehintonianus (Figure 27: 2, 5, 6) LRA3 is mostly weakly expressed. BSA4 well developed (n=11, 42.3%).
3. hintonianus (Figure 27: 4). LRA3 and BSA4 are well developed (n=4, 15.4%).
4. Some specimens demonstrate the condition intermediate between the morphotypes 2 and 3 (n=4, 15.4%).

The posterior dentine tract (distosinus) has a bilobate form typical of *Clethrionomys*. In most cases the posterior tract is only slightly bifurcated (Figure 45: 10c). In some cases the two lobes of the tract are well separated and shifted on the labial and lingual sides of the posterior prism (Figure 45: 9a-b).

Comparison

The molars of the bank vole from Tegelen show typical features of the species *Clethrionomys kretzoi* (Kowalski, 1958). They are: small dimensions, broadly confluent ele-

ments of anteroconid in first lower molars, acrorhiz position of the posterior root of M/2 on the incisor, short and simply built posterior lobe in M3/ and low dentine tracts.

Cl. kretzoi (Kowalski, 1958) from Kadzielnia. The occlusal structure does not differ from the Tegelen material. The Tegelen form may be somewhat smaller; the mean length of M/1 is 2.19 (n=37) compared to 2.27 (n= 10) (calculated from: Kowalski, 1958). The data on hypsodonty of the typical form was published by Carls & Rabeder (1988) as a sinugram. They also gave the mean HH-index for this form: 2.21 (n=20). Judging from this, and also from personal observation it may be tentatively concluded that the type form is slightly less hypsodont than that from Tegelen, which shows the mean HH-index of 2.99 (n=12).

Cl. kretzoi from Schernfeld. The very detailed description of the Schernfeld material enables a close comparison with the Tegelen data. The principle measurements and indices for both forms are given in Table 27.

Cl. kretzoi from Psekups. Another example of the close resemblance to the Tegelen form. The North Caucasian vole may be slightly larger (the mean length of M/1 is 2.37, n=7). The mean HH-index is 2.93 (n=5) (Tesakov, 1996). All other measurements fall into the range of the Tegelen form.

Cl. kretzoi from Liventzovka 2. L.P. Alexandrova (1976) described a small vole under the name *Pliomys kretzoi*. The mean length of the M/1 is 2.31 (n=13). HH-index ranges from 2.78 to 3.61, with a mean of 3.34 (n=8). Thus, the form seems to be slightly more hypsodont than the Tegelen example and the form from Psekups (Tesakov, 1996).

Cl. kretzoi from Kotlovina 3. The small vole described by Topachevsky & Nesin (1989) has the characteristic morphology of *Cl. kretzoi*. The form, however, shows larger dimensions (mean length of M/1 is 2.43, n=14). HH-index of M/1 ranges from 3.08 to 3.99, with the mean 3.51 (n=8) (Tesakov, 1996).

Clethrionomys mirus and **Clethrionomys** aff. **kretzoi** from Aktogay, South Kazakhstan. Kojamkulova, Savinov, Tutkova and Pak (1987) described *Clethrionomys* molars from the Latest Villanyian - Early Biharian locality Aktogay. In the author's view both forms are conspecific and may be considered as *Cl. mirus* Savinov et Tutkova, 1987. This form is similar to *Cl. kretzoi* in broad confluence of the anteroconid triangles (T4-T5) and the simple structure of upper M3/ : morphotype *simplex* of the posterior lobe and broad confluence of T3-T4. Contrary to *Cl. kretzoi*, the vole from Kazakhstan is larger (the mean value of length of the lower M/1 is 2.5, n=10), has broader confluences of the basic triangles T2-T3 (sometimes T1-T2-T3 are conflu-

ent altogether forming the single dentine field) and a broader confluent anterior loop and T2 in the upper M3/. The most substantial difference is the much more advanced stage of hypsodonty in the Central Asian vole: the HH-index ranges from 3.5 to 4.5 (personal observations), which is indeed higher than in modern *Cl. glareolus* even taking into account the larger size of *Cl. mirus*. The combination of primitive and evolved characters clearly indicates the independent position of *Cl. mirus*. The steppe type character of the accompanying fauna, together with markedly-developed hypsodonty (so far unmatched by any other described Late Villanyian - Early Biharian *Clethrionomys*), support the assumption that *Cl. mirus* was adapted to open landscapes. It is therefore not impossible

to interpret *Cl. mirus* as an ancestor of one of the modern *Alticola* lineage's. The additional material from the Novaya Shulba locality in eastern Kazakhstan (the mixed Villanyian-Early Biharian association) ascribed to *Cl. mirus* (Tutkova, 1988), does not seemingly belong to the species.

Comments

This is the second most common species in the Tegelen vole assemblage. It is a very typical late Villanyian species, close to the type population from Poland and to the South Russian samples from the Psekups and Liventzovka 2 localities. The M/1 have broadly fused elements of anteroconid.

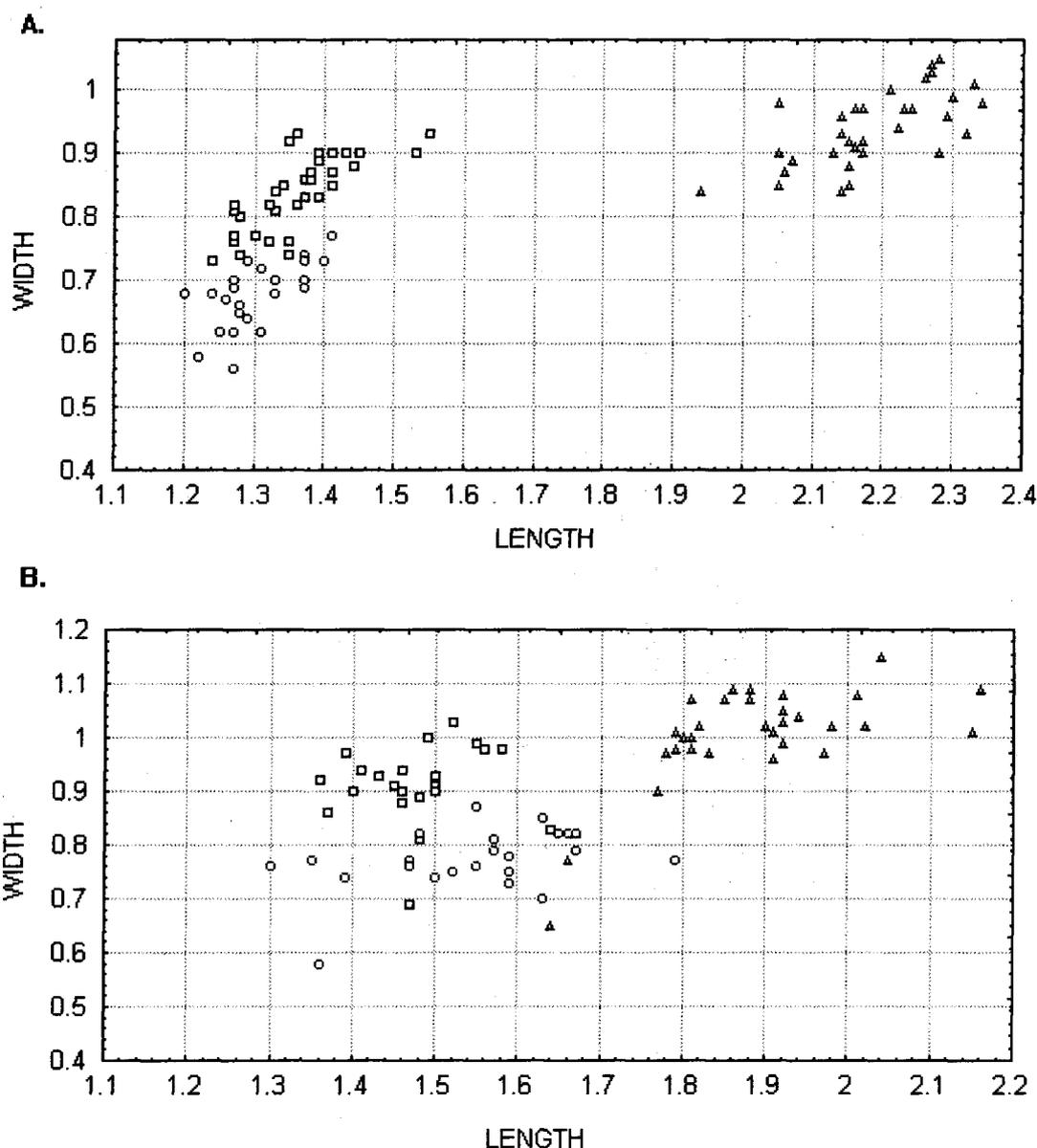


Figure 39
Clethrionomys kretzoi,
Tegelen. Scatter diagram of
length and width.
A - Lower molars, B - Upper
molars. Triangles - M1/1,
squares - M2/2, circles - M3/3.

Table 21
Dimensions of
Clethrionomys kretzoi,
Tegelen, M/1.

Variable	n	Mean	Minimum	Maximum	Standard deviation	Standard error
Length	37	2.19	1.94	2.34	0.09	0.02
Width	42	0.94	0.82	1.05	0.06	0.01
Anteroconid index	37	43.41	37.45	47.83	2.78	0.46
Anterosinuid	10	2.20	1.96	2.50	0.21	0.07
Hyposinuid	12	2.16	1.74	2.50	0.19	0.06
Hyposinulid	17	2.03	1.58	2.46	0.24	0.06
HH-index	12	2.99	2.35	3.51	0.29	0.08

Table 22
Dimensions of
Clethrionomys kretzoi,
Tegelen, M/2.

Variable	n	Mean	Minimum	Maximum	Standard deviation	Standard error
Length	34	1.36	1.24	1.55	0.07	0.01
Width	35	0.84	0.73	0.93	0.06	0.01
Anterosinuid	13	2.10	1.58	2.45	0.23	0.06
Hyposinuid	15	1.68	1.33	1.90	0.16	0.04
Hyposinulid	16	1.70	1.44	2.15	0.19	0.05
HH-index	14	2.37	1.96	2.77	0.21	0.06

Table 23
Dimensions of
Clethrionomys kretzoi,
Tegelen, M/3.

Variable	n	Mean	Minimum	Maximum	Standard deviation	Standard error
Length	23	1.30	1.20	1.41	0.06	0.01
Width	23	0.68	0.56	0.77	0.05	0.01
Anterosinuid	6	1.93	1.74	2.17	0.15	0.06
Hyposinuid	11	1.00	0.65	1.25	0.16	0.05
Hyposinulid	13	1.01	0.82	1.20	0.13	0.04
HH-index	11	1.43	1.05	1.65	0.18	0.06

Table 24
Dimensions of
Clethrionomys kretzoi,
Tegelen, M1/.

Variable	n	Mean	Minimum	Maximum	Standard deviation	Standard error
Length	32	1.88	1.64	2.16	0.12	0.02
Width	34	1.00	0.65	1.15	0.10	0.02
Anterosinus	15	2.03	1.85	2.50	0.18	0.05
Anterosinulus	17	1.63	1.34	2.01	0.16	0.05
Protosinus	18	1.78	0.38	2.28	0.42	0.10
Distosinus	12	2.41	2.17	2.70	0.18	0.05
PA-index	15	2.73	1.89	3.38	0.36	0.09

Table 25
Dimensions of
Clethrionomys kretzoi,
Tegelen, M2/.

Variable	n	Mean	Minimum	Maximum	Standard deviation	Standard error
Length	23	1.47	1.36	1.64	0.07	0.01
Width	25	0.92	0.69	1.03	0.07	0.01
Anterosinus	6	2.00	1.58	2.28	0.25	0.10
Protosinus	5	1.82	1.63	2.07	0.18	0.08
Distosinus	4	1.94	1.79	2.23	0.20	0.10
PA-index	5	2.76	2.50	3.00	0.22	0.10

Table 26
Dimensions of
Clethrionomys kretzoi,
Tegelen, M3/.

Variable	n	Mean	Minimum	Maximum	Standard deviation	Standard error
Length	24	1.55	1.30	1.79	0.12	0.02
Width	25	0.77	0.58	0.87	0.06	0.01
Anterosinus	12	1.48	0.63	1.90	0.33	0.09
Protosinus	15	1.22	0.54	1.63	0.29	0.08
Distosinus	16	0.71	0.33	1.33	0.22	0.06
PA-index	12	1.92	0.83	2.31	0.42	0.12

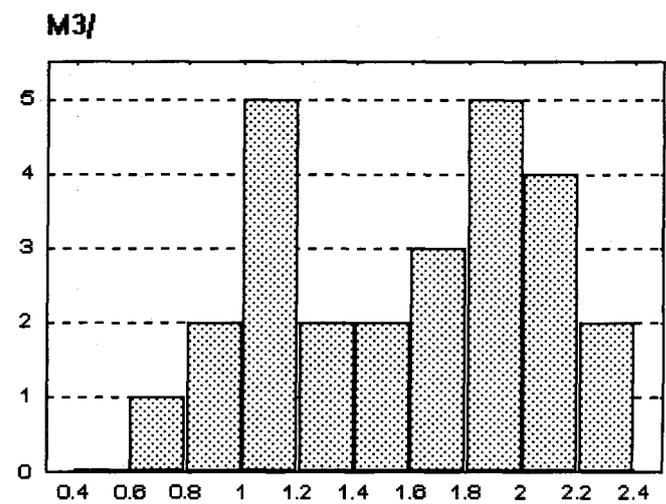
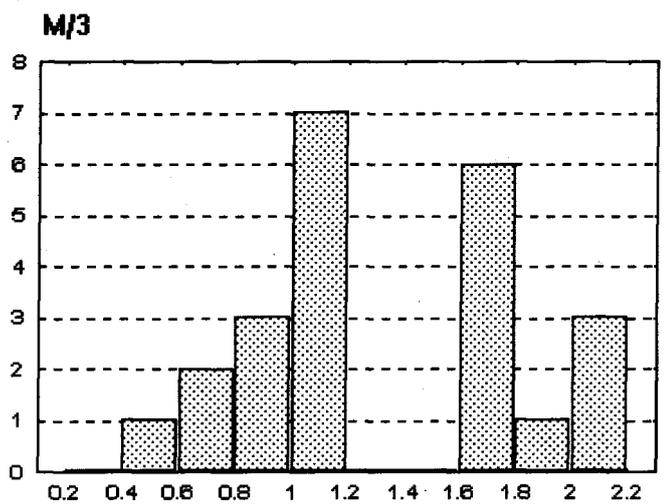
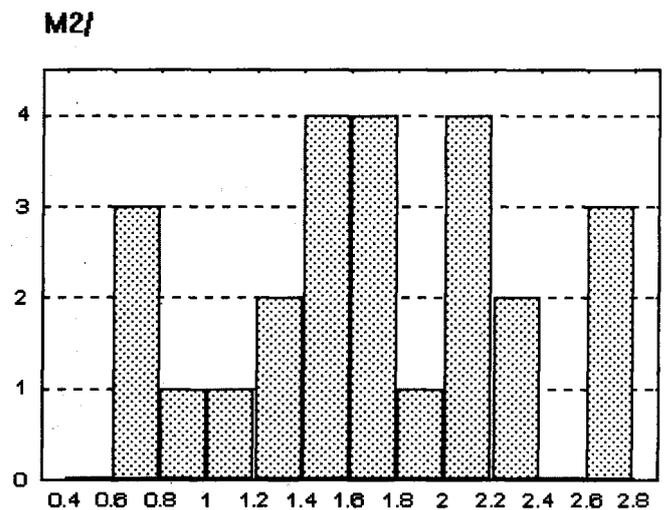
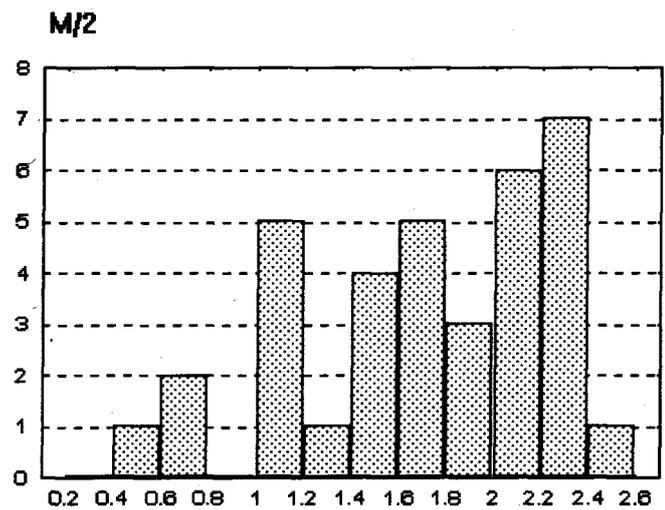
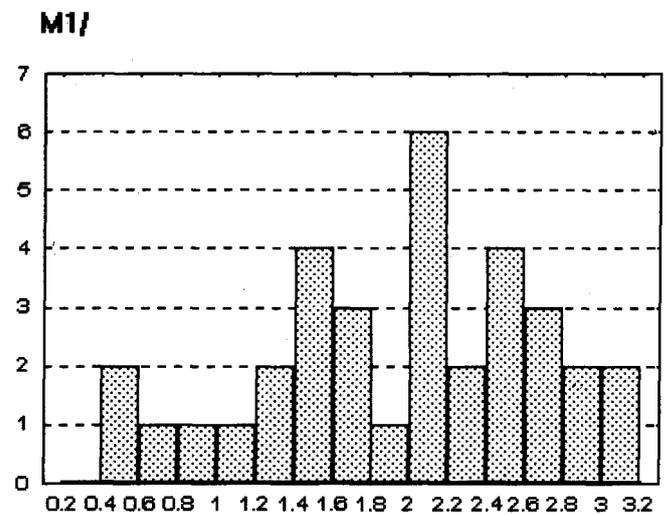
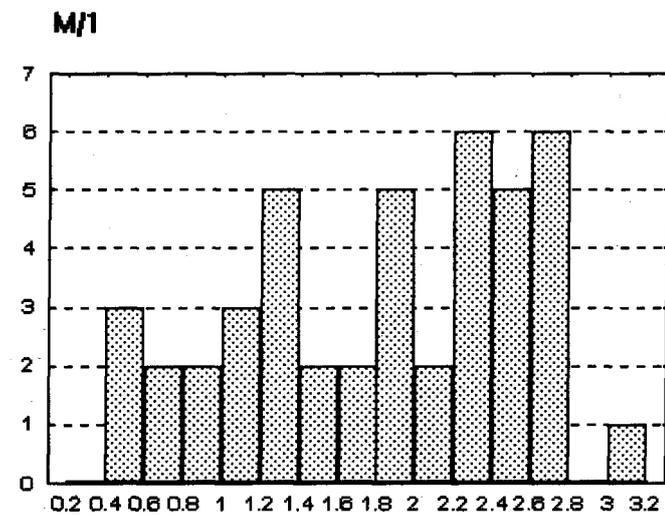


Figure 40
Clethrionomys kretzoi, Tegelen. Frequency histogram of crown height.

The taxonomy of small *Clethrionomys* of the Late Pliocene is complicated by numerous described forms, most of which are insufficiently known. Here the writer follows Rabeder (1981) and Carls & Rabeder (1988) in synonymizing most of the Late Pliocene (MN17) species in the single form, *Cl. kretzoi* (Kowalski, 1958).

It is worth noting that the small *Clethrionomys* from eastern Europe are typically larger than the corresponding forms from western Europe. This eastward increase of dimensions may be a manifestation of forest-steppe conditions in eastern Europe in comparison to the true forest environment of western regions.

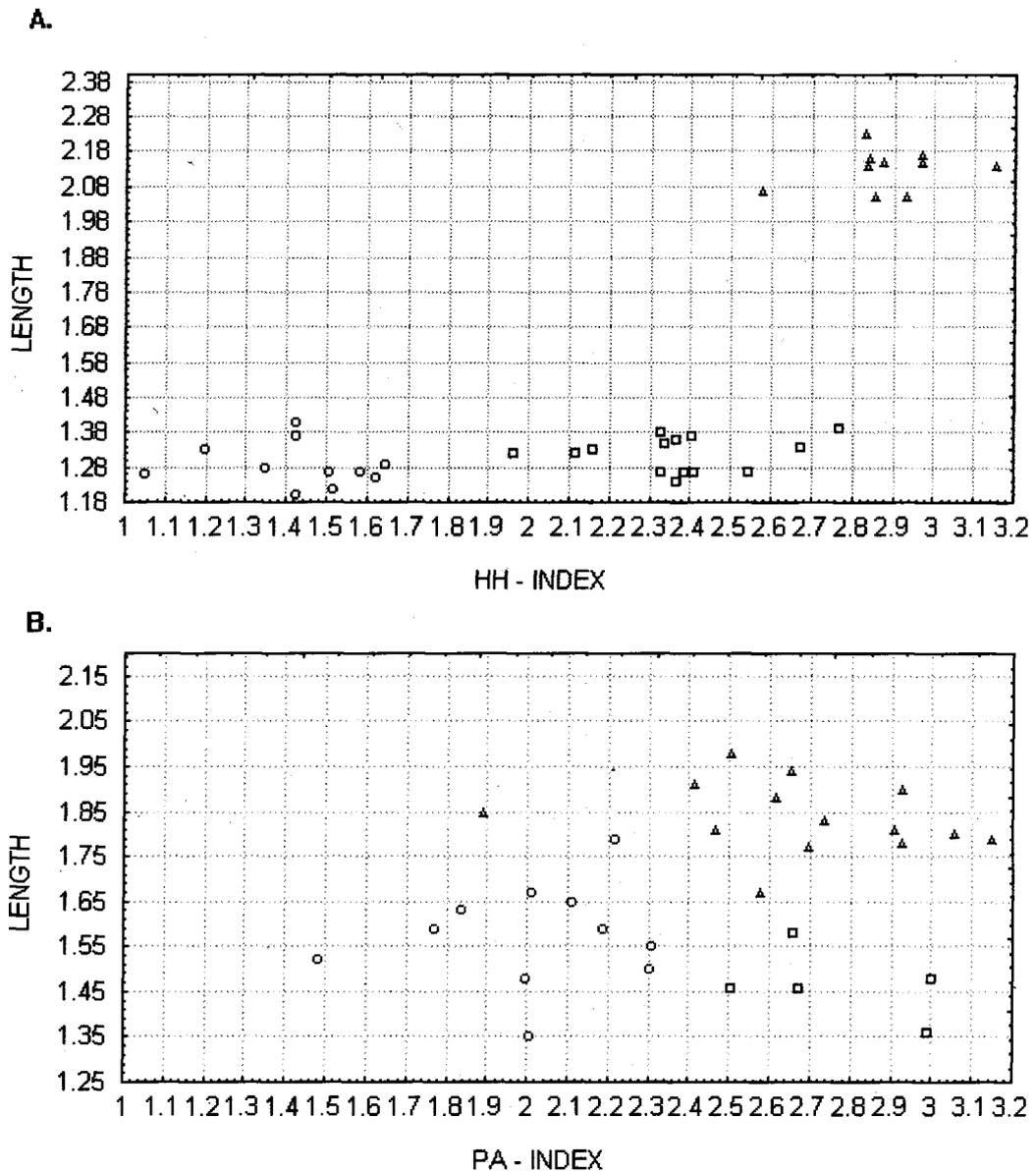
In general, *Cl. kretzoi* is one of the earliest known mem-

bers of the modern *Cl. glareolus* evolutionary line (Rabeder, 1981; Carls & Rabeder, 1988). The lineage shows a very rapid increase in hypsodonty in the late Villanyian (Tesakov, 1996). This allows the differentiation of even the temporally very close populations, such as those at Tegelen and Schernfeld.

Genus *Ungaromys* Kormos, 1932

These are small arvicolines with thick mostly radial enamel, broadly confluent elements of occlusal surfaces of molars and lacking cement.

Figure 41
Clethrionomys kretzoi,
Tegelen. Sinugram. A - Lower
molars, B - Upper molars.
Triangles - M1/1, squares -
M2/2, circles - M3/3.



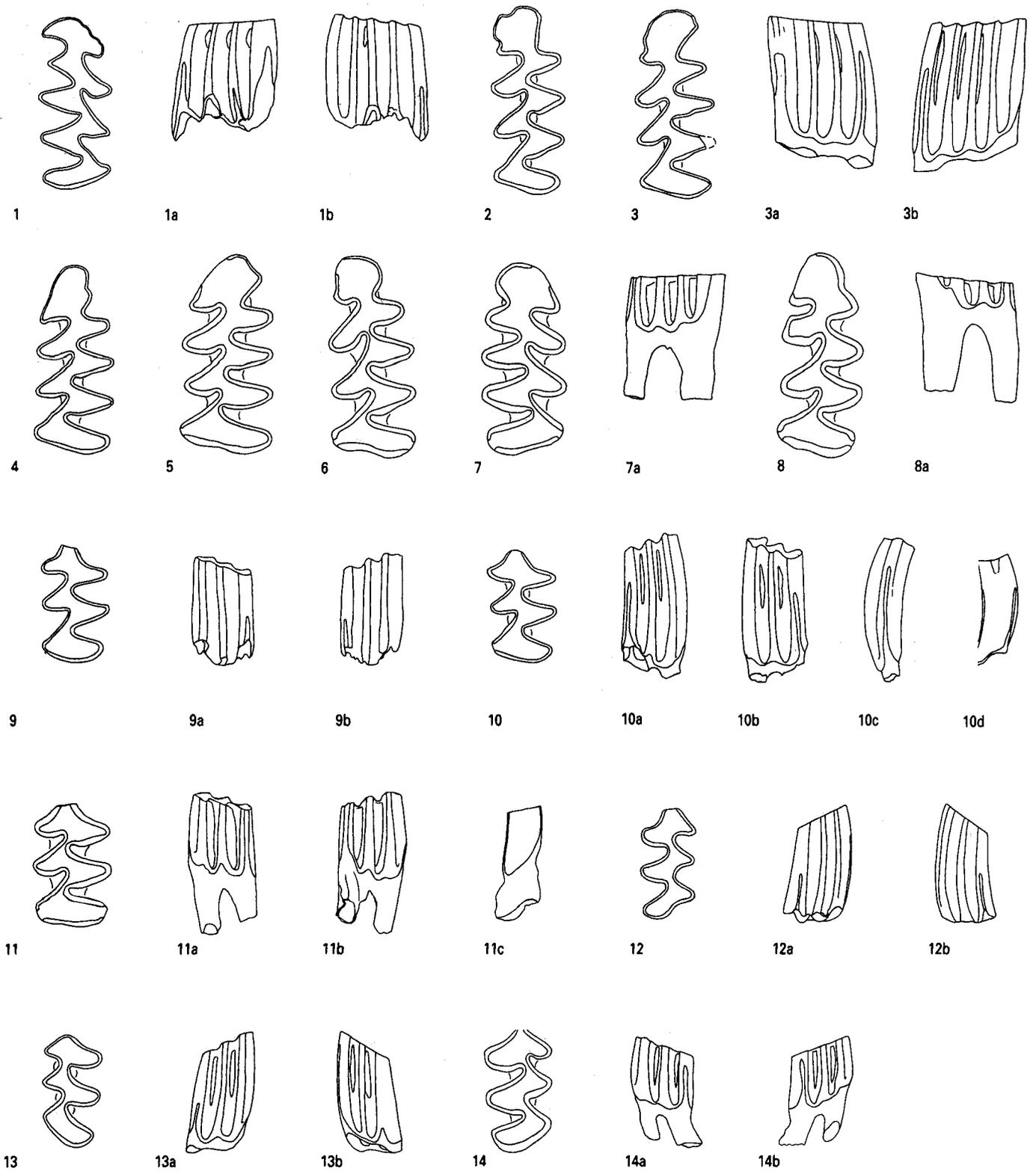


Figure 42

Lower molars (M/1, M/2 and M/3) of *Clethrionomys kretzoi*, Tegelen.

1-8: M/1, 9-11: M/2, 12-14: M/3: occlusal surface; 1a, 3a, 7a-9a, 10b, 11a-13a, 14b: labial side; 1b, 3b, 9b, 10a, 11b-13b, 14a: lingual side; 10c: anterior side; 10d, 11c: posterior side. - 1 - Te628, 2 - Te785, 3 - Te630, 4 - Te224, 5 - Te832, 6 - Te794, 7 - Te795, 8 - Te833, 9 - Te206, 10 - Te705, 11 - Te704, 12 - Te767, 13 - Te683, 14 - Te088. Occlusal view 15x, lateral view 7.5x.

The genus is often considered to be a member of the tribe Ellobiini (not Ellobiini, see Pavlinov et al., 1995) or at least considered to have some affinity with the mole voles of the genus *Ellobius* (Van der Meulen, 1973; Gromov & Polyakov, 1977; Rabeder, 1980).

Rabeder (1981) regarded both *Ungaromys* and *Ellobius* as the stems of the early vole radiation. Carls & Rabeder (1988) proposed a different scheme. Because of the distinct 'Miomomys' characters (enamel islets, *Miomomys* ridge etc.) they regarded *Ungaromys* as a member of the *Miomomys* s.l. group. They assumed that the original *Miomomys* morphology is camouflaged in *Ungaromys* by morphological specialisation. Topachevsky & Recovets (1982) de-

scribed several species of *Ellobius* (*Ellobius*) from the Latest Villanyian and Early Biharian of the Ukraine. They also display some 'Miomomys' features like a weak *Miomomys*-ridge. The earliest species *Ellobius palaeotalpinus* (including *Ellobius tiligulensis*) from the Latest Villanyian faunas of Kryzhanovka 4 and Tiligul (Schevtschenko, 1965, Topachevsky & Recovets, 1982; Tesakov, 1993a) show much less evolved dentine tracts than the broadly synchronous *Ungaromys* from West and Central Europe. The other differences are: a much more developed mimosinoid in the lower M/1 and a hyposinus in upper M1-M2/, unfused middle (protocone) root and the anterior root in upper M1/, much more reduced third molars in Latest Villanyian -

Figure 43
Clethrionomys kretzoi,
Tegelen. Scatter diagram of
relative length of anteroconid
of M/1 (A/L) and crown
height.

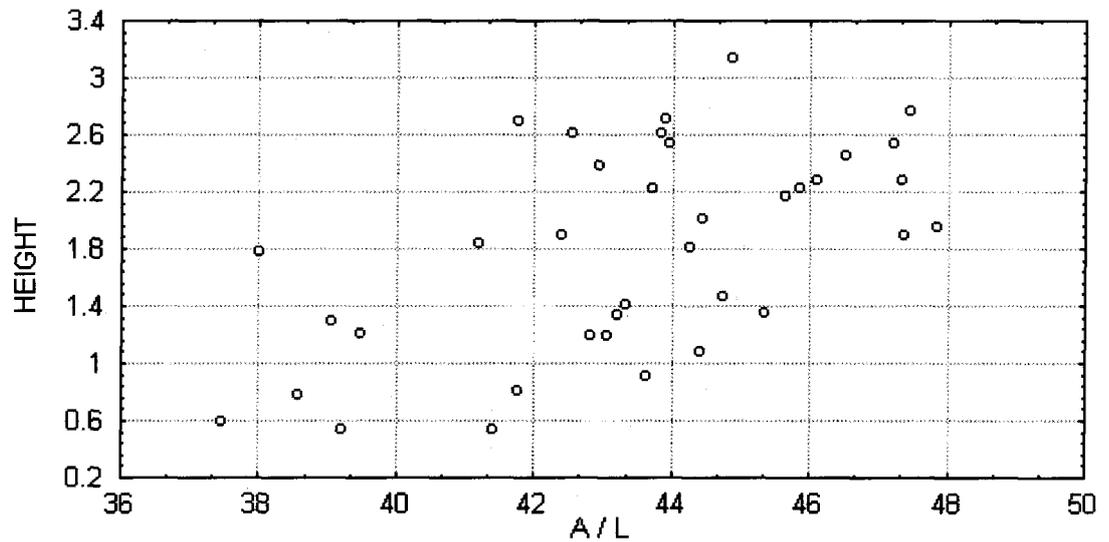
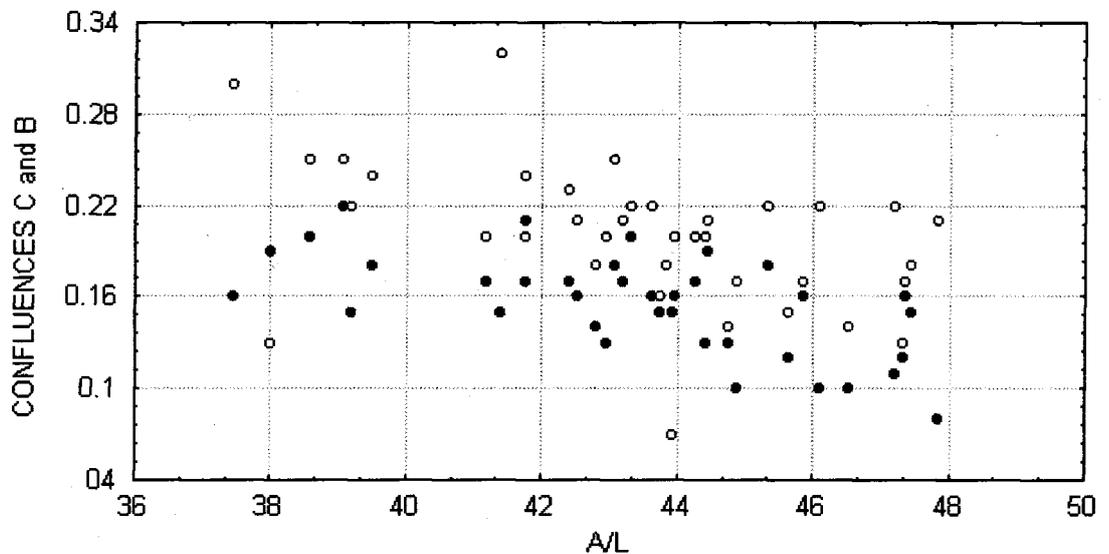


Figure 44
Clethrionomys kretzoi,
Tegelen. M/1. Scatter
diagram of relative length of
anteroconid (A/L) and
confluences B (white circles)
and C (black circles).



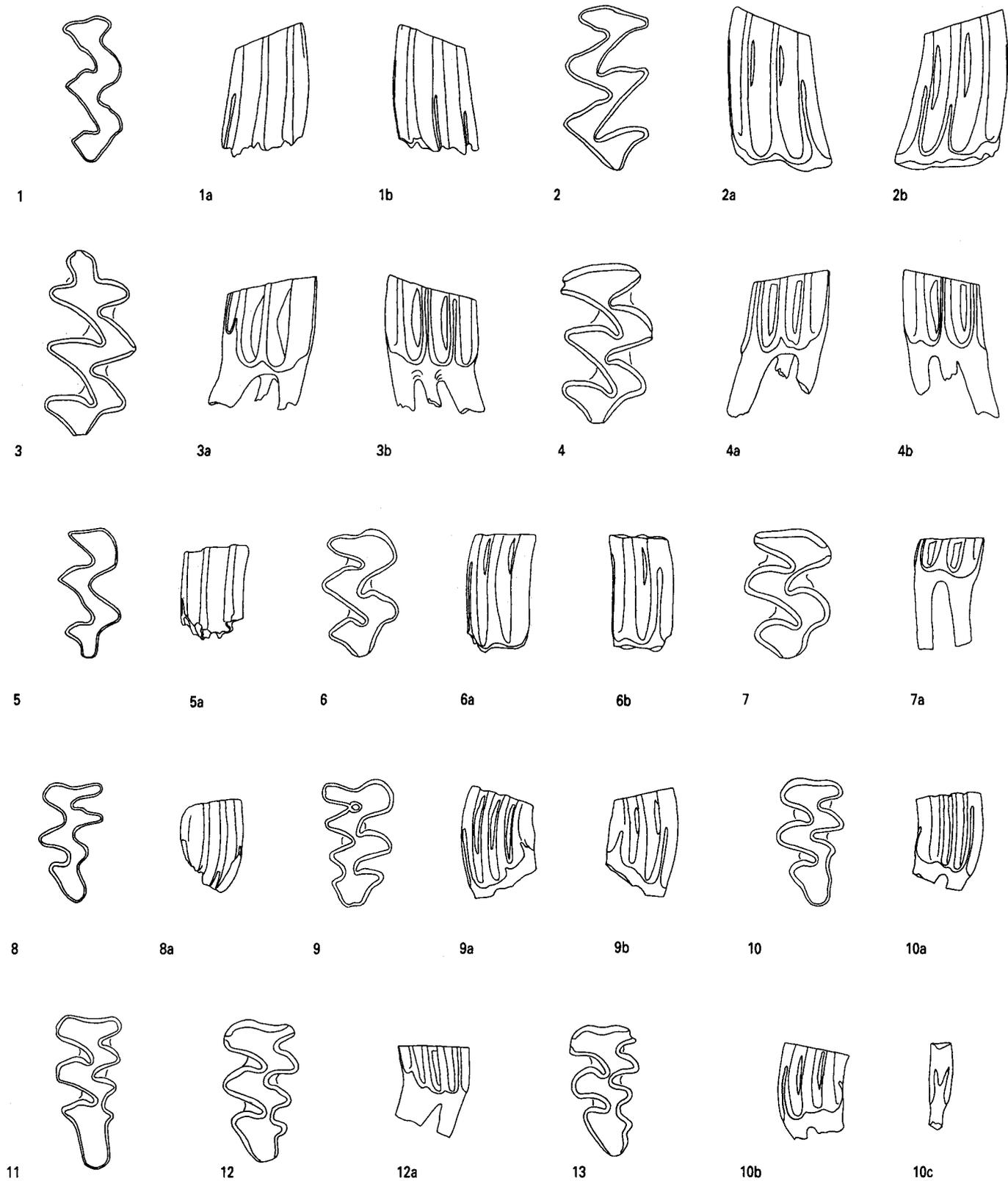


Figure 45

Upper molars (M1, M2 and M3) of *Clethrionomys kretzoi*, Tegelen.

1-4: M1, 5-7: M2, 8-13: M3; occlusal surface; 1a-10a, 12a: labial side; 1b-4b, 6b, 9b, 10b: lingual side; 10c: posterior side. - 1 - Te816, 2 - Te732, 3 - Te769, 4 - Te058, 5 - Te038, 6 - Te838, 7 - Te4314, 8 - Te093, 9 - Te559, 10 - Te354, 11 - Te044, 12 - Te129, 13 - Te282.

Occlusal view 15x, lateral view 7,5x.

Early Biharian *Ellobius* from the Black Sea area. This data allows the distinct origin of both lineages from the common arvicoline ancestors to be inferred. It is likely that both *Ungaromys* and *Ellobius* share some ancestors only at the base of the proto-*Miomys* radiation and cannot be attributed to the same tribe. The similar morphological features of the dentition, like confluent dentine areas in the occlusal surface, thick undifferentiated enamel, and the pleurorhiz position of the lower M/2 are results of the parallel evolution in the direction of the specialised fossoriality. It is worth noting that the vole evolution in North America independently produced a very similar form - *Atopomys* (Zakrzewski, 1975).

The early history of *Ungaromys* (the species *U. altenburgensis* and '*Germanomys helleri*') should be clarified in more detail.

***Ungaromys dehmi* Carls et Rabeder, 1988**

Figures 2D, 47-52, Tables 28 - 34.

1976 *Ungaromys* sp.; A. van der Meulen, The smaller... : p.16-17.

1976 *Ungaromys nanus* Kormos; F. Malec & H. Tobien, Die Säugerreste-führenden... : p.133, Abb.6.

1988 *Ungaromys dehmi* n.sp.; N. Carls & G. Rabeder, Die Arvicoliden... : p.199-213.

1994 *Ungaromys* sp.; B. Sala et al., Villanyian arvicolids... : p.4, plate 1, fig.1-3.

1994 cf. *Ellobius* Fischer; B. Sala et al., Villanyian arvicolids... : p.4, plate 1, fig.4-6.

Material studied

Tegelen, 35 M/1, 26 M/2, 12 M/3, 18 M1/, 24 M2/, 9 M3/ (totally 124 specimens).

Description

The smallest vole of the Tegelen fauna (Tables 28 - 33, Figure 47). The occlusal surfaces show broadly confluent pattern. The enamel is thick and undifferentiated. Histologically, the enamel is mostly composed of radial enamel with the discrete lammellar enamel at the tips of salient angles (Von Koenigswald, 1980, Rabeder, 1981, Carls & Rabeder, 1988).

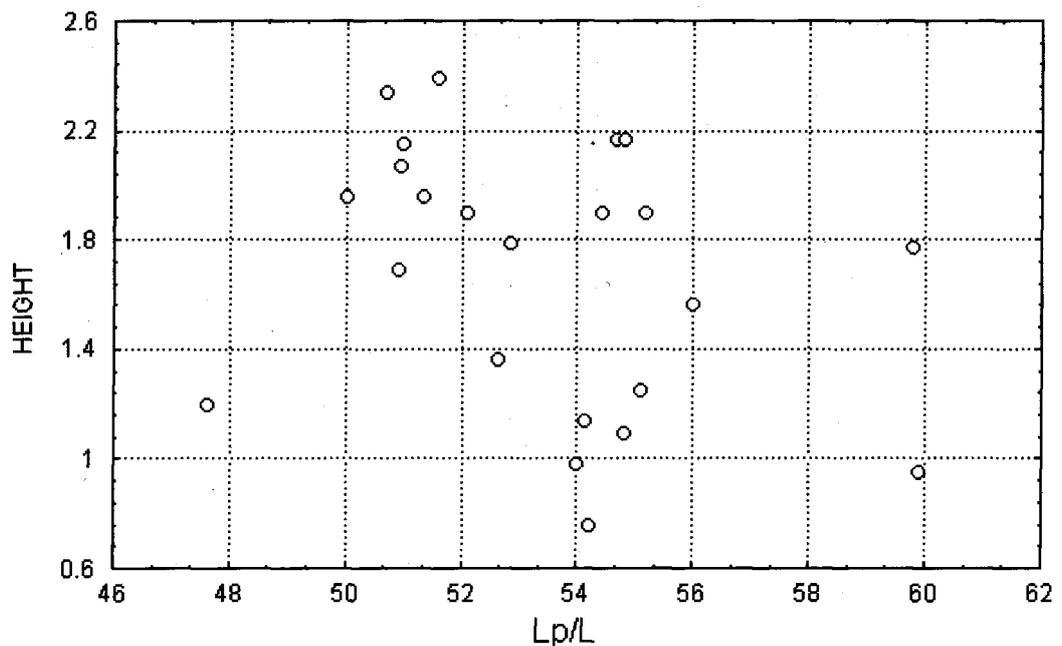
Age distribution

Root formation stages (Figure 2D). The rooted (rhizodont) stage is shown by 69.1% of specimens (n=85). The intermediate (merorhiz) stage is represented by 28.5% of specimens (n=35). Only 2.4% belong to the arhiz stage (n=3).

Crown height distribution (Figure 48). Most molars show a distinct peak related to young (high-crowned) individuals and a lower peak corresponding to higher senile mortality. These are characters of a classical attritional age frequency profile. It may indicate the non-catastrophic mortality pattern in the population(s) of *Ungaromys dehmi* which contributed to the Tegelen fossil assemblage.

In the upper and lower M3 only one 'young' peak is recorded. This is probably due to under-represented low-crowned old individuals. They are very small and have better chances to be lost and overlooked during sorting. Moreover, the eruption of the third molars seems to be retarded in *Ungaromys dehmi* as compared to the anterior teeth.

Figure 46
Clethrionomys kretzoi,
Tegelen. M3/. Scatter
diagram of the relative length
of posterior lobe (Lp/L)
and
crown height.



Dentine tracts

Ungaromys dehmi has rather lodentine tracts. The data is summarized in Figure 49 and in Tables 28 - 33.

M/1

Anteroconid complex is weakly subdivided into the anteroconid cap and anteroconid triangles (T4-T5). The cap has a roundish form and shows only slight variation. In older individuals the anterior cap fuses with the anteroconid triangles due to BRA3 and LRA4 growing more shallow (Figure 50: 6). In one rootless juvenile specimen (Figure 50: 1) the osteodentine trace of an enamel islet is visible. Two other molars display traces of an enamel islet in older stages: one specimen has the crown height of 2.42 mm (merorhiz stage) and the other - 2.28 (merorhiz - rhizodont transition). The *Miomys*-ridge occurs in 6 specimens (Figure 50: 2 - 4). All of them are young and have crown heights ranging from 2.42 to 1.85 mm.; which is about 30% of this age group. The relative length of the anteroconid (A/L) decreases from 46-42% in younger individuals to 40-36 in older individuals with worn molars (Figure 51). The anteroconid triangles are constantly broadly confluent with the T3-T2 rhombus. The labial dentine tracts are interrupted by wear when the roots are already well developed.

M/2

The molar consists of posterior loop, and two pairs of confluent triangles: T1-T2, and T3-T4 (Figure 50: 7 - 9). In younger individuals BRA3 and LRA3 may be slightly deeper and the anterior portion of the occlusal surface is more pointed than in older specimens. In younger specimens there is a slight trend to subdivision of T1 and T2 (Figure 50: 7). The posterior root is situated completely labially from the incisor (the pleurohiz position) (Figure 50: 9b). The LRA1 is somewhat (0.16 - 0.22 mm) less deep than LRA2 when viewed from the lingual side of the crown (Figure 50: 8b, 9d). This probably results from the tight contact of the posterior root and the incisor. It may indicate relatively recent development of a fully pleurohiz condition in the Tegelen *Ungaromys*.

M/3

The molar is composed of posterior loop and two pairs of broadly confluent triangles. In some younger specimens (Figure 50: 10, 12) T1 and T2 may be partly subdivided by the vergent BRA1. Deep LRA3 occurs in the very young individual (Figure 50: 10). With wear the occlusal outline become more rounded, T1-T2 confluence increases. Two roots are present in old specimens. The anterosinus may be shifted to the labial side of the anterior wall of the molar.

Table 27
Size and dentine tracts measurements of *Clethrionomys kretzoi* from Tegelen and *Clethrionomys kretzoi* from Schernfeld.

	TEGELEN			SCHERNFELD			Difference in means (%)
	Mean	Range	n	Mean	Range	n	
M/1							
Length	2.19	1.94 - 2.34	37	2.13	1.89 - 2.3	40	+ 2.8
HH-index	2.99	2.35 - 3.51	12	3.09	2.44 - 3.55	40	- 3.2
M/2							
Length	1.36	1.24 - 1.55	34	1.33	1.24 - 1.43	12	+ 2.2
HH-index	2.37	1.96 - 2.77	14	2.44	1.79 - 2.70	12	- 2.9
M/3							
Length	1.3	1.20 - 1.41	23	1.18	1.08 - 1.33	13	+ 9.2
HH-index	1.43	1.05 - 1.65	11	1.63	1.29 -	13	- 12.3
M1/							
Length	1.88	1.64 - 2.16	32	1.73	1.66 - 1.87	25	+5.9
PA-index	2.72	1.89 - 3.38	15	3.04	2.51 - 3.51	25	- 10.5
M2/							
Length	1.47	1.36 - 1.64	23	1.46	1.33 - 1.84	20	+0.7
PA-index	2.76	2.50 - 2.99	5	2.62	2.29 - 2.96	17	+3.7
M3/							
Length	1.55	1.30 - 1.79	24	1.56	1.38 - 1.70	32	- 0.7
PA-index	1.92	0.83 - 2.31	12	2.02	1.68 - 2.41	27	- 5.0

Table 28
Dimensions of
Ungaromys dehmi,
Tegelen, M/1.

Variable	n	Mean	Minimum	Maximum	Standard deviation	Standard error
Length	31	2.04	1.85	2.16	0.08	0.02
Width	32	0.94	0.73	1.03	0.06	0.01
Anteroconid index	31	40.85	35.81	46.23	2.78	0.50
Anterosinuid	19	1.81	1.44	2.07	0.20	0.05
Hyposinuid	20	1.66	1.41	1.90	0.15	0.03
Hyposinulid	28	0.82	0.44	1.20	0.19	0.04
HH-index	20	1.87	1.48	2.16	0.20	0.05

Table 29
Dimensions of
Ungaromys dehmi,
Tegelen, M/2.

Variable	n	Mean	Minimum	Maximum	Standard deviation	Standard error
Length	26	1.35	1.19	1.49	0.07	0.01
Width	26	0.84	0.66	0.91	0.05	0.01
Anterosinuid	20	1.53	1.20	2.06	0.23	0.05
Hyposinuid	20	1.24	0.98	1.63	0.15	0.03
Hyposinulid	23	0.82	0.27	1.09	0.19	0.04
HH-index	20	1.50	1.10	1.74	0.16	0.04

Table 30
Dimensions of
Ungaromys dehmi,
Tegelen, M/3.

Variable	n	Mean	Minimum	Maximum	Standard deviation	Standard error
Length	12	1.06	0.91	1.24	0.11	0.03
Width	12	0.59	0.47	0.68	0.06	0.02
Anterosinuid	11	1.16	0.82	1.36	0.19	0.06
Hyposinuid	12	0.46	0.32	0.63	0.10	0.03
Hyposinulid	12	0.37	0.22	0.54	0.11	0.03
HH-index	12	0.60	0.42	0.76	0.12	0.03

Table 31
Dimensions of
Ungaromys dehmi,
Tegelen, M1/.

Variable	n	Mean	Minimum	Maximum	Standard deviation	Standard error
Length	18	1.83	1.68	1.95	0.07	0.02
Width	18	0.99	0.88	1.10	0.06	0.01
Anterosinus	16	1.48	1.09	1.71	0.21	0.05
Anterosinulus	17	0.86	0.60	1.14	0.15	0.04
Protosinus	17	0.53	0.38	0.65	0.07	0.02
Distosinus	14	1.61	1.25	1.96	0.21	0.06
PA-index	16	1.58	1.22	1.81	0.19	0.05
AA-index	16	1.72	1.34	2.01	0.22	0.06

Table 32
Dimensions of
Ungaromys dehmi,
Tegelen, M2/.

Variable	n	Mean	Minimum	Maximum	Standard deviation	Standard error
Length	23	1.49	1.38	1.58	0.05	0.01
Width	23	0.85	0.70	0.96	0.07	0.01
Anterosinus	21	0.83	0.63	1.09	0.13	0.03
Protosinus	22	0.63	0.38	0.82	0.13	0.03
Distosinus	19	1.13	0.87	1.41	0.14	0.03
PA-index	21	1.05	0.81	1.30	0.14	0.03

Table 33
Dimensions of
Ungaromys dehmi,
Tegelen, M3/.

Variable	n	Mean	Minimum	Maximum	Standard deviation	Standard error
Length	9	1.18	1.02	1.25	0.08	0.03
Width	9	0.65	0.56	0.74	0.05	0.02
Anterosinus	9	0.47	0.30	0.71	0.13	0.04
Protosinus	9	0.42	0.27	0.49	0.08	0.03
Distosinus	8	0.50	0.27	0.71	0.13	0.05
PA-index	9	0.63	0.40	0.86	0.13	0.04

M1/

The molar of the characteristic arvicoline form. Anterior loop and four alternative triangles are broadly confluent in younger individuals. Progressive wear reduces the connections between anterior loop and T1, and between T2 and T3 (Figure 52: 7 - 9). BRA3 and LRA3 are weak or undeveloped. Of 11 rooted specimens, 8 have two roots: the very small middle root is fused with the anterior one (Figure 52: 2b) and 3 still display 3 roots, although the middle root is still very close to the anterior one.

The dentine tracts shows the typical *Ungaromys* pattern with the anterosinus higher than protosinus (Rabeder, 1981, Carls & Rabeder, 1988). Besides hyposinus is clearly developed and ranges from 0.43 to 1.01 mm with the mean of 0.65 (n=16).

M2/

The molar shows the typical structure with the anterior loop and three alternating triangles. Younger specimens have broadly confluent elements of the occlusal surface. The connections between the anterior loop and T2, and, less so, T3 - T4 decrease with wear (Figure 52: 4 - 7). BRA3 and LRA2 are weakly manifest. BRA3 may disappear with wear (Figure 52: 7). The dentine tracts are low and the hyposinus is almost undeveloped.

M3/

The molar shows one dentine field of the occlusal surface which is weakly subdivided into two parts between the T2 and T3-T4-PL complex. The posterior enamel islet (Figure 52: 8 - 9) is present in the youngest individuals until the crown height of 1.5 - 1.4 mm.

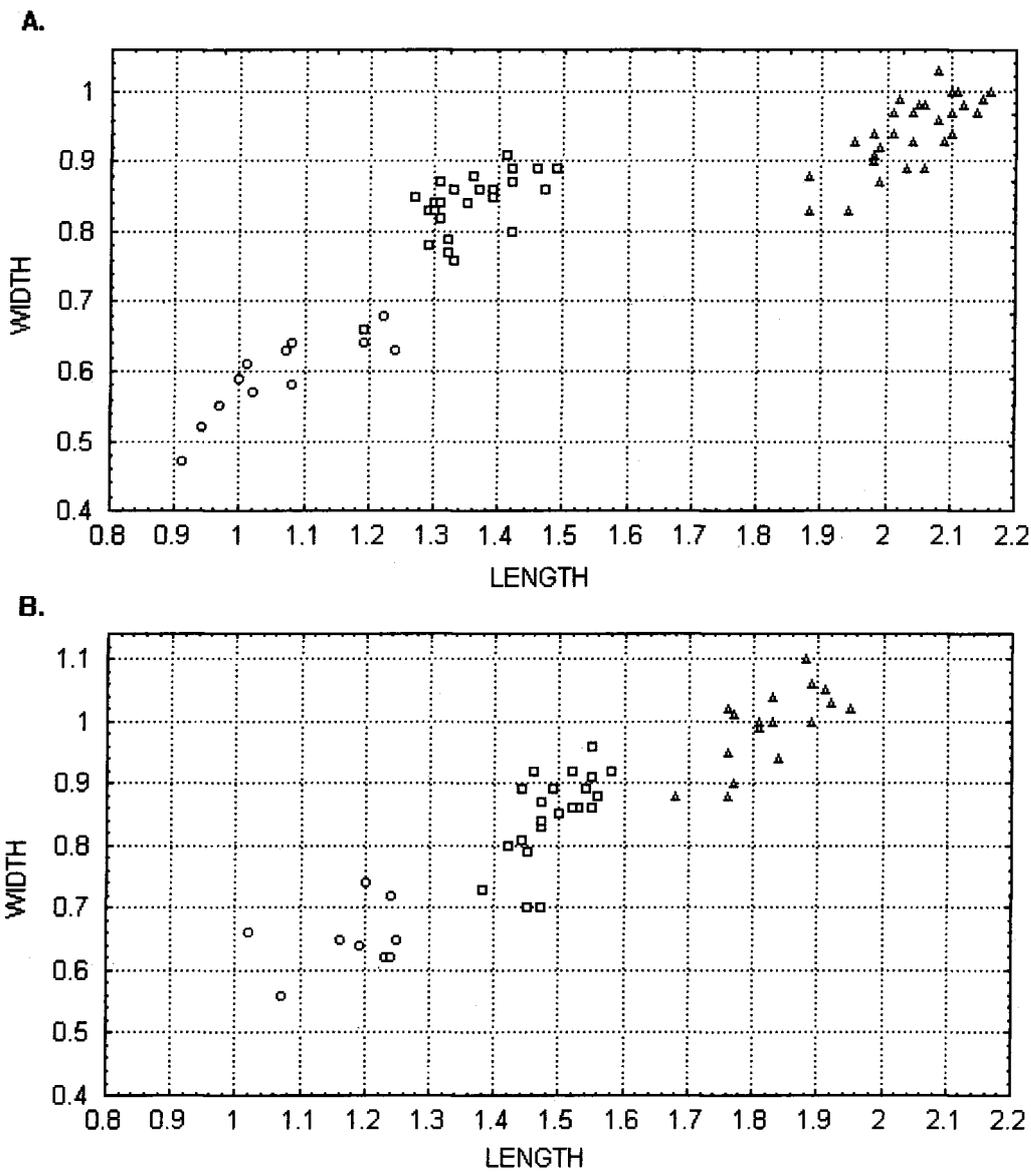


Figure 47
Ungaromys dehmi, Tegelen.
Scatter diagram of length and width. A - Lower molars, B - Upper molars. Triangles - M1/1, squares - M2/2, circles - M3/3.

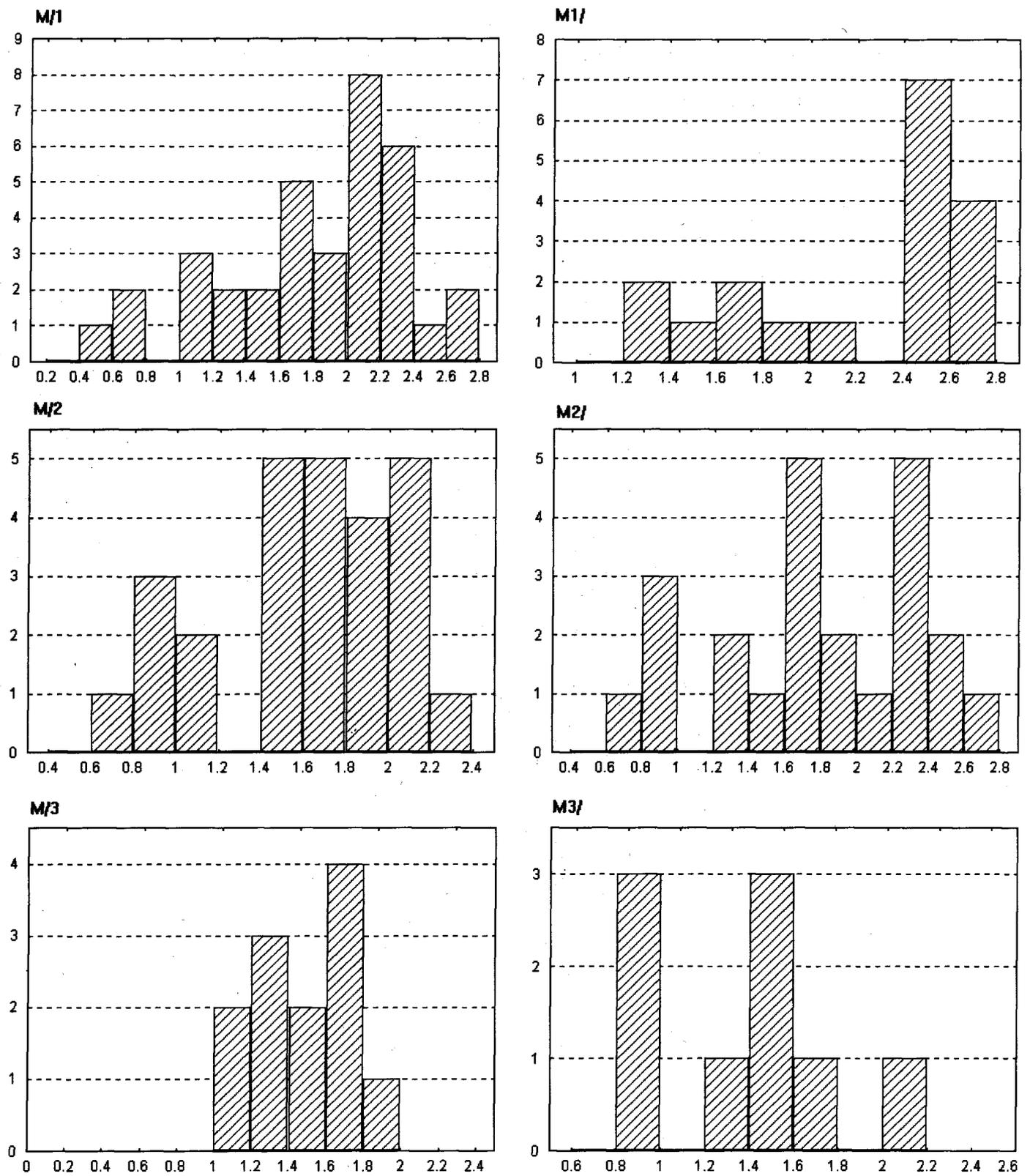


Figure 48
Ungaromys dehmi, Tegelen. Frequency histogram of crown height.

Comparison

Comparison with *U. dehmi* from Schernfeld.

The *Ungaromys* from Tegelen is very close to *Ungaromys dehmi* from Schernfeld (Carls & Rabeder, 1988) both in size and morphology. Some measurements and indices for both forms are summarized in the Table 34.

As it is evident from the Table 34, the Tegelen *Ungaromys* is slightly smaller than the Schernfeld form (2.8% on average). At the same time the dentine tracts as reflected in the HH, PA, and AA-indices are much lower and the range of variation is shifted to distinctly lower values in the Tegelen form. This is a good indication of the lower evolutionary level of the Tegelen *Ungaromys*.

The other character which is worth mentioning is the stages of root formation. According to Carls & Rabeder (1988), most of the *Ungaromys* molars "are so young that

they do not possess roots yet". This is likely to be translated into the arhiz or merorhiz stages. This is in obvious contrast to the Tegelen *Ungaromys*, which shows predominant rooted stage (Figure 2D). Most probably this difference in rooted specimens frequency means the less evolved stage recorded in the Tegelen form. It is in agreement with the lower dentine tracts of the Tegelen form, in comparison to that from Schernfeld.

Ungaromys sp. from Rivoli Veronese. Sala, Masini & Torre (1994) described this form from the Late Villanyian of northern Italy. Three figured specimens of M/1 closely parallel the morphology of *Ungaromys dehmi* from Tegelen and the type locality of Schernfeld. Judging from the scale given (Sala et al., 1994, Plate 1), the illustrated dentine tracts falls into the range of variation of the Tegelen material.

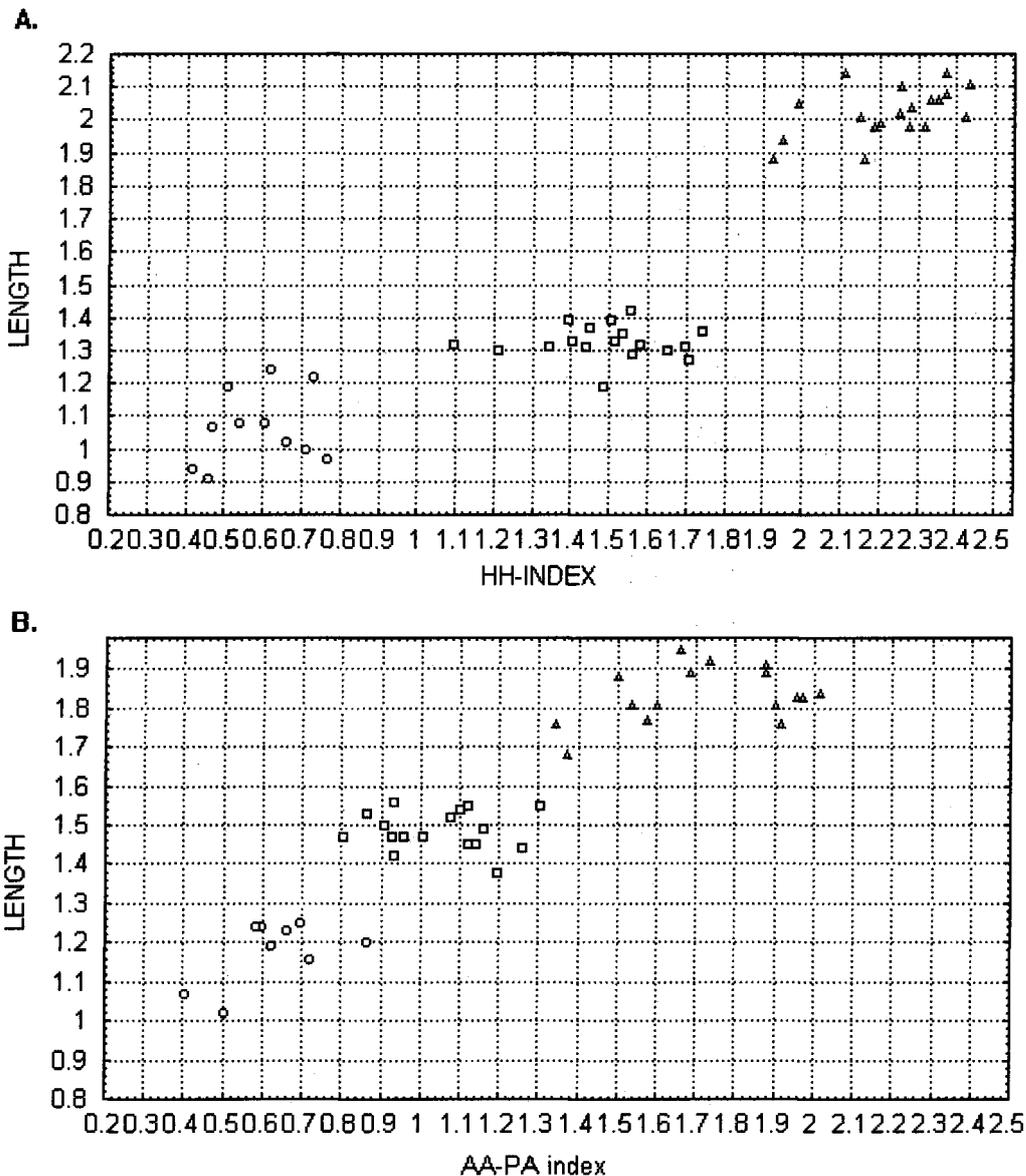


Figure 49
Ungaromys dehmi, Tegelen.
Sinugram. A - Lower molars,
B - Upper molars.
Triangles - M1/1, squares -
M2/2, circles - M3/3.

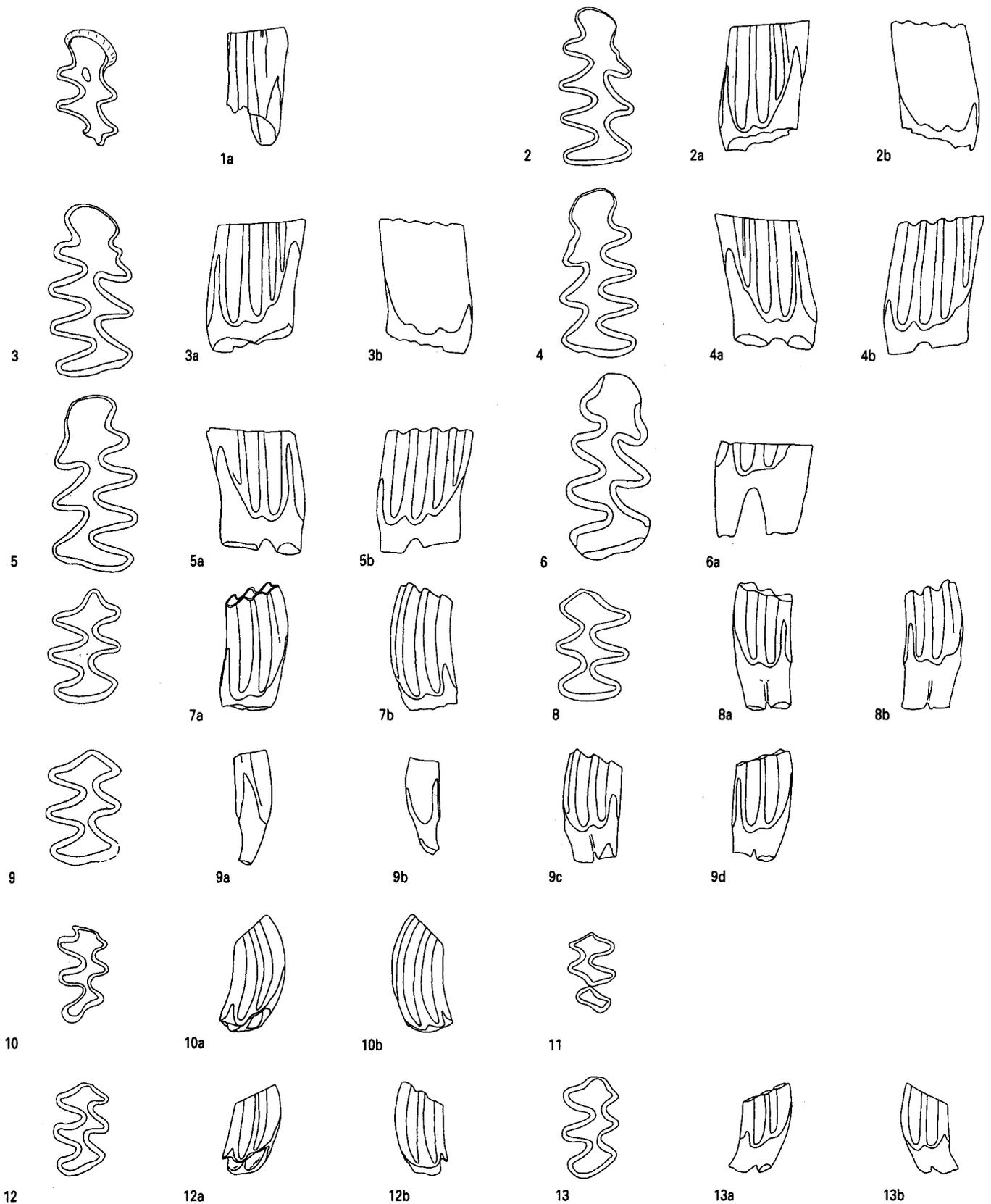


Figure 50

Lower molars (M/1, M/2 and M/3) of *Ungaromys dehmi*, Tegelen.

1-6: M/1, 7-9: M/2, 10-13: M/3: occlusal surface; 1a-8a, 9c, 10a, 12a, 13a: labial side; 2b-5b, 7b, 8b, 9d, 10b, 12b, 13b:

lingual side; 9a: anterior side; 9b: posterior side. - 1 - Te842, 2 - Te578, 3 - Te786, 4 - Te562, 5 - Te611, 6 - Te576, 7 - Te791, 8 - Te892, 9 - Te564, 10 - Te702, 11 - Te774, 12 - Te772, 13 - Te871. Occlusal view 15x, lateral view 7,5x.

cf. *Ellobius* from Rivoli Veronese. The material tentatively referred to the mole voles of the genus *Ellobius* (Sala et al., 1994) is in the author's opinion the integer part of the Rivoli Veronese *Ungaromys* sample. The three illustrated M/1 (Sala et al., 1994, Plate 1, Figure 4 - 6) most probably represent ontogenetically younger stages (merorhiz or early rhizodont). This accounts for the slender occlusal outlines and the better developed anteroconids. The larger dimensions discussed fall into the range of variation of *Ungaromys* from Tegelen and Schernfeld.

Ungaromys nanus Kormos, 1933 from Deutsch-Altenburg 21 and 2C1 (Rabeder, 1981). Judging from the published illustrations, this form has more confluent elements of the anteroconid and somewhat higher dentine tracts than *Ungaromys dehmi* from Tegelen.

Ungaromys meuleni Rabeder, 1981. This form originally described as *Ungaromys nanus* Kormos (Van der Meulen, 1973), was then named as *Ungaromys meuleni* by Rabeder (1981). Rabeder diagnosed the new species on the basis of higher evolutionary level as compared to the type *Ungaromys nanus* from Betfia 2. Here the author accepts this scheme. However, analysis of the type material is needed to substantiate this attribution. The *Ungaromys meuleni* Rabeder from Monte Peglia (the *Mimomys blanci* association) is distinctly more evolved in the dentine tracts in comparison to the Tegelen *Ungaromys* form. In M/1, the hyposinuid has a mean value of 2.2 mm (n=3), the hyposinulid's mean value is 1.7 (n=5). In its dimensions the Early Biharian form is comparable to the Villanyian species. Dentine tracts of the first upper molars are also higher than in Tegelen.

Comments

The small, probably underground voles of the genus *Ungaromys* are common elements of the Villanyian and early Biharian faunas of western and central Europe. In eastern Europe the group is replaced by morphological and, most probably, ecologically-vicarious mole voles of the genus *Ellobius*. Thus, there are no reliable reports of the joint occurrence of the both genera. The cf. *Ellobius* reported from the Rivoli Veronese MN17 fauna of Italy, is most probably identical to *Ungaromys dehmi*.

The Tegelen vole assemblage

The representation of the vole species of the Tegelen fauna is given in the Figure 53. The most common form is *Mimomys tigliensis* nov. sp.. *Clethrionomys kretzoi* is the second most abundant species. *Mimomys reidi*, *Ungaromys dehmi* and *Mimomys pliocaenicus* complete the list of forms. *P. pitymyoides* is exceptionally rare.

The general appearance of the fauna is mesophilous. The abundance of *Clethrionomys*, which is regarded to be a forest indicator, the diverse *Mimomys* group, the absence of indicators of open/arid landscapes, such as *Borsodia* together all point to this conclusion.

In its subdominant role of *Clethrionomys*, the Tegelen assemblage differs from most other European Villanyian faunas. One of the few faunas with a high content of the fossil bank voles, it is broadly synchronous with the forest fauna of Psekups in the North Caucasus (Tesakov, 1995, 1996).

Large *Mimomys pliocaenicus* are sometimes thought to have an aquatic adaptation. No direct evidence in support of this hypothesis is given in the literature. Indirectly it may

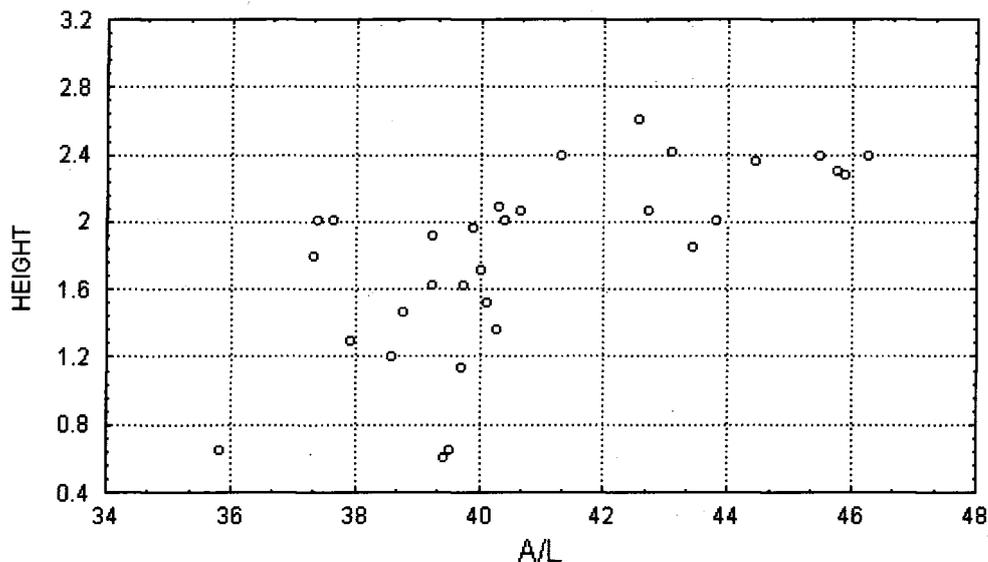


Figure 51
Ungaromys dehmi, Tegelen.
Scatter diagram of relative length of anteroconid of M/1 (A/L) and crown height.

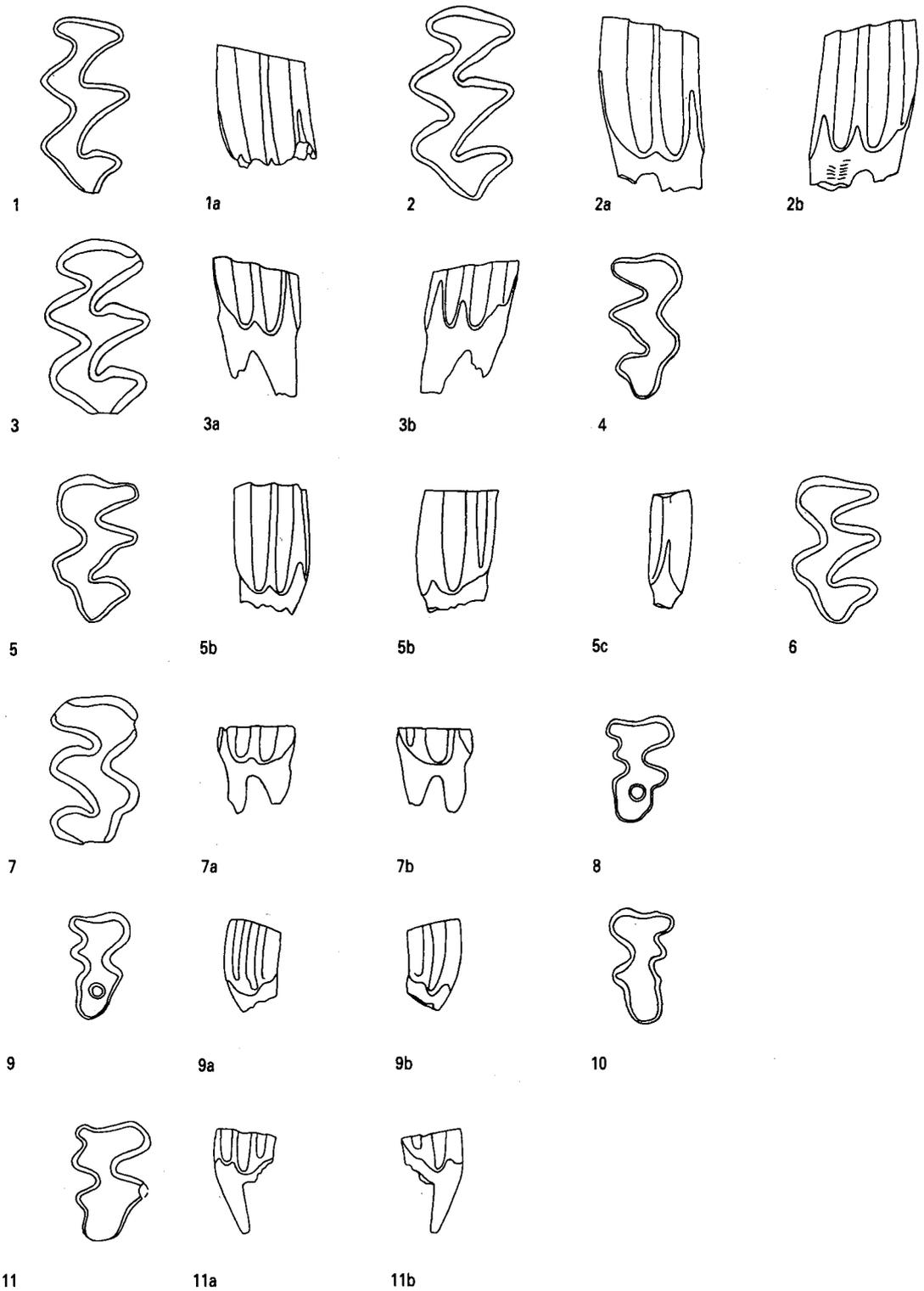


Figure 52

Upper molars (M1/, M2/ and M3/) of *Ungaromys dehmi*, Tegelen. 1 - 3: M1/, 4 - 7: M2/, 8-11: M3/: occlusal surface: 1a-3a, 5a, 7a, 9a, 11a: labial side; 2b, 3b, 5b, 7b, 9b, 11b: lingual side; 5c: posterior side. - 1 - Te790, 2 - Te788, 3 - Te239, 4 - Te905, 5 - Te580, 6 - Te577, 7 - Te907, 8 - Te930, 9 - Te565, 10 - Te929, 11 - Te926. Occlusal view 15x, lateral view 7,5x.

be confirmed by the fact that the large *Mimomys* are rare or absent in open landscape faunas in eastern Europe. The high diversity of presumably aquatic forms in the Tegelen fauna (desmanines and beavers) also suggests an aquatic mode of life for the large *M. pliocaenicus* too.

The most abundant *M. tigliensis* may be considered as a generalized vole species occupying diverse meadow and forest biotopes. The abundance of forms of the *M. tigliensis*-*M. tornensis* lineage in Villanyian faunas throughout Europe may indicate the appearance of the ecological equivalents of the grey voles (*Microtus* s.l.) long before the actual appearance of the latter.

Analysis of age profiles (see description of species) apparently supports the concept of non-catastrophic, attritional type of bone accumulation in the locality.

Biochronology

The biochronology of the Villanyian - Biharian transition is a controversial subject. This transition roughly corresponds to the current conventional Plio-Pleistocene boundary. However, the existing data do not permit correlation of the boundary precisely with the Villanyian-Biharian boundary. In terms of small mammal assemblages, the Villanyian land mammal age embraces faunas with domi-

nant rooted voles of the *Mimomys* group. The Biharian is the time of rootless voles (*Microtus* s.l.) dominated communities. There are several main points of view on the exact position of the boundary between the two ages. According to Kretzoi's (1956) original concept Villanyian comprises the diversified *Mimomys* faunas. The first rootless *Microtus* s.l. (*Allophaiomys deucalion*) appear as an insignificant admixture to these diverse *Mimomys* faunas (Villany 5, Vceláre 5). These transitional faunas are thus regarded as Villanyian (Kretzoi, 1956; Van der Meulen, 1973; 1974; Rabeder, 1981; 1986; Carls & Rabeder, 1988; Horáček & Lozek, 1988). This approach is based on the structure of small mammal communities. The other view is strictly biostratigraphic (Fejfar & Heinrich, 1990). According to this concept, the lower limit of Biharian is defined by the first appearance of *Allophaiomys*. It is clear that beyond western Europe, in different regions of the Holarctic, the dispersal of *Allophaiomys* and, less so, the restructuring of small mammal communities could not be simultaneous. So the Villanyian-Biharian boundary may be considerably diachronous beyond (west-central-eastern) Europe. Indeed the first appearance of *Allophaiomys* is a rather unreliable basis for correlations even within Europe. Thus the 'community' approach is followed here. The boundary between the Villanyian and Biharian should be drawn at

	TEGELEN			SCHERNFELD			Difference in means (%)
	Mean	Range	n	Mean	Range	n	
M/1							
Length	2.04	1.85 - 2.16	31	2.08	1.88 - 2.35	50	- 1.9
HH-index	1.87	1.48 - 2.16	20	2.10	1.66 - 2.62	50	- 11.0
M/2							
Length	1.35	1.19 - 1.49	26	1.38	1.29 - 1.56	19	- 2.2
HH-index	1.50	1.10 - 1.74	20	1.70	1.36 - 2.06	20	- 11.8
M/3							
Length	1.06	0.91 - 1.24	12	1.15	0.92 - 1.24	16	- 7.8
HH-index	0.60	0.42 - 0.76	12	0.76	0.51 - 0.91	16	- 21.0
M1/							
Length	1.83	1.68 - 1.95	18	1.86	1.70 - 2.02	30	- 1.6
PA-index	1.58	1.22 - 1.81	16	1.66	1.21 - 2.39	30	- 4.8
AA-index	1.72	1.34 - 2.01	16	1.96	1.56 - 2.73	30	- 12.3
M2/							
Length	1.49	1.38 - 1.58	23	1.54	1.43 - 1.66	30	- 3.2
PA-index	1.05	0.81 - 1.30	21	1.28	0.91 - 1.86	30	18.0
M3/							
Length	1.18	1.02 - 1.25	9	1.18	1.01 - 1.29	10	0
PA-index	0.63	0.40 - 0.86	9	0.66	0.36 - 1.16	10	- 4.5

Table 34
Size and dentine tracts measurements of *Ungaromys dehmi* from Tegelen and *Ungaromys dehmi* from Schernfeld.

Figure 53
Representation of vole species (%) in the Tegelen fauna.

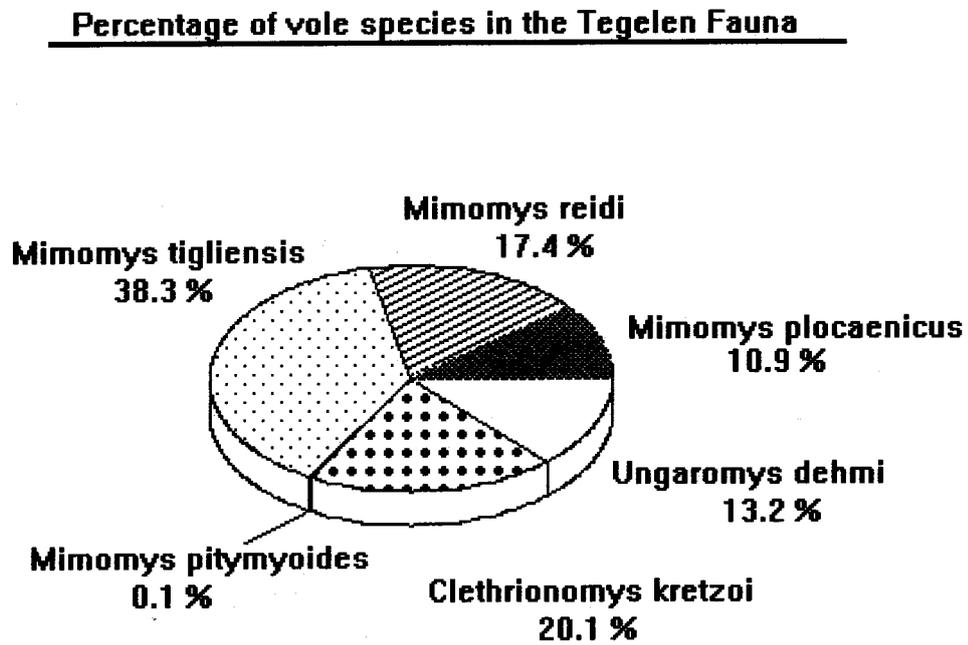
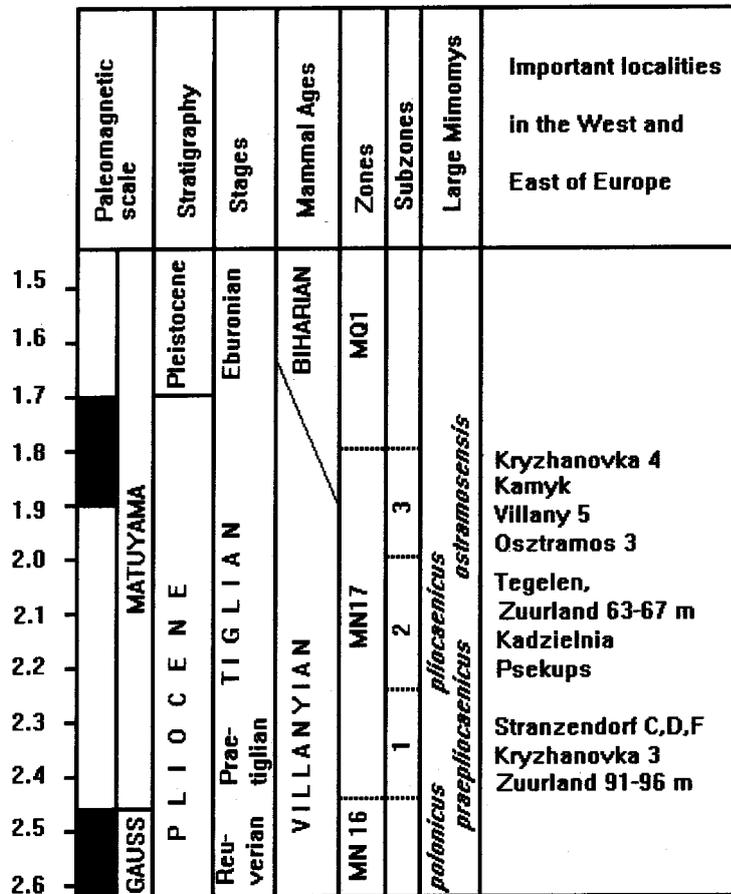


Figure 54
Biostratigraphical scheme of the late Villanyian.



the appearance of *Allophaiomys*-dominated faunas. As was proposed by Fejfar & Heinrich (1990), the Villanyian corresponds to two MN zones, 16 and 17. The Late Villanyian (MN17) is the biozone of *Mimomys pliocaenicus* s.l. This autochthonous European lineage is the best basis for subdivision of the Late Villanyian. Thus, the three morpho-species: *Mimomys praepliocaenicus*, *Mimomys pliocaenicus* and *Mimomys ostramosensis* define three subunits of the Late Villanyian (Figure 54). This division is very close to that proposed by Horáček & Lozek (1988).

The upper subunit (*Mimomys ostramosensis*) comprises faunas including Schernfeld, Villany 5 and Kamyk. The Tegelen fauna is placed within the *Mimomys pliocaenicus* (middle) subunit of the Late Villanyian together with those at East and West Runton, Psekups and Kadzielnia. The lower Villanyian subunit includes faunas like Stranzendorf C, D, F, Kryzhanovka 3 and others.

The Dutch small mammal faunas of the Tiglian correspond mostly to the middle subunit of the Villanyian. These are faunas Tegelen and Zuurland borehole 62-66 metres. The lower subunit is represented by the Zuurland 95 m fauna (*Mimomys praepliocaenicus*) and possibly the small collection from the Tegelen-Maalbeek site. The uppermost Villanyian subunit with *Mimomys ostramosensis* and the first primitive *Allophaiomys deucalion* is so far unknown in the Netherlands. In the most complete Zuurland sequence, the middle Late Villanyian faunas are capped by the Early Biharian assemblages with numerous *Allophaiomys* of a rather progressive type. A notable gap thus occurs in the sequence as known at present.

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