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New findings on the rare and peculiar genus *Lartetomys* (Cricetidae, Rodentia, Mammalia)

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Key-words: *Lartetomys*, Cricetidae incertae sedis, Rodentia, Mammalia, Middle Miocene

ABSTRACT

In this paper newly collected material on the rare and peculiar cricetid genus *Lartetomys*, MEIN & FREUDENTHAL, 1971 is described. Material from four new localities is compared with the type material from Vieux-Collonges (France, MN 4/MN 5) and is described as *Lartetomys* cf. *zapfei* MEIN & FREUDENTHAL, 1971. A description of hitherto unknown tooth positions is given. Some old characteristics of that species have been critically revised and improved. The systematic position, the stratigraphic range, and geographic distribution of this peculiar species are discussed.

ZUSAMMENFASSUNG

Von einer der seltensten miozänen Cricetiden-Gattungen Europas, *Lartetomys* MEIN & FREUDENTHAL, 1971 wird von vier Lokalitäten neu aufgesammeltes Material beschrieben und mit dem Originalmaterial von der Typuslokalität Vieux-Collonges (Frankreich, MN 4/MN 5) verglichen. Das neue Material wird in die Nähe der Art *Lartetomys zapfei* MEIN & FREUDENTHAL, 1971 gestellt. Bisher nicht belegte Zahnpositionen werden erstmals beschrieben sowie von früheren Autoren aufgeführte Zahnmerkmale kritisch untersucht. Die systematische Stellung sowie die stratigraphische und geographische Verbreitung werden diskutiert.

Introduction/Historical review

In their publication on the Middle Miocene Slovakian locality Devínska Nová Ves (Neudorf an der March), Schaub & Zapfe (1953) described scanty material (1 m_1) of a large, peculiar cricetid with characteristic thick enamel and strongly shortened anteroconid, which they recognized as a new species. However, due to the poor record, they refrained from establishing a new species and attributed the only tooth to the genus known at that time, *Cricetodon* LARTET, 1851.

Based on new material from the French karstic fissure filling Vieux-Collonges, Mein & Freudenthal (1971a) established the genus *Lartetomys*. Their diagnosis based on only 7 teeth, which were attributed to two different species; a large one, *Lartetomys mirabilis* and a small one, *Lartetomys zapfei*. Based on the dentition, *Lartetomys mirabilis* showed affinities to the genus *Cricetodon* LARTET, 1851, whereas *Lartetomys zapfei* showed affinities to the genus *Democricetodon* FAHLBUSCH, 1964. For that reason the original diagnosis emphasized the possibility of the existence of two independent genera. Mein & Freudenthal (1971a) based their classification of

European cricetids on the morphology of maxilla and mandible. As no maxilla and mandible of *Lartetomys* had been found, the genus *Lartetomys* was enlisted as Cricetidae incertae sedis.

New Localities and their material

Remains of the genus *Lartetomys* are extremely rare. Until today, only 11 localities, two of them still unpublished, have yielded scanty material of that peculiar cricetid (Tab. 1). The newly collected material originates from four localities. Three of them were found in the course of a project established by the Swiss National Science Foundation and one was supported by the Polish Scientific Committee. During the last ten years, systematic prospecting of micromammal sites in the Upper Freshwater Molasse of Switzerland (MN 4–MN 9) has been intensified. Large amounts of sediment have been washed and picked out, but only three localities yielded scanty material of *Lartetomys*. During a sojourn at the Natural History Museum

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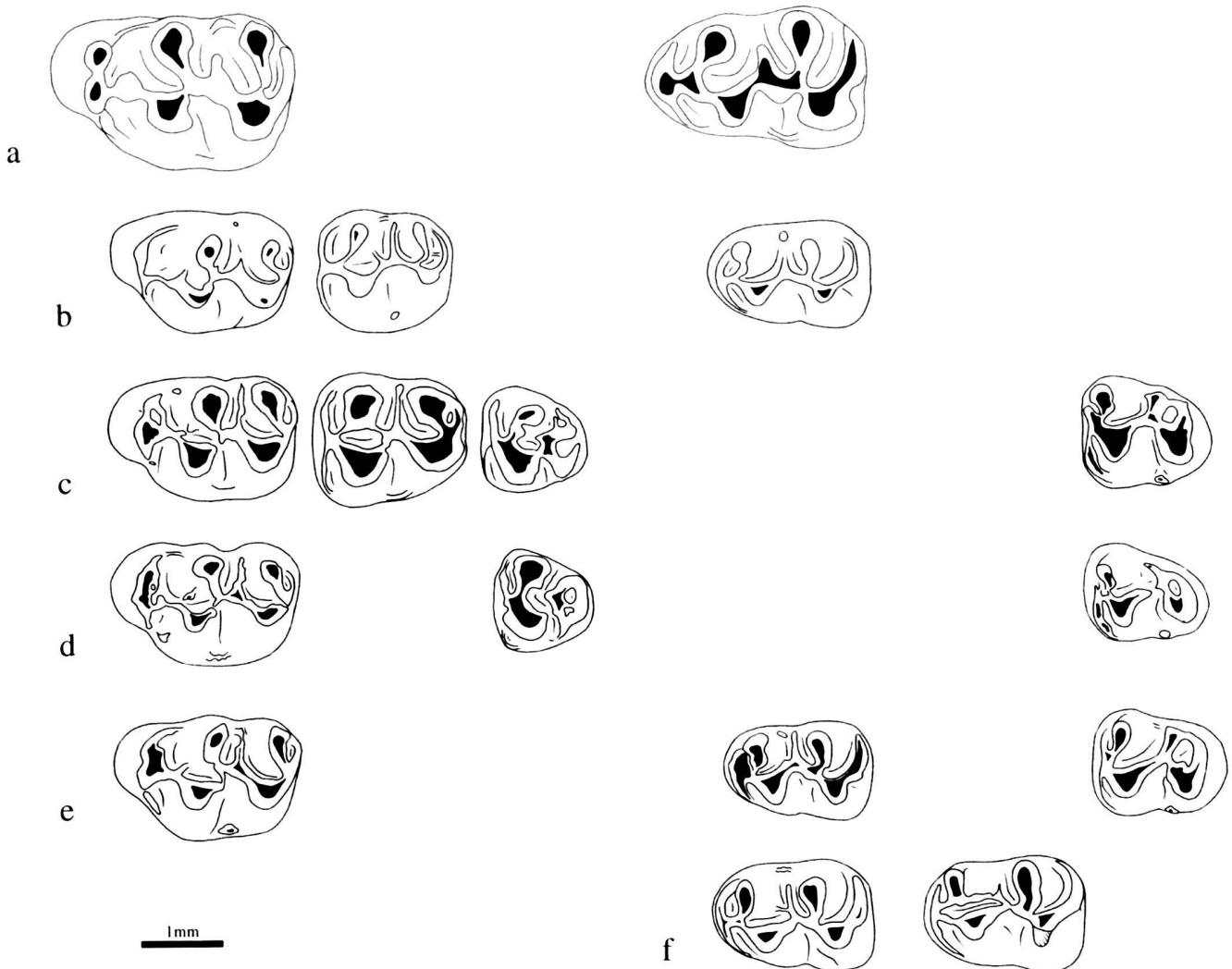


Fig. 1. Dentition (M^1 – M^3 and m_1 – m_3) of *Lartetomys zapfei* and *Lartetomys mirabilis* from different localities. All figures 12.5:1.

- a. *Lartetomys mirabilis* from Vieux-Collonges.
 M^1 sin. F.S.L. 65660, holotype. m_1 dext. (invers) F.S.L. 65661, paratype.
- b. *Lartetomys zapfei* from Vieux-Collonges.
 M^1 sin. F.S.L. 65662, holotype. m_1 sin. F.S.L. 65665, paratype.
- c. *Lartetomys* cf. *zapfei* from Uzwil-Nutzenbuech.
 M^1 dext. (invers) Uzw. 1, M^2 sin. Uzw. 2, M^3 dext. (invers) Uzw. 3, m_3 sin. Uzw. 4.
- d. *Lartetomys* cf. *zapfei* from Chatzloch.
 M^1 dext. (invers) Caz. 9, M^3 dext. (invers) Caz. 10, m_3 dext. (invers) Caz. 11.
- e. *Lartetomys* cf. *zapfei* from Belchatów B.
 M^1 sin. MF/2235/1, m_1 sin. MF/2235/2, m_3 sin. MF/2235/3.
- f. *Lartetomys* cf. *zapfei* from Neudorf. Redrawn from Fejfar (1974).
 m_1 sin. 733924, m_1 dext. (invers) 733925.

of Basle, A. Garapich recognized the presence of *Lartetomys* in the Polish fauna Belchatów B. Although the total number of all newly collected teeth is only 14, we have decided to publish that material due to the general scarcity of the genus *Lartetomys*, the insufficient knowledge of its tooth morphology, and its poorly known stratigraphical and geographical range.

Measurement and determination of the new material

Based on the tooth morphology; thick enamel, undivided anterocone, extremely short anteroconid and some other features and also based on the size, we are dealing with a species closely related to *Lartetomys zapfei* MEIN & FREUDENTHAL, 1971.

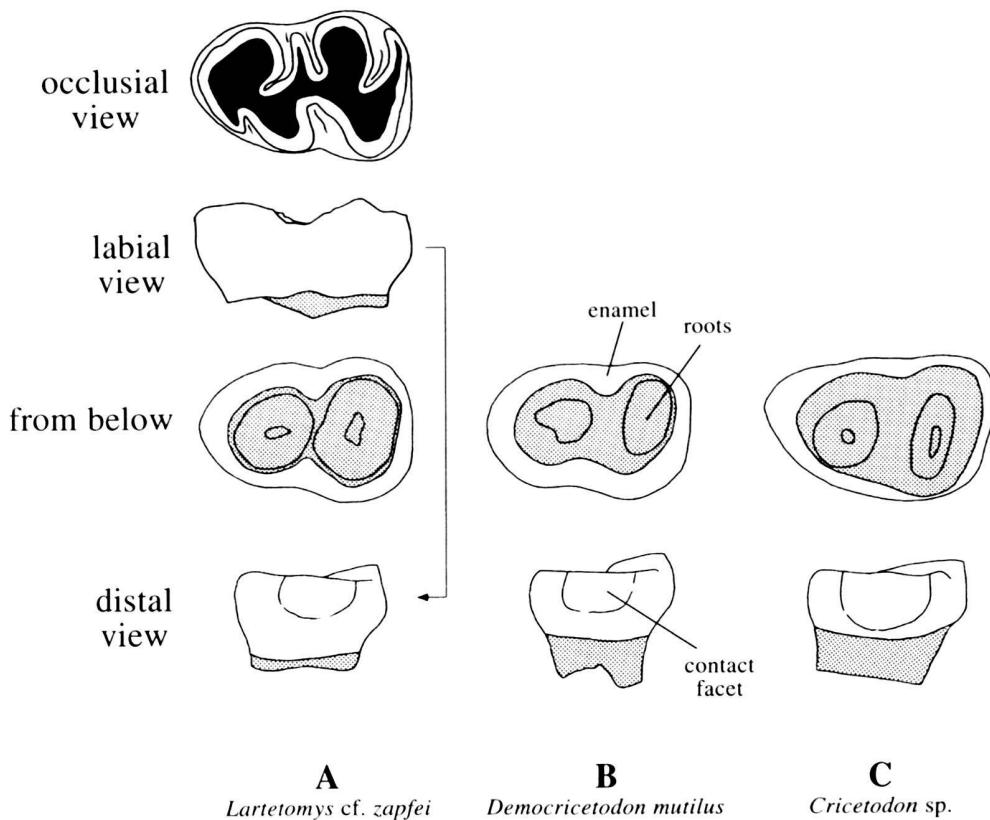


Fig. 2. Severely worn m_1 of *Lartetomys* cf. *zapfei* from Belchatów B in occlusal and lingual view, from below and in distal view compared with severely worn m_1 of *Cricetodon* sp. from Rümikon (MN 6) and severely worn m_1 of *Democricetodon mutilus* from Vermes 1 (MN 5), both from below and distal view. Not to scale.

A: *Lartetomys* cf. *zapfei* from Belchatów B. m_1 dext. (invers) MF/2235/4.

B: *Cricetodon* sp. from Rümikon. m_1 sin. Rüm. 9.

C: *Democricetodon mutilus* from Vermes 1. m_1 sin. KV. 89.

Description of the new material

Terminology after Mein & Freudenthal (1971b).

Locality Uzwil-Nutzenbuech (Fig. 1, c)

M^1 dext.

The anterocone is broad, with only a minor tendency to splitting. The labial cingulum joins the paracone. The massive anterolophule is placed centrally behind the anterocone. A protolophule I exists only rudimentally. The connection protocone-entoloph is interrupted. The thin mesoloph is long, attached to the base of the metacone and reaching the labial border of the tooth. On the lingual side a small entostyl is visible. The metalophule is directed backwards and joins the posteroloph behind the hypocone. The posteroloph is short and joins the metacone, so the posterosinus is very small. Three roots are identifiable.

M^2 sin.

The M^2 is longer than it is broad. The labial anteroloph is well developed, better than the lingual part. The first synclines are very narrow. The long, marked mesoloph reaches the labial border of the tooth and ends in a small mesostyl. The thick, massive posteroloph joins the metacone and encloses, as for M^1 , a small posterosinus. Three roots are identifiable.

M^3 dext.

The anteroloph is strongly asymmetrical. In both teeth the labial part of the anteroloph is well developed. The labial part of the anteroloph is strongly reduced in one specimen and absent in the other [This feature differs from the original description given by Mein & Freudenthal 1981]. Both hypocone and metacone are strongly reduced. In one specimen the anterior part of the tooth is almost completely separated from the posterior part.

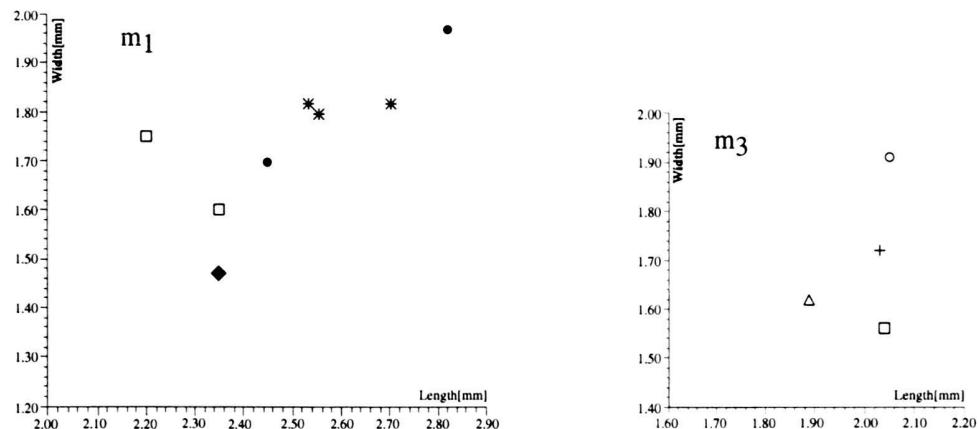
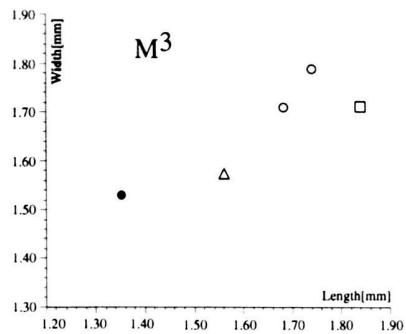
m_3 dext.

The anterolophid is strongly asymmetrical, the lingual part strongly reduced. The massive labial anterolophid is long and ends at the base of the protoconid. The protoconid is prominent, the metaconid relatively small. A marked ectostylyid is placed at the base of the prominent hypoconid. The entoconid is very small, the hypolophid extremely shortened. The hypoconid builds up most of the the posterior part of the tooth, the posteroloph is short, joining the entoconid. The posterosinusid is small.

Locality Chatzloch (Fig. 1, d)

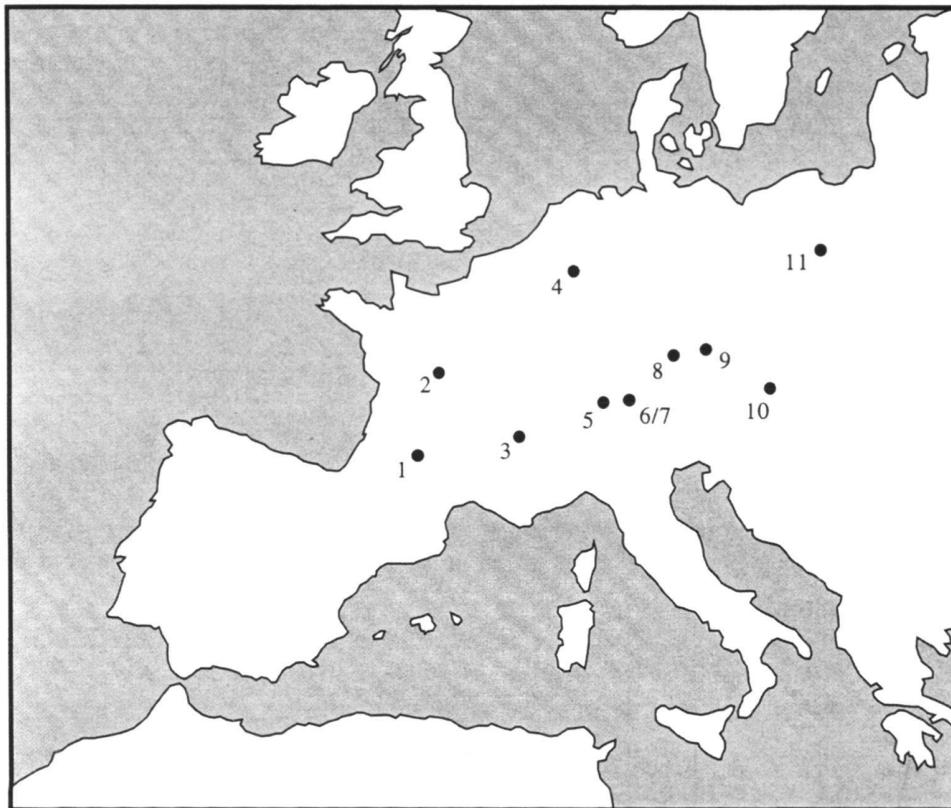
M^1 dext.

The broad and simple anterocone shows only a minor tendency to splitting. The posterior part of the anterocone on the



● <i>Lartetomys zapfei</i>	Vieux-Collonges	MN 4/MN 5	Values after Mein & Freudenthal (1981)
* <i>Lartetomys cf. zapfei</i>	Neudorf	MN 6	Values after Fejfar (1974)
○ <i>Lartetomys cf. zapfei</i>	Uzwil-Nutzenbuech	MN 6	
△ <i>Lartetomys cf. zapfei</i>	Chatzloch	MN 6	
□ <i>Lartetomys cf. zapfei</i>	Belchatów B	MN 6	
◆ <i>Lartetomys cf. zapfei</i>	Pont Levoy-Thenay	MN 5	Values after Ginsburg & Sen (1977)
+	Rümikon	MN 6	
■ <i>Lartetomys cf. zapfei</i>	Strakonice	MN 5	Values after Fejfar (1974)

Fig. 3. Scatter-diagrams of the molars of *Lartetomys zapfei* from different localities.



1 Birosse (Castelnau d'Arbieu)

2 Pont Levoy - Thenay

3 Vieux-Collonges

4 Hambach

5 Chatzloch

6 Rümikon

7 Uzwil-Nutzenbuech

8 Petersbuch

9 Strakonice

10 Neudorf

11 Belchatów B

Fig. 4. Geographical map of Europe showing the distribution of localities yielding findings of *Lartetomys*.

other hand is complicated, and the anterolophule is placed more lingually. A trace of a protolophule I may be seen at the base of the paracone. The connection protocone-entoloph is interrupted. On the lingual side the sinus is closed by a marked wall. The mesoloph is long and attached to the base of the metacone. The metalophule is massive and indistinctly separated from the hypocone. The posteroloph is short, encloses a small posterosinus and is fused with the metacone.

M^3 dext.

The anteroloph is asymmetrical, on the labial side well developed, on the lingual side practically absent. The protocone is not connected with the hypocone, so the anterior part of the tooth is completely separated by a ditch from the posterior part.

m^3 dext.

The anterolophid is strongly asymmetrical, the lingual part is absent. The labial anterolophid is long, descending to the base

of the protoconid. The protoconid is elongated, the following ectolophid interrupted. A marked ectostyliid is placed in front of the base of the hypoconid. The hypoconid itself is massive, in contrast to the very small, reduced entoconid. A kind of forward entoconid spur points towards the metaconid.

Locality Belchatów B (Fig. 1, e)

M^1 sin.

The M^1 shows a simple, broad anterocone with a tendency to splitting. The well-developed labial cingulum joins the paracone at its base. The lingual cingulum is also well developed. The anterocone is connected with the protocone by a lingually displaced anterolophule, which shows a well developed protolophule I. The paracone shows a short ectoloph, which is connected with the mesoloph. On the lingual side a small entostyl is placed at the aperture of the sinus. The mesoloph is long, reaching the labial border of the tooth, but is not at-

Tab. 1. List of localities yielding *Lartetomys*. There are further localities in France and in the Upper Freshwater Molasse of Bavaria (Germany), but this material was not available, nor is it published.

Locality	Country	Age	Literature
Vieux-Collonges	F	MN 4/MN 5	Mein 1958, Mein & Freudenthal 1971a
Neudorf (Devínska Nová Ves)	SK	MN 6	Schaub & Zapfe 1953
Strakonice	CZ	MN 5	Fejfar 1974
Pont Levoy-Thenay	F	MN 5	Ginsburg & Sen 1977
Birosse (Castelnau d'Arbieu)	F	MN 5	Baudelot & Collier 1978
Uzwil-Nutzenbuech	CH	MN 5/MN 6	Reichenbacher et al. 1998
Chatzloch	CH	MN 5/MN 6	Kälin 1997
Belchatów B	PL	MN 5/MN 6	Kowalski 1997
Rümikon	CH	MN 6	Fischli & Weber 1916, Engesser 1990: 130
Hambach	D	MN 6	Mörs 1997
Petersbuch 32	D	MN 6/MN 7	unpublished material Coll. M. Rummel

Tab. 2. Relative frequency of the genus *Lartetomys* in different cricetid populations.

Locality	No. of teeth (<i>Lartetomys</i>)	% of the cricetid fauna	total No. of the cricetid fauna
Vieux-Collonges	7 teeth	< 0.01%	>100 000
Uzwil-Nutzenbuech	5 teeth	~2%	280
Chatzloch	3 teeth	~2%	142
Belchatów B	5 teeth	~9%	57
Rümikon (new collection)	1 tooth	~0.2%	577

Tab. 3. Measurements of *Lartetomys* cf. *zapfei* from different localities in mm. M1sL = Length of an upper first molar, m2iB = Width of a lower second molar.

Locality	M1sL	M1sB	M2sL	M2sB	M3sL	M3sB	m1iL	m1iB	m2iL	m2iB	m3iL	m3iB
Uzwil-Nutzenbuech	2.97	2.06	2.33	1.88	1.68	1.72					2.05	1.91
					1.74	1.79						
Chatzloch	2.92	1.85			1.56	1.57					1.89	1.62
Belchatów B	2.92	1.81			1.84	1.71	2.35	1.60			2.04	1.56
							2.20	1.75				
Rümikon											2.03	1.72

tached to the base of the metacone. The short posteroloph encloses a small posterosinus. The greatest width is on the line paracone-protocone.

m_1 dext.

This tooth is severely worn (Fig. 2A). As a consequence, the massive anteroconid is fused with the metaconid. The mesolophid is long, nearly reaching the lingual border of the tooth. The sinusid is distinctly directed forwards. A long posterolophid terminates the tooth and encloses a tight posterosinus.

m_1 sin.

The massive, undivided anterolophid is extremely short and nearly fused with the metaconid. An anterolophid has not been formed. The mesolophid is long, reaching the lingual border of the tooth, ending in a mesostyliid. The strong posterolophid is long.

m_3 sin.

In both teeth the anterolophid is strongly asymmetrical. In one of these teeth the lingual anterolophid is poorly developed, in the other, absent. In one specimen a small entoconid is placed at the aperture of the sinusid.

Locality Rümikon

m_3 sin.

This tooth shows a simple tooth-pattern. The anterolophid is strongly asymmetrical, the lingual part absent. The entoconid shows a kind of a forward entoconid spur.

The most striking feature for all of the above described teeth is the thick enamel. Another attribute of the enamel is, that it carries on well under the body of the tooth (Fig. 2A). In this feature, *Lartetomys zapfei* is morphologically closer to *Democricetodon* than to *Cricetodon*.

Conclusions

With the exception of m_2 , all tooth positions of *Lartetomys* cf. *zapfei* are now known. In most features (thick enamel, extremely short anteroconid), the new material of *Lartetomys* cf. *zapfei* corresponds well to the type material of Vieux-Collonges. Nevertheless, there are some minor differences such as the longer mesoloph and the more complicated anterocone in the upper first molar or the narrower first synclines and the backwards directed metalophule in the upper second molar. This is the reason why we cannot assign the new material unreservedly to *Lartetomys zapfei*.

The greatest difference was found in the upper M^3 . According to a cast and the figure in Mein & Freudenthal (1981, Pl. 1, Fig. 7), in the M^3 from Vieux-Collonges the anteroloph is well developed on the labial as well as on the lingual side of the tooth. Additionally, the M^3 from Vieux-Collonges is not showing the characteristic thick enamel. So it is likely that this tooth (paratype, No. F.S.L. 65664) doesn't belong to the genus *Lartetomys* and certainly not to the species *Lartetomys zapfei*.

Since Mein & Freudenthal (1971a) the genus *Lartetomys* is regarded as Cricetidae incertae sedis. Within that genus, the larger species *Lartetomys mirabilis* shows affinities to the genus *Cricetodon*, LARTET, 1851. The species *Lartetomys zapfei* however shows striking affinities to the genus *Democricetodon* FAHLBUSCH, 1964 (see additionally Fig. 2). Based on the exceptionally large dimensions and the characteristic thick enamel it is not possible to include the species *zapfei* into the genus *Democricetodon*. In our opinion, and in agreement with Mein & Freudenthal (1971a) the species *mirabilis* and *zapfei* should be attributed to two different genera. The genus name *Lartetomys* however is occupied by the type species *Lartetomys mirabilis* (Mein & Freudenthal 1971a; p. 31). Therefore a new genus should be established for the species *zapfei*, based on a large amount of material.

As the species *Lartetomys zapfei* may not be incorporated into the genus *Democricetodon*, the systematic position of that peculiar cricetid remains unsolved. A contribution to that problem would be the investigation of the morphology of the maxilla and mandible as well as the structure of the enamel pattern ("Schmelzmuster") of the incisors. The incisors however, are still unknown.

Paleogeographic distribution

Especially during the Middle Miocene, rodent faunas were generally dominated by cricetids. Remains of the cricetid genus *Lartetomys* however seem to be very rare (normally < 1%). Since the first description by Schaub & Zapfe more than 40 years ago, only a few localities have yielded scanty additional material (Tab. 1).

As Figure 4 shows, the genus *Lartetomys* is restricted to central Europe. Remarkably, *Lartetomys* is recorded from two of the northernmost localities in Europe: Hambach, Germany and Belchatów B, Poland. Within those localities, *Lartetomys* seems to be more frequent than in all other mentioned localities (e.g. in Belchatów B 9%).

Stratigraphic range and ecological relations

With one exception (Vieux-Collonges), all findings of the genus *Lartetomys* are restricted to the MN-“zones” 5 and 6. Vieux-Collonges however, represents a karstic fissure filling with a faunal mixture of at least MN 4 and MN 5. So the guaranteed stratigraphic range for this particular cricetid genus is exceptionally short, MN 5 to MN 6.

In the Biozonation of the Upper Freshwater Molasse of Switzerland (in work), which is supported by dated bentonite layers and magnetostratigraphy (Kempf et al. 1997), this time interval correlates with the reference levels of Tobel Hombrichtikon to Rümikon. In numeric ages, the stratigraphic range of *Lartetomys* is restricted to approximately 0.9 Ma, ranging from 15.0 Ma to 14.1 Ma.

Quite remarkably, that time span coincides with the characteristic increase in ground-squirrels (especially *Heteroxerus*), which is recorded for rodent assemblages in Spain by Weerd & Daams (1978: p. 462) and for Central Europe (Swiss Molasse Basin) by Bolliger (1997: p. 510). This increase in ground-squirrels is interpreted by these authors as a shift towards a drier biotope, which correlates with the investigations and results of Van der Meulen & Daams (1992: p. 248). A drier biotope however is generally correlated with less “wet” nourishment and more “hard” nourishment (such as grains and nuts).

A characteristic feature for the teeth of *Lartetomys zapfei* is the striking thickness of the enamel, which gives a marked sturdiness to the teeth. This striking thickness of the enamel may be regarded as a specification and may be due to an adaptation to “harder and drier” food. In the case of *Lartetomys*, this adaption may not have been caused by abrasive foodstuff, which causes rapid tooth wear. It is more likely, that the thick enamel of *Lartetomys* represents a kind of “crack-dentition”.

There are other examples of specifications among cricetids, such as the genus *Melissiodon*, which is characterized by its especially thin enamel and its honeycomb teeth (German “Wabenmuster”). That combination is interpreted as an adaptation to “soft” or frugivorous nourishment (Mein & Freudenthal 1981, Kristkoiz 1992). The genus *Melissiodon* however is believed to have lived in wet habitats (Weerd & Daams 1978, Daams et al. 1988: p. 291).

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