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RESEARCH PAPER

Variation and complexity of the enamel pattern in the first lower molar of the common pine vole *Microtus subterraneus* (L., 1761) (Mammalia: Rodentia: Arvicolinae)

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Abstract. We investigated the variation in complexity of the lower first molar M_1 of the common pine vole *Microtus subterraneus*. Eight different morphotypes were found. The M_1 with additional structures was significantly longer than the '*typica*' morph. This structural gain is not caused by alternating dentin triangles, as known from *Microtus arvalis* or *M. agrestis*, but by a second 'pitymys' field in combination with a complete *anterior lobus*. This morphotype is named '*pitymys* +'. Two possible routes towards increased complexity are described and depicted schematically. It depends on whether, initially, the *anterior lobus* narrows to the '*maskii*' morph, and the new and complete anterior lobe will be constricted in the following step out of the remaining loop. Alternatively, additional anticlines are first formed at the anterior lobe, and the constriction of the second '*pitymys*' rhombus takes place in the next step.

Key words: dental morphology, tooth variability, masticatory efficiency, small mammals

Introduction

The occlusal surfaces of the molars of rodents of the subfamily Arvicolinae show a characteristic pattern of angles and folds along the lingual and labial borders of the teeth. Their shape is of particular diagnostic importance. They are a distinctive feature used for the discrimination of genera and species, but also display considerable intraspecific variation, particularly in the first lower molar M_1 (Kapischke et al. 2009, Kapischke & Kuhlisch 2016, Jentzsch & Lorenz 2019). Such forms can, in turn, occur in different species and genera in similar forms as homologous series (Ognev 1950, Angermann 1974). Minor deviations in form are neglected in classification, which leads to a 'coarsening of the facts' (Angermann 1974). This is evidence of evolutionary and intraspecific shape change (Guthrie 1971, Kapischke et al. 2009, Seelig et al. 2021).

The '*pitymys*' rhombus on M_1 is an important identifying feature of the common pine vole *Microtus subterraneus*, along with twelve other species (Kryštufek et al. 1996, Markova 2014), and is used to distinguish it from other Arvicolinae tooth patterns (Gaffrey 1961, Niethammer & Krapp 1982, Turni

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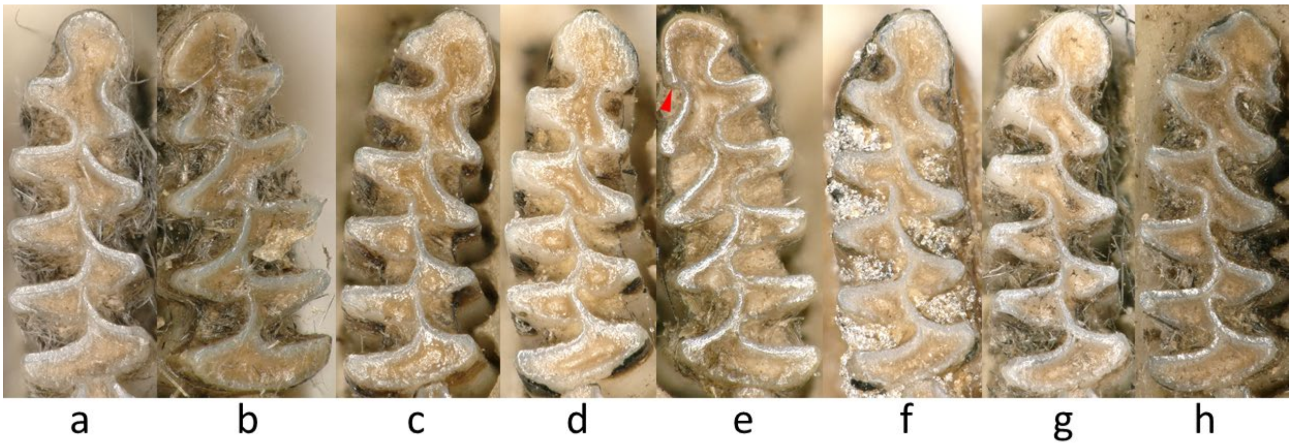

Fig. 1. Variants of the first lower molar (M_1) of the common pine vole, *Microtus subterraneus* (a – '*typica*', b – apical knob swaged, c – lingually additional salient angle on the anterior loop, d – almost '*maskii*', e – buccally implied additional salient angle (red arrow), f – buccally pronounced additional salient angle and incomplete second '*pitymys*' rhombus, g – '*maskii*', h – '*pitymys* +').

1999). The nomenclature of this tooth form dates from the earlier categorisation of the short-eared mouse in the genus *Pitymys* (Kraft & Kapischke 2008).

Based on the respective '*typica*' morph, the variability of molar pattern, especially of M_1, has been described by numerous authors (e.g. Angermann 1974, Zahreddin 1989, Kapischke et al. 2009). Additional data on aberrations of M_1 in *M. subterraneus* populations from different German counties and some single findings from Romania and Bulgaria are presented.

Material and Methods

The skulls and lower jaws were collected at different times and locations in Germany, Bulgaria and Romania (see Table S1). Because it was not always possible to match the mandibles to each other, only the available M_1 are considered below. The material was lent from different collections: Museum Mauritianum Altenburg (28 M_1), Senckenberg Museum of Natural History Görlitz (17), Museum of Natural History Erfurt (2) and the private collection of Dr. Dietrich von Knorre (83), Dr. Martin Trost (16), and the first author (22). A total of 91 left and 77 right M_1 were included, of which 38 M_1 occurred in pairs (Table 1). Most of the material was extracted from owl pellets, and some specimens were trapped. The study refers to the total material because much of the material occurred as single skulls and mandibles or as small series per location. Summarising all the material was beneficial for the length measurements in connection with the occurrence of the various morphs to obtain the greatest possible amount of data for analysis.

The determination of species has been proven by the discriminant analyses of Kraft & Kapischke (2008). Altogether, 168 M_1 were classified according to the criteria for dental morphs proposed by Grummt (1961), Angermann (1974) and Zahreddin (1989) and supplemented by intermediate stages. Only the material from Saxony, Saxony-Anhalt, and Thuringia with at least 28 analysable teeth was used for regional comparisons of the frequency of morphs.

Microsoft Excel (version 2019, Microsoft Corporation, Redmond, Washington, USA) was used for the data collection and processing and the creation of selected diagrams. The IBM SPSS Statistics program (version 23, SPSS Inc., Chicago, Illinois, USA) was used for further descriptive and inferential statistical analyses.

The length measurements of the M_1 were carried out for statistical analyses using the corresponding function of the VHX-5000 digital microscope from KEYENCE. The data for the two different groups ('*typica*' and non '*typica*') were compared. The molar lengths were normally distributed, as shown by the Kolmogorov-Smirnov test and visual analysis using Q-Q diagrams (Weiß 1999). A test for homogeneity of variance between the groups was also carried out for the molar lengths using the Levene test (Weiß 1999). Significant mean differences between the two groups were determined using an independent samples t-test (du Prel et al. 2010).

Results

Morphotypes of M_1

A total of eight different morphotypes were identified (Figs. 1a-h). In general, the M_1 of the common pine vole has a rounded apical knob of the anterior loop, five lingual and four buccal salient angles (5/4), three closed triangles, and the typical '*pitymys*' rhomb (forma '*typica*'; Fig. 1a). Based on this form, the anterior loop can be distinctly swaged in some molars (Fig. 1b)

Table 1. Proportion of the respective morphs in the total number of analysed M_1 per region in % (n = number).

Region	Year of collection	Morph type (n lingual/n buccal salient angles, applied angle in brackets)						
		‘*typica*’ 5/4	apical knob swaged: 5/4	lingually additional salient angle on anterior loop: 6/4	buccally implied additional salient angle on anterior loop: 6/(5)	almost ‘*maskii*’ 5/4	‘*maskii*’ 5/4	‘*pitymys* +’ 6/5
Bulgaria (n = 2)	1974	-	-	-	-	50	50	-
Romania (n = 8)	1993	12.5	-	87.5	-	-	-	-
North Rhine-Westphalia (n = 2)	1990	50	50	-	-	-	-	-
Saxony (n = 28)	1970-2004	7.1	53.6	3.6	-	28.6	7.1	-
Saxony-Anhalt (n = 33)	2004-2018	9.1	18.2	9.1	-	48.5	15.1	-
Thuringia (n = 95)	1968-2017	42.1	28.4	6.3	2.1	17.9	2.1	1.1
Total (n = 168)		28.0	29.1	10.1	1.2	25	6.0	0.6

and shows lingually an additional salient angle (6/4; Fig. 1c) that resembles that of a knight chess piece. The anterior lobe is similar to that of *Microtus oeconomus* (Pallas, 1776), but otherwise, the whole molar has the typical pattern of *M. subterraneus*. Other patterns show almost or completely constricted anterior lobes (5/4, ‘almost *maskii*’, Fig. 1d; 5/4 ‘*maskii*’, Fig. 1g). The latter presents two complete ‘*pitymys*’ rhombuses, but only an incomplete anterior lobe. Another development towards increased molar complexity can be seen in the case of a buccally implied additional salient angle (6/(5); Fig. 1e, red arrow), followed by a buccally pronounced additional salient angle and incomplete second ‘*pitymys*’ rhombus (6/5; Fig. 1f). The most significant increase in structure is shown by an M_1 from Weiden in Thuringia, in which a second ‘*pitymys*’ rhomb appeared and a complete *anterior lobus* with two salient angles was formed (Fig. 1h). To emphasise the existence of a second ‘*pitymys*’ rhomb, we propose the term ‘*pitymys* +’ for this morph. The two similar morphs, ‘*typica*’ and ‘*typica*’ with swaged apical knob, were the most common in our study (57.1%), followed by ‘*maskii*’ and almost ‘*maskii*’ (31%). There are differences between the regions. While the ‘*typica*’ morphs are also the most common in Saxony and Thuringia, those of Saxony-Anhalt revealed the ‘*maskii*’ morph with the highest frequency (Table 1).

Twenty of the 38 pairs of left and right M_1 showed symmetrical structures (52.6%), five in the ‘*typica*’ morph (13.2% of all pairs, 25% of all symmetrical pairs). In the 18 pairs of asymmetric M_1, there was no tendency in favour of one side of the body in relation to the more complex structure: eight pairs showed the more complex structure in the left M_1 and ten pairs in the right. The average length of all first lower molars was 2,350 ± 106.1 µm (mean ± SD). The length of the only M_1 showing the ‘*pitymys*‘ morph was 2,419 µm and belonged to the top fifth (20.8%) of all tooth lengths.

The length of the ‘*typica*’ molars was 2,320.5 ± 93.5 µm, and of the non ‘*typica*’ molars 2,362.0 ± 108.8 µm. The distribution of molar lengths of M_1 among study groups is shown in Fig. 2. There were no differences in the homogeneity of variance in molar length between the groups ($P = 0.424$). However, there were significant differences in molar length between the two groups ($P = 0.022$).

Discussion

While the different enamel types of teeth are mainly functionally determined, the taxonomic value of the

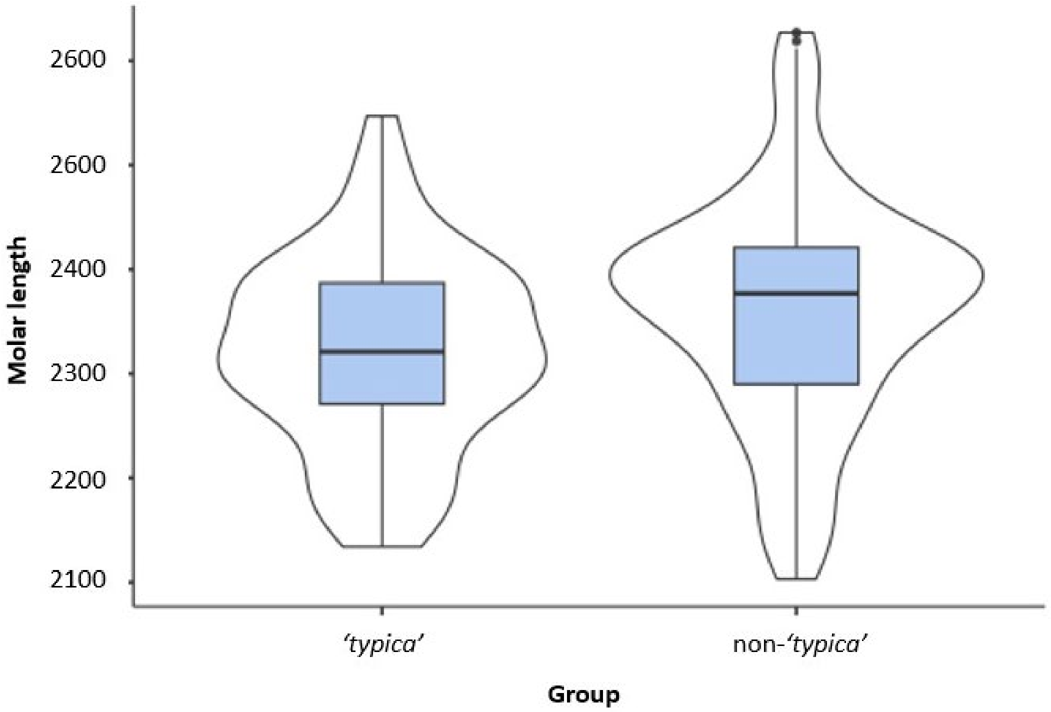

Fig. 2. Violin plot illustrating the distribution of molar lengths (in μm) for the two groups examined.

enamel structures is limited primarily to the level of enamel patterns (von Koenigswald & Pfretzschner 1991). The changes in enamel patterns can be attributed to functional differences (Herrmann 2002), whereby this development is subject to morphological limits (Polly 2012). The complexity of the molars follows a linear morphogenetic gradient along the molar row (Herrmann 2002, Seelig et al. 2021) and environmental factors such as climate or the availability and composition of the diet play a distinct role in the development of such morphs, along with the lifestyle of the species (Renaud et al. 2005, Piras et al. 2012, Seelig et al. 2021). Overall, the changes in the molars are mediated by the ecology of the animals (Seelig et al. 2021). In terms of feeding ecology, this ultimately corresponds to the thesis of von Koenigswald (1982) and Guthrie (1971) that a more complex structure of the tooth surface, i.e. the development of more partial surfaces, increases chewing efficiency and favours the mechanical crushing of hard plant parts.

While numerous identification keys refer to the typical tooth pattern of *M. subterranes* with the three closed dentinal triangles and the '*pitymys*' rhombus (forma '*typica*', e.g. Niethammer & Krapp 1982, Angermann & Hackthal 1995, Turni 1999), there are several publications dealing with different patterns and tooth morphs of this species (e.g. Zahreddin 1989, Kraft & Kapischke 2008, Barkaszi 2017). Many of these patterns are considered to be homologous series that occur in different species of Arvicolinae (Ognev 1950, Angermann 1974).

In most Arvicolinae, the structural gain of the first lower molar M_1 is due to an alternating gain of dentine triangles. In *M. agrestis* (Linnaeus, 1762), for example, the gain is described as starting from five closed dentin triangles ('*typica*') via a sixth buccal (Jentzsch 2006) to a seventh labial triangle (Kapischke et al. 2009). In contrast, our study reveals a different tooth development in *M. subterraneus*. The structural gain is achieved by a second '*pitymys*' field in combination with a complete *anterior lobus* ('*pitymys* +' morph). This morphotype is presented here for the first time. In the monograph of Mohr (1954), Fig. 76 comes closest to this variant, showing the *anterior lobus* of a '*maskii*' morph in which the salient angles of the new lobe are already faintly indicated.

In our mandibles, the increase in the structure of M_1 was accompanied by a significant increase in length. Comparable studies on *M. subterraneus* or other Arvicolinae were not available. Overall, the average lengths of different populations differ slightly from each other. The average value of the M_1 tooth lengths given in Niethammer (1972) is 2.53 mm. The same value for our mixed samples from different locations is lower at 2.35 mm. The average value of the nine mandibles from the Pleistocene from Serbia is between the two at 2.46 mm (Bogićević et al. 2012).

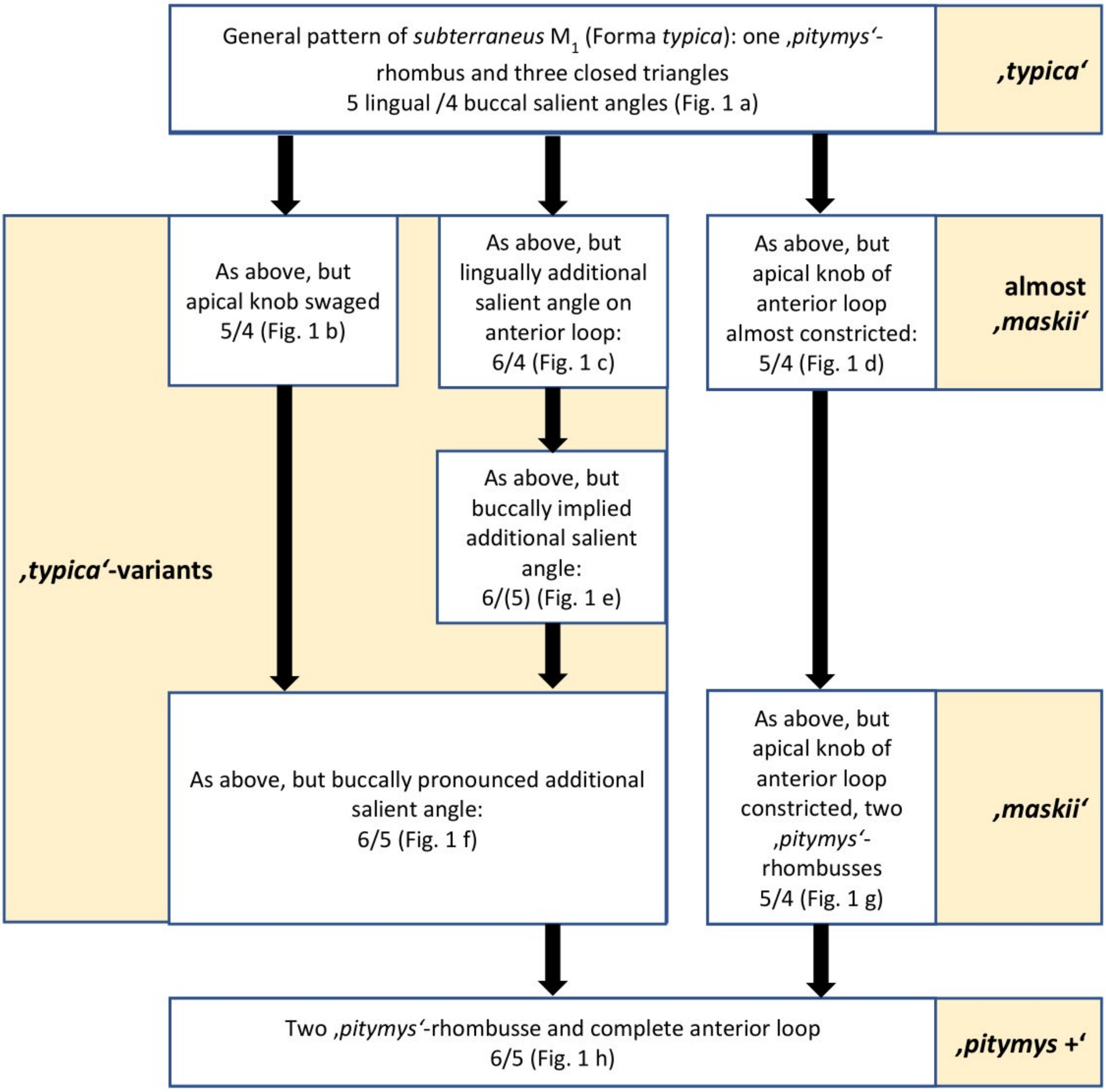

Fig. 3. Theoretically possible ways and intermediate steps of the gain in complexity in the pattern of the first lower molar of the common pine vole *Microtus subterraneus* towards the variant '*pitymys* +'. On the left side, the development runs through various '*typica*' variants, and on the right, through those of '*maskii*'.

These and the cited studies represent solely morphological studies. The extent to which genetic analyses can also substantiate the described intraspecific diversity could not be clarified in the present case due to the age and condition of the material and its origin, primarily from owl pellets. Including genetic data will be an essential approach for future investigations.

Two paths and intermediate steps up to the development of the '*pitymys* +' variant are conceivable (Fig. 3). Depending on whether the *anterior lobus* initially narrows to the '*maskii*' morph (which already shows the second '*pitymys*' rhombus) and the remaining loop subsequently develops to a new and complete anterior lobe, which is known from the '*typica*' morph of this species (Fig. 3, right). In this case, the proportion of '*maskii*' forms and transitions to '*maskii*' usually show high values in *M. subterraneus* specimens (Niethammer 1972, Angermann 1974, Zahreddin 1989, this study). This scenario is in contrast to the mostly low frequency of '*maskii*' patterns in *M. agrestis* and *M. arvalis* (Schimmelpfennig 1991, Jentzsch 2006, Kapischke et al. 2009), in which the increase in the structure is formed via alternating dentine triangles. As an alternative to the first variant, additional anticlines first form at the anterior lobe, and the constriction of the second '*pitymys*' rhombus takes place in the next step (Fig. 3, left).

The various stages proposed here for the development of the '*pitymys* +' variant are theoretical and based on only a small number of some morphotypes. Only ten molars with '*maskii*' 5/4 patterns were available, and only one of the newly described '*pitymys* +' 6/5 morph. This low frequency makes it difficult to generalise about the possible directions of development. Further investigations with a larger dataset would, therefore, be desirable. However, it is difficult to obtain a sizeable local series of the common pine vole from numerous sites, as it is rare in Europe compared to the more common *M. agrestis* and *M. arvalis*. For example, in the Red Lists of Germany, information on the species' occurrence is currently considered inadequate, but an Endangered status can be assumed (Meinig et al. 2009, Trost et al. 2020). Nevertheless, it would be interesting to see whether the significant increase in length of the more complex morphs that we have determined in our investigation is also visible in single local populations and in what proportions the different morphotypes occur in the current series.

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Author Contributions

M. Jentzsch – conceptualisation, methodology, photo documentation, measurements, data analysis and visualisation, writing, original draft, review and editing; A.S. Mühle – photo documentation, measurements, data analysis and visualisation, writing, R. Schreiter – methodology, statistics, data analysis and visualisation, writing. All authors read and approved the final manuscript.

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Supplementary online material

Table S1. Origin and geographical coordinates of the material investigated (https://www.ivb.cz/wp-content/uploads/JVB-vol.-74-2025-Jentzsch-M.-et-al.-Table-S1.pdf).