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

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> Abstract

The variation in complexity of the lower first molar, M_1, of the Field vole, *Microtus agrestis*, is investigated. Two possible routes towards increased complexity are described and are depicted schematically. It is concluded, that increased tooth complexity enhances masticatory efficiency.

> Key words

Arvicolinae, *Microtus agrestis*, dental morphology, enamel pattern, tooth complexity, masticatory efficiency.

Introduction

The grinding surfaces of the persistently growing molars of microtine rodents (Arvicolinae) show a peculiar pattern of salient angles and re-entrant folds along the lingual and labial borders of the teeth. Number, form, and relative size of transversal loops and alternating dental triangles, even though a distinctive feature for the discrimination of genera and species, are subjected to considerable intra-specific variation, in particular in the first lower molar, M_1 (Angermann, 1974; Schimmelpfennig, 1991, Kraft & Kapischke, 2008; 2009; Kapischke & Kraft, in press). In the Field vole, *Microtus agrestis*, variability of molar pattern had been described e.g. by Rörig & Börner (1905), Zimmermann (1956), Reichstein & Reise (1965), Reichstein (1966), Kapischke (1992), Locatelli & Paolucci (1995), and Jentzsch (2006). Aberrations from the general enamel pattern of the lower molars comprise the development of additional transversal loops or an increase in the number of constricted segments. Additional data for populations from different German counties are presented.

Material and methods

In the course of mapping the small mammal fauna of their home counties, the authors were able to sight large series of the Field vole from Bavaria (R. Kraft, M. Hiermeier), Saxony, Brandenburg, and Mecklenburg-Vorpommern (H.-J. Kapischke), and Saxony-Anhalt (M. Jentzsch, H.-J. Kapischke). The bulk of the material was extracted from owl pellets, more than 800 specimens were trapped. For details on localities, collectors, and storage of the samples see Kapischke (1992, in prep.), Jentzsch (2006), and Kraft (2008, p. 8 ff).

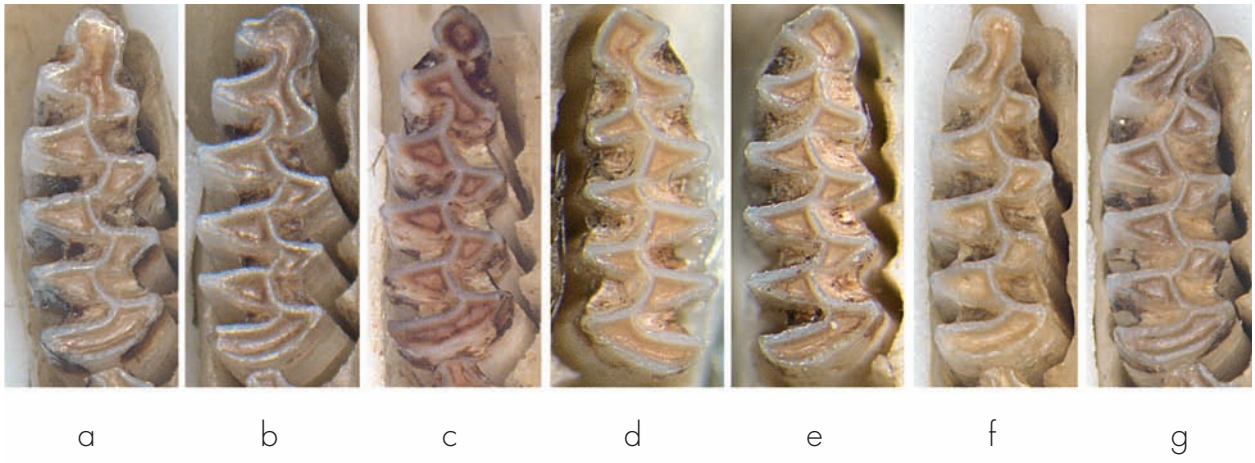

Fig. 1. Variants of the first lower molar of the Field vole, *Microtus agrestis*.

From about 2500 specimens, individuals with aberrant tooth pattern were sort out and classified according to the criteria proposed by ANGERMANN (1974), JENTZSCH (2006), and KRAFT & KAPISCHKE (2008).

Results

In general, the first lower molar of the Field vole has five closed triangles (T1 to T5), a crescent-shaped posterior loop and a more complex anterior one. The latter displays a labial and lingual transversal loop, T6 and T7, respectively (fig. 1 a).

Occurrence of an additional salient angle on anterior loop: the *oeconomus* + -morph

The apical knob of the anterior loop, that is round in most specimens (fig. 1 a), can display a pronounced edge on the lingual side, which represents an extension of the peripheral enamel sheet (fig. 1 b). With an anterior loop, that resembles that of a knight (chess piece), this molar is very similar to that of the Root vole, *Microtus oeconomus* (PALLAS, 1776), but has five instead of four closed triangles between anterior and posterior loop. Therefore, JENTZSCH (2006) proposed the term „*oeconomus*+-morph“ for this molar shape. The plus sign stands for the presence of the additional closed dental triangle. Beside the Field vole, the *oeconomus*+-morph had also been reported for the Common vole, *Microtus arvalis* (PALLAS, 1779), by KRAFT & KAPISCHKE (2008).

After “normal” this is the most common molar form in the Field vole populations. Approximately 25 % of the specimens examined show this additional salient angle on M_1 (Tab. 1). In most cases, this variant is symmetrically present on both sides and just occasionally on one side only.

Constriction of additional dental triangles

Another development towards increased molar complexity is by dividing the anterior loop of M_1 into two or three closed dental fields. This may happen by constriction of the apical knob of the anterior loop, resulting in the *maskii*-morph (fig. 1 c). The resulting rhombus can be partially or completely divided by longitudinal displacement of the angles T6 and T7 in the opposite direction, resulting in a molar with seven alternating dental triangles and a constricted apical knob. This was found in the right M_1 of a specimen from Brandenburg (fig. 1 e, KAPISCHKE, in prep.) and in the left M_1 of another specimen from Bavaria. In the corresponding opposite molars, however, only T6 is forming a closed dental triangle, whereas T7 is still confluent with the apical part of the loop (fig. 1 d) To emphasize the existence of seven closed alternating triangles in an arvicolid M_1, we propose the term “*arvalis/agrestis*++” for this morph, suspecting that this variation eventually will be located in *Microtus arvalis*.

In the specimen from Brandenburg, a small lingual edge or angle appears in outlines on the lingual side of the constricted apical knob (fig. 1 d, e), combining characters of the *arvalis/agrestis*++ morph with that of the *oeconomus*++ variant.

Starting either from the standard form or from the *oeconomus*+-morph, also the labial edge (instead of the apical knob) of the anterior loop can be separated by indentation of the re-entrant fold between T5 and T7, thus forming a sixth closed triangle, T6 (fig. 1 f). Also from this stage, the development of the *arvalis/agrestis*++ morph, is conceivable by successive constriction of T7.

Tab. 1. Occurrence of the described morphs of the first lower molar of Field voles in populations from Bavaria and Saxony-Anhalt

nos. of closed dental tringales between anterior and posterior loop	**5**		**5**		**5**		**6**		**6**		**7**		total	
	maskii-morph		additional salient angle (T8) on anterior loop (*oeconomus+*)		*maskii*-morph + additional salient angle (T8) on anterior loop		labial edge of anterior loop (T6) constricted:		labial edge of anterior loop (T6) constricted: + additional salient angle on anterior loop: (*oeconomus++*)		labial and lingual edge of anterior loop (T6, T7) constricted: („*arvalis/ agrestis++*")			
	fig. 1 c		fig. 1 b		–		fig. 1 f		fig. 1 d, g		fig. 1 e			
	left	**right**	**left**	**right**	**left**	**right**	**left**	**right**	**left**	**right**	**left**	**right**	**left**	**right**
Bavaria	4	4	93	99	3	5	17	17	9	8	1	-1	405	402
	1.0 %	1.0 %	23.0 %	24.6 %	0.7 %	1.2 %	4.2 %	4.2 %	2.2 %	2.0 %	0.2 %	0.2 %	100%	100%
population Drömling, Saxony-Anhalt	0	1	22	25	1	2	2	0	4	3	0	0	93	95
	0.0 %	1.1 %	23.7 %	26.3 %	1.1 %	2.1 %	2.2 %	0.0 %	4.3 %	3.2 &	0.0 %	0.0 %	100%	100%

In the *maskii*-M_1 as well as in other variants, the apical knob of the anterior loop can display a lingual salient angle T8 as in the *oeconomus+* morph (figs. 1 d, e, g). For variants with six closed dental triangles and a pronounced T8 on the anterior loop, the term *oeconomus++* (Kraft & Kapischke, 2008) is appropriate.

While in *Microtus agrestis* a single specimen with seven closed triangles in the M_1 has been already mentioned by Kapischke (1992), only up to six closed triangles are hitherto reported for the Common vole *Microtus arvalis* (e.g. Kraft & Kapischke, 2008, Abb. 3 e, f).

These different routes from the standard form to the most complex (arvalis/agrestis++-) morph are depicted schematically in fig. 2.

Discussion

Gradual development of supernumerary loops and constriction of alternating dental triangles on the M_1 via several intermediate morphs (e.g. *maskii, oeconomus+*, *oeconomus++*), nearly always has its origin in the anterior loop. Hence changes towards increased complexity in the lower molars always start from the mesial part of the tooth. It is noteworthy to mention that the same is reported for several phylogenetic lines within microtine rodents, e.g. in Dicrostonychidae and for the line from *Allophaiomys* to *Microtus* (v. Koenigswald, 1982). When changes do occur in a more distal region of the molar, these are mostly reductions in complexity. Amongst many thousands of individuals of *Microtus arvalis* from the German counties Bavaria and Saxony, Kapischke & Kraft (in press, fig. 1 j, k) were able to find only two specimens that show a supernumerary loop on a more posterior part of the M_1. In the upper molars, however, it is always the posterior end that is subjected to analogous processes (v. Koenigswald, 1980).

It is emphasized by several authors (e.g. Guthrie, 1971), that an increase of enamel loops or triangles enhances masticatory efficiency and reduces abrasion of the grinding surface in microtine molars. Individuals with a more complex M_1 should be favoured within a population due to better exploitation of food. Therefore, such variants can demonstrate changes in the evolution of arvicolids from forms with a simple molar tooth pattern to those with a more complex one (v. Koenigswald, 1982).

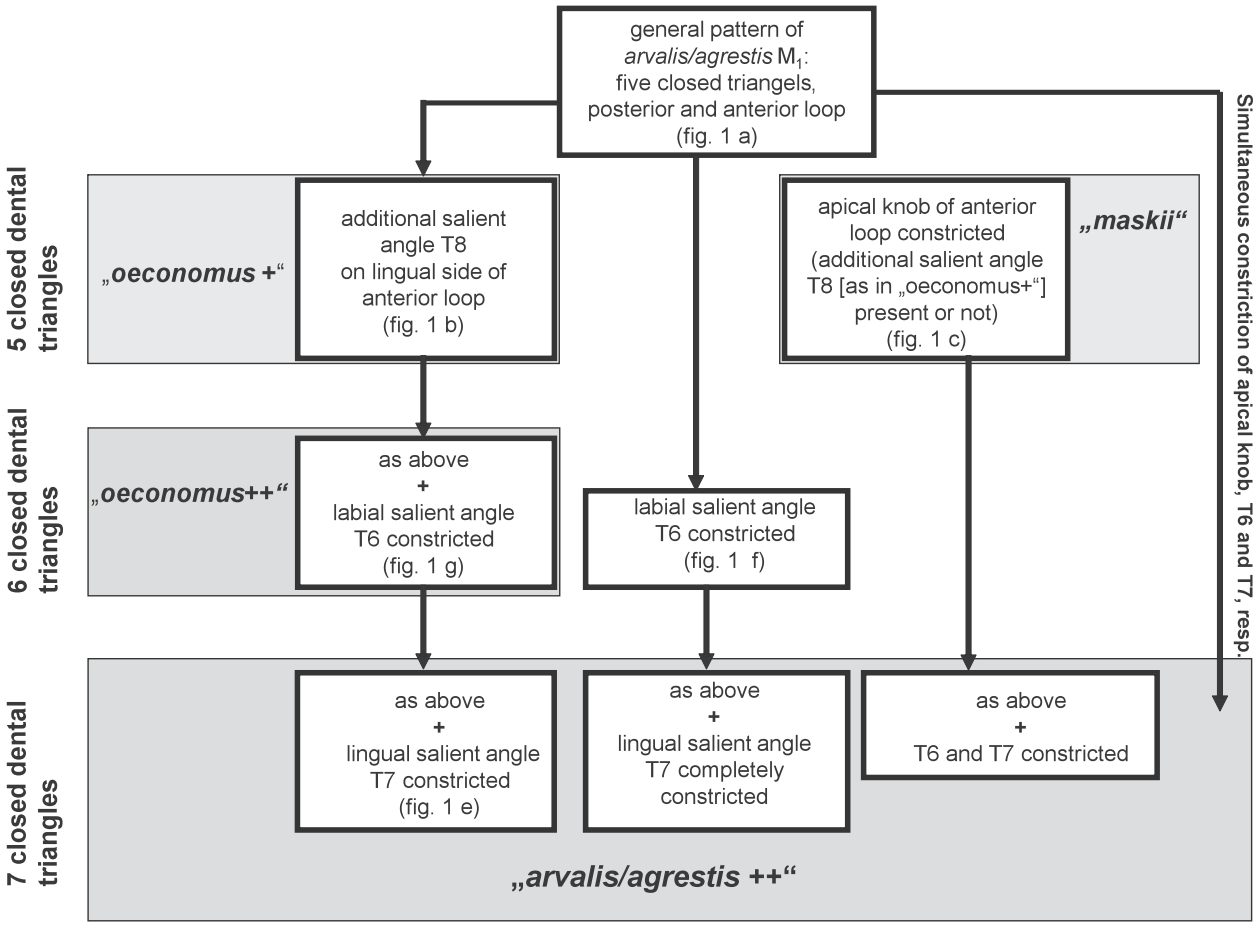

Fig. 2. Scheme of theoretical routes to complexity in the first lower molar of the Field vole, *Microtus agrestis*

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