

ENAMEL DIFFERENTIATIONS IN MYOXID INCISORS AND THEIR SYSTEMATIC SIGNIFICANCE

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ABSTRACT – Based on enamel microstructure of lower incisors, extant and fossil myoxids can be arranged into three groups. In the first group, Hunter-Schreger bands retain the plesiomorphic state, a transverse orientation. An oblique orientation is found in the second, and in the third group a longitudinal orientation is achieved. This additional morphological character should enter into phylogenetic and systematic discussions. This modification of the schmelzmuster is so far exclusively found in myoxids. Even if parallel evolution within myoxids cannot be excluded, a reversal of the direction of differentiation is most unlikely.

Key words: Enamel incisors, Myoxidae, Systematics.

RIASSUNTO – *Differenziazione dello smalto negli incisivi dei Mioxidi e suo significato sistematico* – I Mioxidi esistenti e fossili possono essere riuniti in tre gruppi in base alla microstruttura dello smalto degli incisivi inferiori. Nel primo gruppo, le bande Hunter-Schreger mantengono lo stato plesiomorfico, ovvero un orientamento trasversale. L'orientamento è obliquo nel secondo gruppo e longitudinale nel terzo. Questo ulteriore carattere morfologico dovrebbe essere incluso nelle discussioni di sistematica e filogenesi. Questa modificazione del tipo di smalto è stata finora riscontrata solo nei Mioxidi. Anche se non è possibile escludere una evoluzione parallela tra i Mioxidi, una inversione nella direzione di differenziamento è più improbabile.

Parole chiave: Smalto incisivi, Myoxidae, Sistematica.

INTRODUCTION

The ultrastructure of dental enamel has been shown to provide characters significant for biomechanical as well as systematic analyses. In most rodents, the incisor enamel is usually two-layered with a portio interna formed by Hunter-Schreger bands (HSB) and a portio externa formed by radial enamel. The thickness of the Hunter-Schreger bands may be used to differentiate major rodent groups (Korvenkontio, 1934; Wahlert, 1968), but the orientation of the interprismatic matrix (IPM) is of great significance, too (Boyde, 1984; Martin, 1992). Incisor enamel offers additional characters for systematic analysis that can be investigated in material of both fossil and extant taxa. Of the various levels of complexity within the enamel ultrastructure (Koenigswald & Clemens, 1992), that of schmelzmuster, the occurrence of different enamel types within one tooth, is significant for myoxid incisors. Although the Myoxidae have uniserial HSB, as do the Sciuromorpha and Myomorpha, the orientation of the HSB in the Myoxidae may differ from the transverse direction that is common among most rodents, a fact first recorded by Korvenkontio (1934).

RESULTS

Koenigswald (1993) investigated several fossil and recent Myoxidae including *Selevinia* (Table 1) and grouped them according to the modified schmelzmuster of the lower incisors. Since extensive descriptions and SEM-micrographs are presented there, only a brief summary will be given here.

SCHMELZMUSTER OF INCISORS IN RODENTS AS AN OUTGROUP

The schmelzmuster of the incisors of a wide range of rodents was investigated in order to specify the plesiomorphic character state for myoxids. In the Sciuromorpha and in myoinorph rodents the portio interna consists of uniserial HSB that are transversely oriented. The interprismatic matrix (IPM) is parallel to the prisms or at an angle to them in more derived taxa. In highly derived stages the IPM is at right angles to the layers of decussating prisms and reinforces a third direction; such a condition occurs in the Muridae (sensu latu). The outer layer, the portio externa, is formed by radial enamel in which all prisms are parallel and rise apically; the IPM is mostly at an right angles to the prisms. The outermost part of the portio externa may be formed by a fairly thin layer of prismless enamel, termed Plex by Martin (1992); it normally carries the pigmentation of the enamel (Dotsch & Koenigswald, 1978).

The schmelzmuster of lower and upper incisors is identical in all but the highly derived stage. If differences occur, the upper incisors tend to be more conservative (Fig. 1).

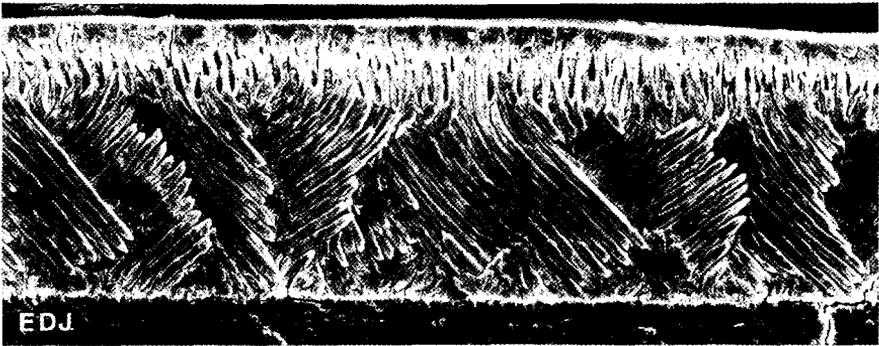


Fig. 1 – Micrograph of cross-section of the upper incisor of *Graphiurus murinus* [KOF 1536] with uniserial Hunter Schreger bands parallel to the occlusal surface. Most myoxids retain this orientation in the upper incisors. Bar equals 30 μ m. EDJ = Enamel dentine junction.

Variations of this plesiomorphic schmelzmuster were found in *Marmota* where the HSB change in thickness (Koenigswald, 1990).

Several rodent lineages have convergently modified the orientation of HSB of lower incisors. In the Rhizomyidae (*Tachyoryctes*), Spalacidae (*Spalax*), Myospalacinae (*Myospalax* and *Prosiphneus*) the HSB, seen in tangential view, rise from both sides apically and show an anticline in the middle (Korvenkontio, 1934; Koenigswald, 1993). In contrast the Dipodoidea (*Allactaga*, *Alactagulus*, *Jaculus* and *Pygeretmus*) show vertical HSB without a central anticline;

Tab. 1 – Myoxid taxa investigated for this study: The material was determined (det.) and dedicated (ded.) by many helpful colleagues. Abbreviations for collections the material came from: NHMB = Naturhistorisches Museum Basel, Switzerland; BSPM = Bayerische Staatssammlung für Hist. Geol. u. Paläontologie, Munich, Germany; KOE = Enamel collection Koenigswald, Institute of Paleontology, Bonn, Germany; SMF = Senckenberg Museum, Frankfurt a.M., Germany; SMNS = Staatliches Museum für Naturkunde, Stuttgart, Germany; ZPP = Paleozoological Institute of the Polish Academy of Science, Warsaw, Poland; ZMM = Zoologisches Museum of the Lomonosov University, Moscow, Russia.

<i>Anthracoqlis nitarnoi</i> Engesser 1983,	upper Miocene, Bacinello VI,	KOE 1557 det. B. Engesser ex NHMB
<i>Dryomys nitedula</i> , (Pallas 1778),	extant, Kleinmalm, Niedere, Tauern, Austria	KOE 923 ex Col. Niethammer 1227
<i>Dryomys nitedula</i> (Pallas 1778),	extant, Jugoslawia,	KOE 1504 ex SMF19 791
<i>Eliomys (Hypnomys) isp.</i> ,	upper Pleistocene or Holocene, Pen Majol (Mallorca)	KOE 1002, det. H. de Bruijn
<i>Eliomys (Maltamys) golicheri</i> (Bruijn 1966);	Pleistocene, Mnaidra Gap, Malta,	KOE 999 det. H. de Bruijn
<i>Eliomys (Maltamys) wiedingensis</i> Zammit Maempel & Bruijn 1982,	Pleistocene, (<i>Leithia-casteri</i> -Stufe), Għar-Dalam-Cave Malta,	KOE 1505 leg. G. Storch 1970
<i>Eliomys (Tyrrhenoglis) majori</i> Engesser 1976,	upper Pliocene, Capo Figari (Sardinia),	KOE 1559 det. B. Engesser ex NHMB
<i>Eliomys quercinus</i> (L. 1766),	extant	KOE 961 ex Slg J. Niethammer
<i>Eliomys quercinus</i> (L. 1766),	extant, Trier/Mosel,	KOE 966 ex Col. J. Niethammer
<i>Gilwavis</i> sp.	Oligocene, Le Bretou (MN 32),	KOE 1639 det. J.L.Hartenberger
<i>Girulus japonicus</i> (Schinz 1845),	extant, Japan,	KOE 1500, Shusaku Minato ded
<i>Graphiurus murinus</i> (Desmarest 1822),	Kanyawara, extant	KOE 1536 ex SMNS 26323
<i>Graphiurus</i> sp.,	Rietfontein/Windhoek,	KOE 963 ex Col. J. Niethammer
<i>Muscardinus avellanarius</i> (L. 1758),	extant,	KOE 962 ex Col. J. Niethammer
<i>Muscardinus avellanarius</i> (L. 1758),	extant, Mosel,	KOE 965 Col. J. Niethammer
<i>Microdyromys miocaenicus</i> Baudelot 1965 ,	Miocene (MN 6), Sansan	KOE 1558 det. B. Engesser ex NHMB
<i>Microdyromys aegericii</i> Baudelot 1972,	Miocene (MN 6), Steinberg/Nördlinger Ries,	KOE 995, 1560 ex BSPM 1970 XVIII
<i>Microdyromys biradiculw</i> Mayr 1979,	Miocene (MN4), Petersbuch 2, Frankische Alb,	KOE 1550, 1563 ex BSPM
<i>Myomimus qafzensis</i> Haas 1973,	upper Pleistocene, Qafze, LAYER 17, Israel,	KOE 1539, det. E. Tchernov
<i>Myomimus roachi</i> (Bate 1937),	extant, Edirne/Turkey,	KOE 1503 ex SMF 77286
<i>Myomimus roachi</i> (Bate 1937),	upper Pleistocene, Ilayonim Cave, LAYER B, Israel,	KOE 1538, det. E. Tchernov
<i>Myoxus glis</i> (L. 1766),	extant, Tübingen	KOE 35
<i>"Peridromys brailloni"</i> (Thaler 1966),	Petersbuch 2, Frankische Alb, Miocene (MN4),	KOE 1549, 1562 ex BSPM
<i>Plioselevinia gromovi</i> Suliniski 1962,	Pliocene, Weze/Poland	KOE 994 ex ZPP M.Z. VIII. Vm - 328/1
<i>Selevinia belpakdalaensis</i> Belosludov & Rashanov 1938;	extant, Kazakistan, Karagandinskaia obl. Ulatau,	KOE 912 ex ZMM S-110990 leg. I Stogov 1977
<i>Selevinia belpakdalaensis</i> Belosludov & Bashanov 1938;	rezent, Kazakistan, Dzherkazganskaia obl. 40 km S of Karsakpai,	KOE 913 ex ZMM S-145124, leg. I Stogov 09.1977

in a transverse section the HSB are aligned like a fan (Koenigswald, 1993); the IP is always at an angle to the prisms. Vertical HSB were found in Eomyidae as well, but here they appear in transverse section to be folded or angled (Wahlert & Koenigswald, 1985).

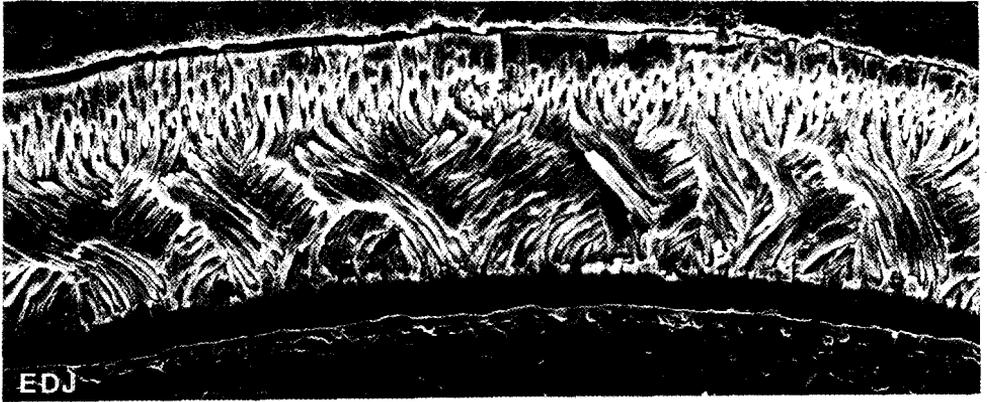


Fig. 2 – Micrograph of a cross-section of the lower incisor of *Myoxus glis* [KOE 35] with uniserial Hunter Schreger bands almost parallel to the occlusal surface. This is characteristic for group 1. The transverse orientation is shared with most rodents and regarded as the least derived character stage. Bar equals 30 μm . EDJ = Enamel dentine junction.

The various groups preserve radial enamel in the portio externa even if the orientation of the HSB is modified.

This short survey indicates that within a few rodent groups the orientation of the HSB has been modified in different ways, but no obvious correlation of these modifications can be found either to a specific diet or to a predominant activity like borrowing.

The modifications of the schmelzmuster in the Myoxidae are described according to three groups of significantly different orientation of the HSB.

FIRST MYOXID GROUP

The extant *Myoxus glis*, *Glirulus japonicus*, and the Oligocene *Gliravus* sp. share a uniform schmelzmuster. In the lower incisors the portio interna is of transversely oriented, uniserial HSB (Fig. 2). Only in the middle, between the mesial and lateral sides, are the HSB slightly inclined. The IPM is parallel to the prisms. The prisms change direction abruptly where they turn into the radial enamel of the portio externa, and the prisms disappear within the Plex, which is very thick in these genera.

The upper incisors retain the strict transverse orientation of the HSB. The radial enamel of the portio externa is only visible in the innermost part of this layer. The main part of this layer is formed by a Plex.

SECOND MYOXID GROUP

This group contains *Anthracoqlis marinoi*, *Dryomys nitedula*, *Eliomys quercinus*, *Eliomys (Hypnomys) sp.*, *Eliomys (Maltamys) gollcheri*, *Eliomys (Maltamys) wiedincitensis*, *Eliomys (Tyrrhenoglis) majori*, *Leithia melitensis*, *Microdryomys miocaenicus*, and "*Peridyromys*" *brailloni*. The schmelzmuster of the lower incisors is characterized by diagonally oriented HSB in the portio interna (Fig. 3). They rise from the lateral to the mesial side with about 45° to the longitudinal axis of the tooth. The IPM is parallel to the prisms. The portio externa is formed by a well developed prismatic enamel. The orientation of the prisms is not quite apical as in radial enamel; instead, the prisms are rotated laterally and retain the right angle to the rotated HSB. In contrast to the portio interna, the IPM is at right angles to the prisms within the portio externa. A Plex is very thin or missing.

The upper incisors retain an unmodified schmelzmuster with transversely oriented HSB and radial enamel.

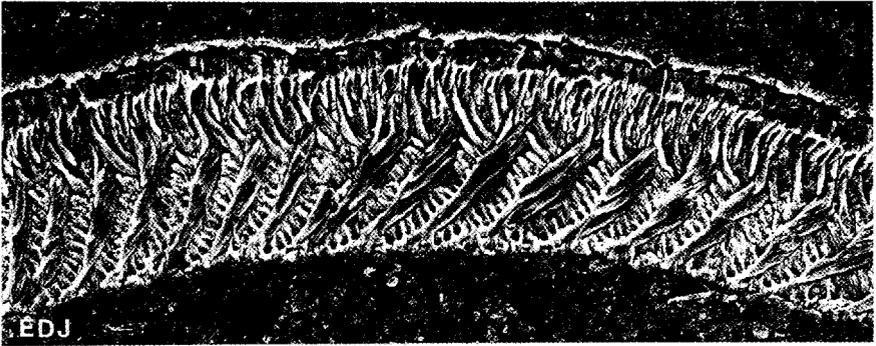


Fig. 3 – Micrograph of a cross-section of the lower incisor of *Dryomys nitedula* [KOE 963] with uniserial HSB intersecting the cross-section with about 45° typical for group 2. Bar equals $30 \mu\text{m}$.

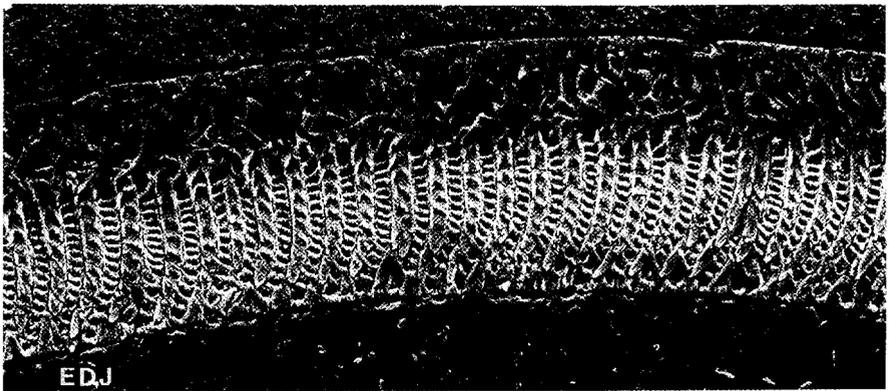


Fig. 4 – Micrograph of a cross-section of the lower incisor of *Muscardinus avellanarius* [KOE 923] with longitudinally oriented uniserial HSB in the portio interna. This is typical for the most derived group, group 3. Close to the EDJ, the interprismatic matrix forms an angle with the prisms. The portio externa is formed by tangential enamel. Bar equal $30 \mu\text{m}$. EDJ = Enamel dentine junction.

THIRD MYOXID CROUP

Of the taxa studied the following species belong to this group: *Graphiurus murinus*, *Graphiurus* sp., *Miodyronzys aegercii*, *Miodyromys biradiculus*, *Muscardinus avellanarius*, *Myomimus qafzensis*, *Myomimus roachi*, *Plioselevinia gromovi*, and *Selevinia betpakdalaensis*. The schmelzmuster of the lower incisors is characterized by a strictly longitudinal orientation of the HSB within the portio interna (Fig. 4). While prisms of one band rise apically, those of the neighboring bands descend. The IPM is basically parallel to the prisms but a distinctive inner zone with IPM at an angle is present in most genera. The portio externa is formed by tangential enamel with prisms directed mesially and thus retaining a right angle to the prisms of the portio interna. A Plex, if present, is very thin.

The upper incisors retain the unmodified schmelzmuster as in the second group.

DISCUSSION

In comparison to other rodents the tendency to rotate the HSB within the portio interna while retaining a consistent angular relationship with prisms of the portio externa is a synapomorphic character for Myoxidae including *Selevinia*, which was previously regarded as an independent family.

Within the Myoxidae the three groups that are distinguished by the schmelzmuster of the lower incisors are not identical with the subfamilies proposed by Bruijn (1966, 1967) or Daams (1981) based on the molar morphology or those by Wahlert et al. (1993) based on cranial foramina. However, these systems disagree with each other as well.

Therefore the question must be asked: Are these three groups, defined by the schmelzmuster, phylogenetic clades or evolutionary grades? The direction of modification is obvious; according to outgroup comparison with other rodents, we can assume that transversely oriented HSB and radial enamel form the basic schmelzmuster. Therefore the three groups distinguished may be regarded as grades with an increasing rotation of the schmelzmuster.

In addition, the least derived myoxid group, which contains *Gliravus*, *Glirulus*, and *Myoxus*, is characterized by a thick Plex as a synapomorphy. According to the schmelzmuster *Muscardinus* does not fit into this group, even if cranial foramina indicate such a relationship (Wahlert et al., 1993). Several characters found in soft tissues indicate a highly derived position of *Muscardinus* that is very different from *Myoxus* (Bugge, 1985; Kratochvil, 1973; Vorontzov, 1967).

For the second group with diagonal HSB no proper synapomorphy has yet been found, and therefore it could be a transitional evolutionary grade towards the third group. However, it is striking that in the material investigated no transitional forms between the first and the second as well as between the second and the third groups were found. The systematic significance of this character is demonstrated by the fact that all taxa studied of the *Eliomys*-group (Meulen & Bruijn, 1982) belong to this one group. *Eliomys* and *Dryomys* are united by the arrangement of cranial foramina (Wahlert et al., 1993).

The third group is very uniform with longitudinally oriented HSB and the tangential enamel in the portio externa. Slight differences are found in the extend

of an inner zone with IPM oriented at an angle to the prisms. Even if the third group is only a grade but not a clade, some important phylogenetic information is obvious from the schmelzmuster. At least in this character the genera within this group, *Graphiurus*, *Miodyromys*, *Muscardinus*, *Myomimus*, *Plioseleviniu*, and *Selevinia*, are highly derived. The presence of this derived condition in *Miodyromys* from the Miocene MN6 indicates the great antiquity of this schmelzmuster. It is noteworthy that *Graphiurus* fits very well into this group with a highly derived schmelzmuster.

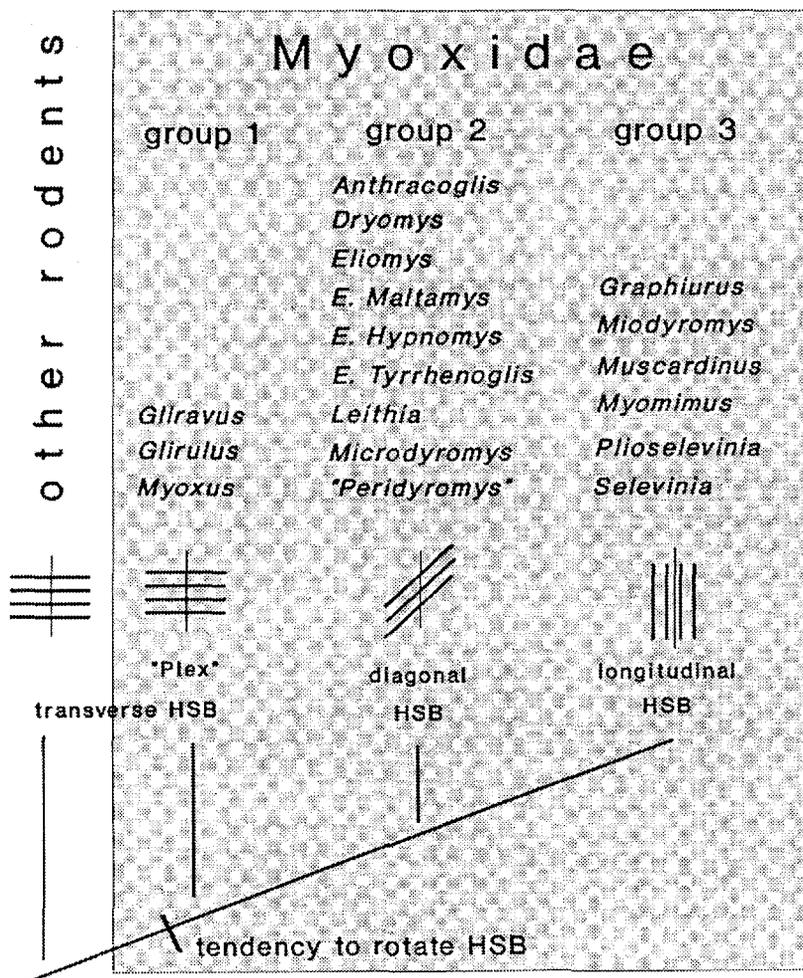


Fig. 5 – Grouping of fossil and extant myoxids according to the transverse, diagonal or longitudinal orientation of the Hunter-Schreger bands (HSB) in the lower incisors.

The idea to exclude *Graphiurus* from the Myoxidae as proposed by Vianey-Liaud & Jaeger (1993) and discussed by Storch (1995) is not supported by the structure of the enamel. On the contrary, *Graphiurus* shares a highly derived schmelzmuster with group 3 among the Myoxidae which is not known from any

other rodent outside this group. *Anomalurus*, which is discussed as the most likely sister group of *Graphiurus*, definitely has transverse HSB (Korvenkontio, 1934) and does not show any tendency to modify this plesiomorphic character in the direction of *Graphiurus*.

With the expectation of some degree of parallel evolution within the Myoxidae in molar morphology, in schmelzmuster, and perhaps in cranial foramina, I think it is much to early to transfer the three groups based on the schmelzmuster into specific systematic taxa. The aim of this paper is not to solve systematic problems by the analysis of the enamel only, but to draw attention to an additional character which can be checked out in fossil and recent material and which has a very clearly defined direction of evolution. Even if the schmelzmuster represents only grades, it would be very helpful since no genus from the first or second group should be derived from the third one. Therefore, the analysis of the highly diverse schmelzmuster in Myoxidae will contribute significantly to the systematic understanding of the this family as soon as the majority of the fossil genera are available for detailed inspection.

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