

Oligocene-Miocene Vertebrates from the Valley of Lakes (Central Mongolia): Morphology, phylogenetic and stratigraphic implications

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10. The enamel microstructure of molars and incisors of Paleogene and early Neogene rodents from Mongolia

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With 6 figures in the text and 1 table

Summary

The schmelzmuster of molars and incisors was studied in various taxonomic groups of fossil Mongolian rodents, which derived mainly from the joint Austrian-Mongolian expedition of the years 1995 to 1997 (FWF-Project: P-10505-GEO). The first-time joint discussion of molar and incisor enamel microstructure corroborated their independent evolution. In their molars, the Mongolian rodents show all three elementary types, the P-, S-, and the C-type of schmelzmuster, characterizing the various rodent families. The Mongolian material is phylogenetically important because of the stratigraphically earliest occurrences of the highly derived C-type schmelzmuster in the molars. Due to the limited number of clearly identified incisors, the Mongolian material shows only a selection of the expected schmelzmuster diversity. The incisors show schmelzmuster with multiserial as well as uniserial HSB.

Zusammenfassung

Das Molaren- und Inzisivenschmelzmuster in verschiedenen taxonomischen Gruppen fossiler Nagetiere aus der Mongolei wurde untersucht. Das Untersuchungsmaterial stammt zum Großteil von der in den Jahren 1995–1997 durchgeführten Österreichisch-Mongolischen Expedition (FWF-Projekt P-10505-GEO). Erstmals werden Molaren- und Inzisiven-Mikrostrukturen gemeinsam betrachtet, wodurch ihre eigenständige Evolution untermauert wird. Die Molaren der mongolischen Nagetiere zeigen die drei grundlegenden Schmelzmuster-Typen, den P-, S- und C-Typ, mit denen sich die verschiedenen Nagerfamilien kennzeichnen lassen. Das Fossilmaterial aus der Mongolei ist phylogenetisch von besonderer Bedeutung, da es eines der stratigraphisch ältesten Nachweise für den hochentwickelten C-Typ liefert. Aufgrund der begrenzten Anzahl eindeutig identifizierter Inzisiven, beinhaltet das Material nur einen Ausschnitt der erwarteten Schmelzmuster-Diversität. Die Inzisiven zeigen Schmelzmuster mit multiserialen als auch mit uniserialen HSB.

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Introduction

Mammalian teeth are used for crushing, grinding, and cutting. It is always the hardness of the enamel, which makes these tools so efficient in the process of energy intake. Thus enamel should be hard but not brittle and must not fracture in an uncontrolled fashion. Many structural details of the mammalian enamel microstructure can be interpreted as a protection against cracking (PFRETZSCHNER 1988, KOENIGSWALD & PFRETZSCHNER 1991). Different mammalian clades developed different ways to protect the enamel and reached different levels of enamel structural complexity. Thus tooth enamel contributes many aspects to the discussion of biomechanics, systematic, and phylogenetic investigations.

Tooth enamel is especially well suited for comparative studies since the highly mineralized material is often well preserved in the fossil record. Another advantage of the enamel microstructure is the very limited individual variation at the schmelzmuster level. The enamel formation is controlled by genetic and epigenetic factors and does not show reorganization during lifetime, as it is the case in bones. Thus, the teeth of fossil and extant mammals can be investigated with exactly the same method.

The enamel of rodent incisors is a classical field of microscopic investigation. KORVENKONTIO (1934) provided the first comprehensive analysis of a large sample of fossil and Recent mammalian taxa. Additional data were published by WAHLERT (1968). Detailed investigations of specific groups were conducted for the Caviomorpha (MARTIN 1992), the Myodonta (KALTHOFF 2000), the Eomyidae (WAHLERT & KOENIGSWALD 1985), and the Gliridae (KOENIGSWALD 1993). MARTIN (1997, 1999, 2004) described the incisor enamel of the earliest rodents and their sister groups among Glires.

The structural diversification of rodent molar enamel evolved independently from that in the incisors (KOENIGSWALD 1997a). The investigation of the enamel in rodent molars started with the Arvicolinae (KOENIGSWALD 1980, RABEDER 1981). It turned out that they show one of the highest degrees of complexity among mammals. Later the enamel of euhypsodont rodent molars was studied (KOENIGSWALD et al. 1994), and only recently a major survey of the molar enamel of most of the rodent families was published (KOENIGSWALD 2004a, 2004b).

In the present study, the results of molar and incisor enamel microstructure analysis in various rodents from the Mongolian Oligocene and early Miocene are summarized. In addition to material provided by several museum collections, the bulk of the material studied here comes from the joint Austrian-Mongolian expeditions of the years 1995 to 1997 (HÖCK et al. 1999) and were generously provided by Dozentin Dr. G. DAXNER-HÖCK, Vienna. Although some data have been partially published already, this report compares the molar enamel and the incisor enamel for the first time. It also provides a correlation between stratigraphy and the occurrence of the various schmelzmusters of Mongolian rodents.

Terminology used for the investigation of enamel

A glossary of the terms used for the description of mammalian enamel microstructure was published by KOENIGSWALD & SANDER (1997). For the better understanding, the

most relevant terms are explained here. Mammalian enamel is composed of *prisms* and *interprismatic matrix* (IPM). Prisms start at the *enamel dentine junction* (EDJ) and continue to the *outer enamel surface* (OES). Between the EDJ and the OES, prisms often change their direction. The various enamel types differ in the direction of the prisms and the orientation of the IPM.

The most relevant enamel types in rodent teeth are firstly *radial enamel* (RE) in which the prisms are parallel and rise more or less straight towards the occlusal surface. Secondly, layers of decussating prisms, which are parallel in each layer, form *Hunter Schreger-bands* (HSB). The prisms of adjacent layers decussate at a high angle, often at 90°. For rodent incisors, the thickness of these layers as measured in the number of cross-sections of prisms is of great significance. In rodent incisors, KORVENKONTIO (1934) distinguished *uniseriate enamel* (one prism thick bands), *pauciseriate enamel* (2-4 prisms) and *multiseriate enamel* (bands 5-12 prisms thick). In addition to the thickness of the HSB, features like the orientation of the IPM and of the prisms are important. MARTIN (1992) gives a detailed redefinition of KORVENKONTIO's pauciseriate and multiseriate enamel that includes the orientation of the IPM. HSB that are only one prism thick occur in molars of myodont rodents as well; here they are called *lamellar enamel* (KOENIGSWALD 1980, 1997b).

Several different enamel types may contribute to the enamel cap of a single tooth, and this three-dimensional arrangement of the enamel types is called *schmelzmuster* (KOENIGSWALD 1980). Within a dentition, the *schmelzmuster* of the different tooth categories may differ, especially when they show a very different morphology and function, as do molars and incisors in rodents.

In most cases, the *schmelzmuster* of the cheek teeth is similar in the upper and lower dentition, but may well differ in rodents between upper and lower incisors. If so, the lower incisor as the active gnawing tooth is generally more derived than the upper one. Thus the *schmelzmuster* of the lower incisors is more important for any systematic-phylogenetic interpretation.

Different types of *schmelzmuster* were defined for rodent molars (KOENIGSWALD 2004a) and for myomorph rodent incisors (KALTHOFF 2000). Those for the molars are designated by capital letters (P, S, and C) and those for incisors by numbers, which may be specified by small letters (e.g. 1a, 3a). For practical reasons, we follow largely the systematic scheme of MCKENNA & BELL (1997, 2002).

The *schmelzmuster* in molars

Despite the great morphological variability among rodent molars the diversity of the *schmelzmuster* is limited (Fig. 1). The *schmelzmuster* of rodent molars can be studied best in vertical sections. In brachyodont molars only three basic types of *schmelzmuster* were recognized. But these types are modified in various genera, especially when molars become hypsodont or even euhypsodont.

The least derived *schmelzmuster* in rodent molars is characterized by radial enamel only (P-type). The plesiomorphic type of *schmelzmuster* was found in some fossil Sciuromorpha, some Sciuravida, and Anomaluromorpha, but also in a few distinct myomorph rodents, which are fairly derived (KOENIGSWALD 2004a and b).

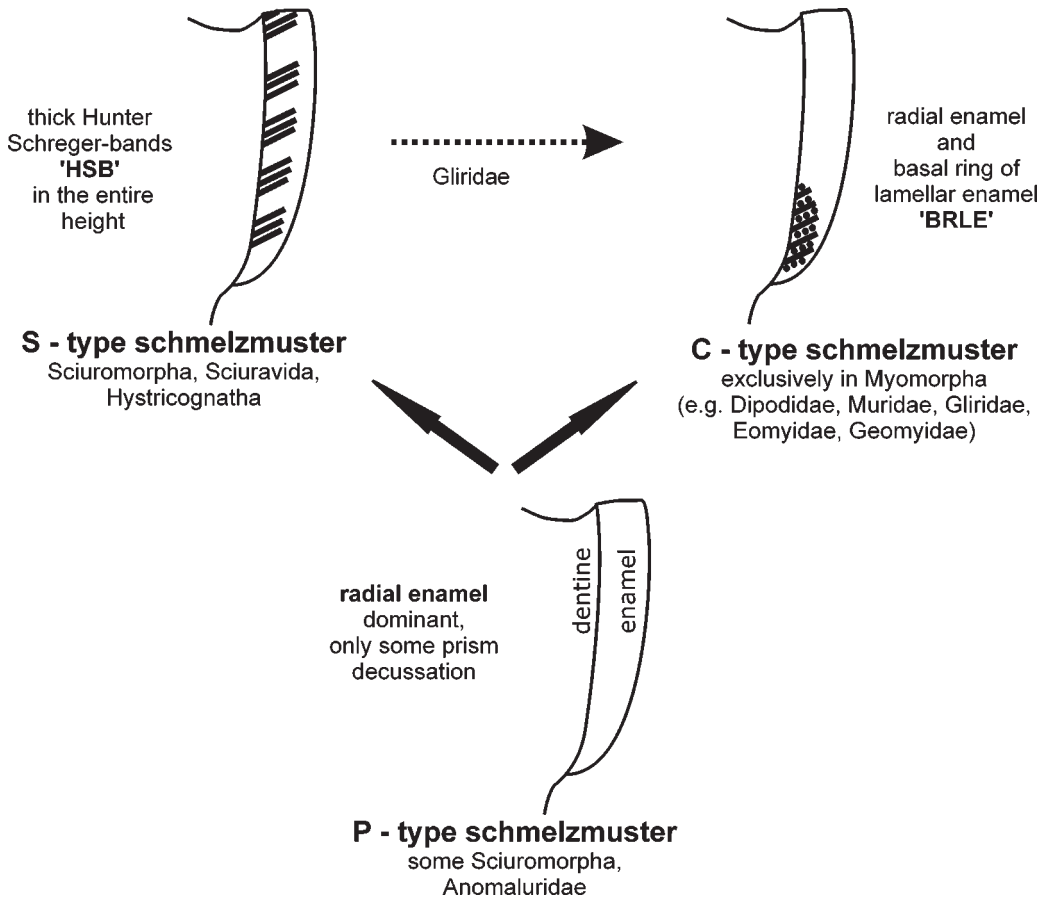


Fig. 1: The three basic types of schmelzmuster in rodent molars (after KOENIGSWALD 2004a). The P-type with radial enamel gave rise to the S-type with thick Hunter Schreger-bands and the C-type with the basal ring of lamellar enamel (BRLE). As an exception in glirids the BRLE evolved from the S-type schmelzmuster.

The teeth of most insectivores show a very similar schmelzmuster containing only radial enamel. This indicates the plesiomorphic character of this schmelzmuster. A more sophisticated differentiation of the schmelzmuster occurs in most mammals only with increasing body size going along with higher mastication forces. About the size of a hare or a hedgehog seems to mark the threshold above which HSB are introduced. This happened in the various mammalian lineages convergently (KOENIGSWALD 1997b).

Rodents are the only group of mammals to have HSB in their incisors and molars despite being much smaller than the above mentioned size limit. In molars, HSB are introduced in two different ways. Several groups (Sciuromorpha, Pedetidae within the Anomaluromorpha, Sciuravida, and Hystricognatha) evolved thick HSB in the entire height of the sidewalls of their cheek teeth. This derived type of schmelzmuster is defined as the S-type, of which *Sciurus* is a good example. The widespread occurrence of the S-type schmelzmuster indicates a convergent evolution in the various groups.

The various families of the Myodonta, Glirimorpha, and Geomorpha share a very different way to strengthen their enamel. In almost all investigated taxa a ring of lamellar enamel was found to surround the base of the crown while the upper part is formed by radial enamel. This "basal ring of lamellar enamel" was defined as BRLE (KOENIGSWALD 2004a). This highly derived schmelzmuster is called the C-type schmelzmuster since it was detected in the genus *Cricetus* for the first time (KOENIGSWALD 1980). This C-type schmelzmuster occurs very regularly in Dipodidae, Muridae, Eomyidae, Geomyidae, and Gliridae. The fossil record shows that the C-type schmelzmuster is derived from the P-type, except in Gliridae where it obviously is derived from the S-type schmelzmuster (KOENIGSWALD 2004a and b). Thus the BRLE does not form a synapomorphy of the Myomorpha (Fig. 1).

The schmelzmuster of the incisors

The continuously growing (euhypsodont) rodent incisors are covered with enamel only on the labial side. This enamel is generally two-layered, and a *Portio interna* (PI or inner region) can be distinguished from a *Portio externa* (PE or outer region). The PE is mostly formed by radial enamel and shows little differentiation except a variation in thickness. On the other hand, the enamel type forming the PI is highly important. Primitive rodents (Sciuravida and Ischyromyidae) are generally characterized by pauciserial enamel. The first true rodent so far known, *Acritoparamys*, has pauciserial enamel in the PI (MARTIN 1992, 1999). This schmelzmuster gave rise to the multiserial enamel in Hystricognatha (MARTIN 1992). The uniserial enamel characterizing the Sciurida and Myodonta was derived from pauciserial enamel as well. While in Sciurida the IPM is mostly parallel to the prism direction, in most derived Myomorpha a distinct angle between prisms and IPM forms an additional structural reinforcement. Within the Myomorpha, some rodent groups like the glirids show a further differentiation of the schmelzmuster since the initially transverse orientation of the bands compared to the growing axis of the tooth is modified to a longitudinal orientation (KOENIGSWALD 1993).

Most extant hamsters (Cricetinae) have transversely oriented HSB, but, surprisingly, some fossil hamsters and other myodont rodents show a much greater differentiation of the schmelzmuster. KALTHOFF (2000) defined different types of schmelzmuster in Myodonta, which vary in the orientation of the bands and the IPM. Within the myodont rodents, no less than 32 types and subtypes of schmelzmuster could be distinguished. Some of them occur both in lower and upper incisors, others are restricted either to lower or upper incisors. The 32 types and subtypes can be roughly categorized into four groups: (1) schmelzmuster with transversely oriented HSB and those with both transversely and diagonally oriented HSB (types 1 to 4); (2) schmelzmuster with diagonally oriented HSB (types 5 and 6); (3) schmelzmuster with longitudinally oriented HSB (types 7 and 8); and (4) schmelzmuster with longitudinally oriented HSB and a central syncline (types 9 to 11) (KALTHOFF 2000). In the Mongolian material, main types 1, 3, and 7 are represented (Fig. 2, Tab. 1).

Material and methods

Stratigraphically, the fossils are attributed to the Mongolian faunal horizons defined by HÖCK et al. (1999) (see Tab. 1). If known, specimens are listed with both their catalogue number of the collection of origin as well as their enamel collection number (KOE prefix).

Acronyms indicate the origin of the material as follows:

AMNH – American Museum of Natural History, New York.

CMNH – Carnegie Museum of Natural History, Pittsburgh (Dr. Mary Dawson).

DAS – Geological Institute, Mongolian Academy of Sciences, Ulaan Baatar (Dr. Demberelyin Dashzeveg).

KOE – indicates the numbers of the prepared specimen in the enamel collection of the Institute of Paleontology at the University of Bonn.

NHMW – Naturhistorisches Museum Wien, collected by the joint Austrian-Mongolian Expedition 1995-1997 (Dr. Gudrun DAXNER-HÖCK).

MYOMORPHA

Dipodidae

Heosminthus minutus, early Oligocene, Hsanda Gol Formation, Taatsiin Gol, TGR-AB/21, faunal horizon B; NHMW 2001z0033/0009/6 (molar), KOE 3620. Fig. 3a.

Heterosminthus gansus, late Miocene, Builstyn Khudang, BUK-A/12+14, faunal horizon E; NHMW 2001z0039/0002 (molar) and 0003 (I inf.), KOE 3217. Figs 3b, 5a, 5b.

Pappocricetodontinae

Pappocricetodon antiquus, Irдинmanhan, middle Eocene, Shuanghung Fissure D, Mongolia; CMNH (molar), KOE 3629. Fig. 3c.

Pappocricetodon antiquus, middle Eocene, IVPP V11018.611 - Loc. 93006, Shanghuang Quarry of Liyang County, Jiangsu Province, China; CMNH (I inf.), KOE 1842. Fig. 5c.

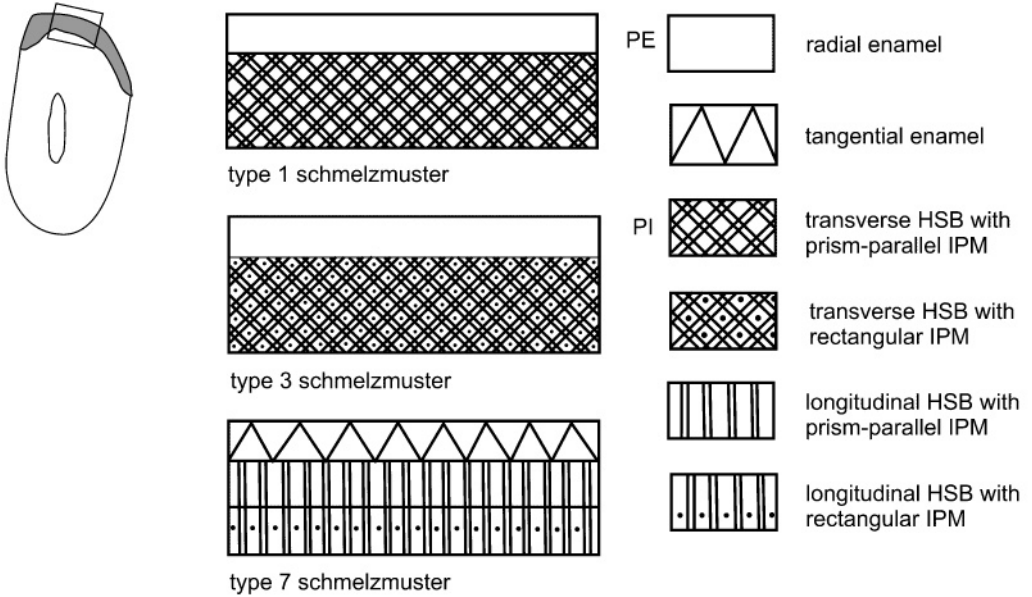
Muridae

Selenomys mimicus, early Oligocene, Hsanda Gol Formation, Tatal Gol (TAT-Basis), faunal horizon A; NHMW 2005z0087/0001 (molar) and 0002 (I inf.), KOE 2482. Figs 4a, 5d.

Cricetopidae

Cricetops dormitor, early Oligocene, Hsanda Gol Formation, Tatal Gol, (TAT-Basis), faunal horizon A; NHMW 2005z0088/0001 (molar) and 0002 (I inf.), KOE 3608 and KOE 2481. Fig. 4b.

Uniserial schmelzmuster types (best seen in transverse view)



Multiserial schmelzmuster (best seen in longitudinal view)

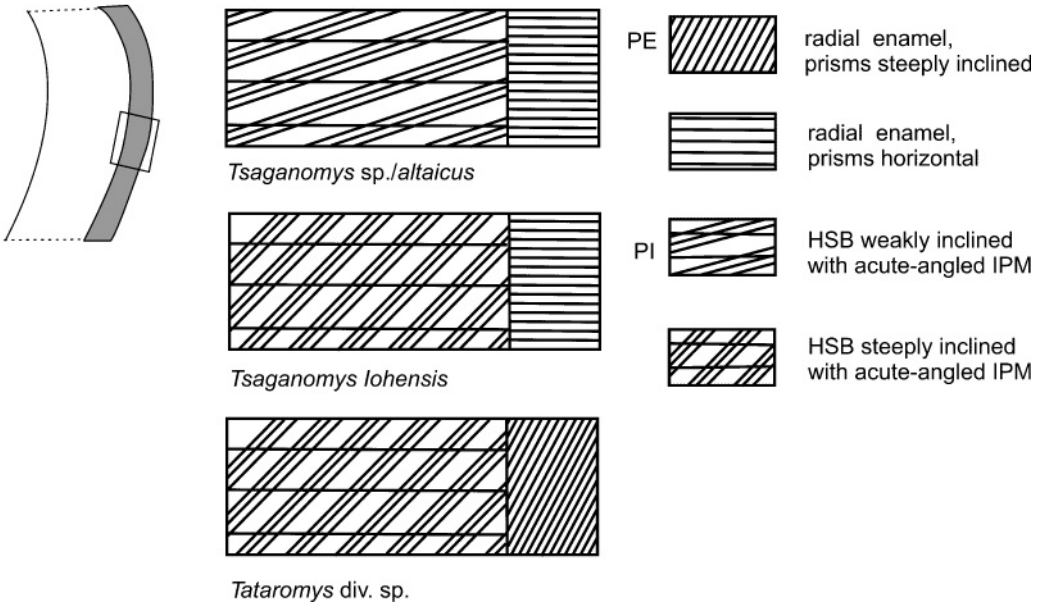


Fig. 2: Uniserial schmelzmuster types and multiserial schmelzmusters present in the analyzed rodent incisors from Mongolia (after MARTIN 1992 and KALTHOFF 2000)

Eucricetodontini

Eucricetodon sp. 2, late Oligocene, Hsanda Gol Formation, Taatsiin Gol (TGR-C), faunal horizon C; NHMW 2005z0089/0001 (molar), KOE 3609.

Tachyoryctoidinae

Tachyoryctoides kokonorensis, transition Oligocene-Miocene, Loh Formation, Unkheltseg (UNCH-A/3), faunal horizon D; NHMW 2005z0091/0002 (molar), KOE 3610 and KOE 3654. Fig. 4c.

Tachyoryctoides sp., transition Oligocene-Miocene, Loh Formation, Unkheltseg (UNCH-A/3), faunal horizon D; NHMW 2005z0091/0001 (I inf.), KOE 3120. Fig. 6a.

SCIURAVIDA

Cylindrodontinae

Ardynomys sp., late Eocene, Khoer Dzan, Ergilin Dzo Formation, Sevkhui Member; DAS PSS, 27/175 (I inf.), KOE 3127. Fig. 6b.

Ardynomys sp., late Eocene, Ardyn Obo Formation; AMNH 92219 A (I inf.), KOE 3255.

Ardynomys sp., late Eocene, Ardyn Obo Formation; AMNH 125647 (I inf.), KOE 847 (specimen published in MARTIN 1992).

Ardynomys russeli, late Eocene, Alag Tsav, ex DAS (molar), KOE 3658. Fig. 4d.

Ctenodactylidae

Tataromys sp., late Oligocene, Ulantatal (UTL 1), Alahan Zuoxi, Inner Mongolia; N. SCHMIDT-KITTLER (Mainz), KOE 1889 (molar and I inf.). Figs. 4e, 6c.

Tataromys sp. (small), late Oligocene, Ulantatal (UTL 1), Alahan Zuoxi, Inner Mongolia, N. SCHMIDT-KITTLER (Mainz), KOE 892 (I inf., published in MARTIN 1992 as *Leptotataromys*).

Tataromys sp. (large), late Oligocene, Ulantatal (UTL 1), Alahan Zuoxi, Inner Mongolia, N. SCHMIDT-KITTLER (Mainz), KOE 893 (I inf., published in MARTIN 1992 as *Leptotataromys*).

HYSTRICOGNATHA

Tsaganomys sp., early Oligocene, Hsanda Gol Formation, Tatal Gol (TAT), faunal horizon A; NHMW 2005z0092/0001 (molar), KOE 3655. Fig. 4f.

Tsaganomyidae indet., early Oligocene, Hsanda Gol Formation, Tatal Gol (TAT-Basis), faunal horizon A; NHMW 2005z0092/0002 (I inf.), KOE 2480. Fig. 6d.

Tsaganomys sp., early Oligocene, Hsanda Gol Formation, Tsagan Nor Basin, Outer Mongolia; AMNH 84328 (I sup.), KOE 853 (specimen published in MARTIN 1992).

Tsaganomys altaicus, early Oligocene, Hsanda Gol Formation, Tsagan Nor Basin, Outer Mongolia; AMNH 85202 (I inf.), KOE 854 (specimen published in MARTIN 1992).

Tsaganomys lohensis, early Oligocene, Hsanda Gol Formation, Tsagan Nor Basin, Outer Mongolia; AMNH 21661 (I sup.), KOE 848 (specimen published in MARTIN 1992 as *Cyclomys*).

Tsaganomys sp., early Oligocene, Hsanda Gol Formation, Tsagan Nor Basin, Outer Mongolia; AMNH 82289 (I inf.), KOE 849.

In rodent enamel preparation, either an entire tooth is taken or a small piece is cut off with a diamond-coated minidrill disk. For easier handling the specimen is embedded in polyester resin and, after hardening, cut in transverse and in longitudinal section. The next stages are grinding and polishing with 1200 corundum powder and subsequently 2-5 seconds of etching with 2N HCl to make the enamel details visible. After ultrasonic cleaning with distilled water, the specimen is mounted on a SEM stub and sputter coated with gold (circa 3 minutes). The teeth were studied and digitally documented with a CAMSCAN MV 2300 at magnifications from 100 to 2,500x. For the incisors, the description of the enamel microstructure always refers to a zone near the sagittal plane (FLYNN & WAHLERT 1978).

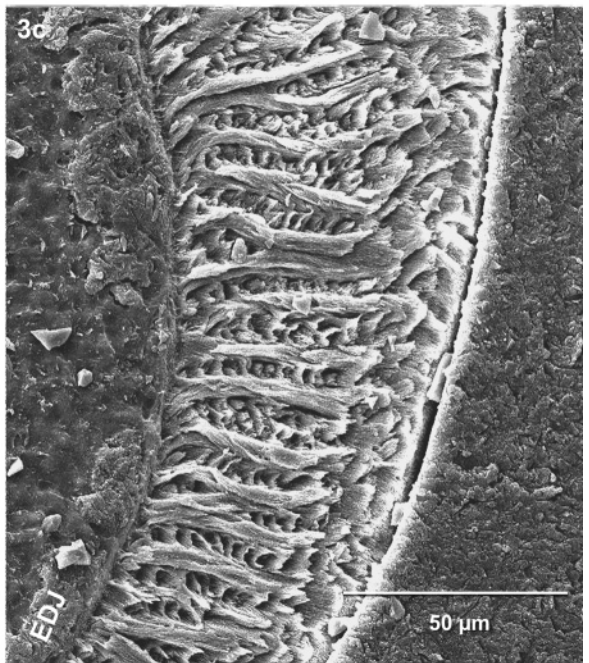
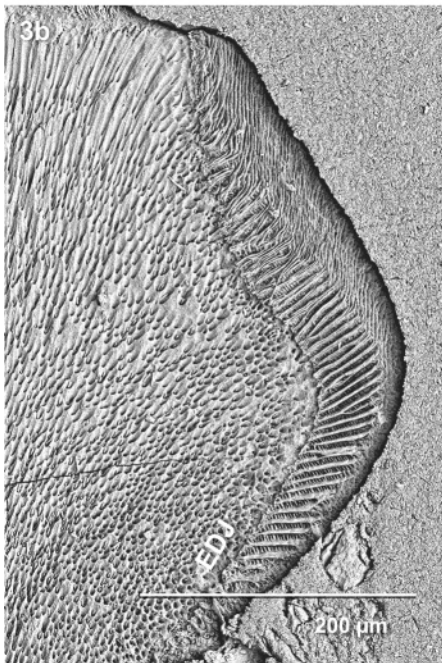
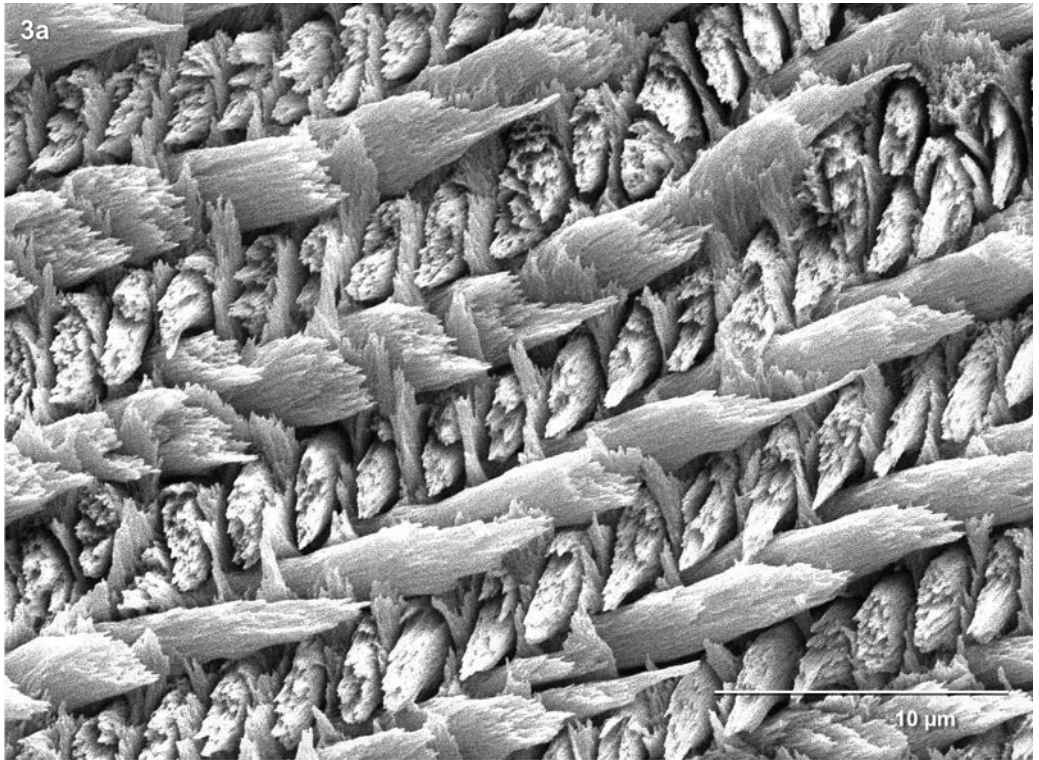
Enamel microstructure of the Mongolian rodents

Dipodidae

A molar of *Heosminthus minutus* from the early Oligocene shows well-developed lamellar enamel at the base of the tooth crown (Fig. 3a). This is the earliest documentation of the C-type schmelzmuster in the Dipodidae so far. For the systematic position of *Heosminthus* within the dipodids see DAXNER-HÖCK (2001). According to the phylogenetic and palaeogeographical reconstruction by DAWSON (2003), dipodids separated early from the "cricetids" and reached Europe only after the Grande Coupure (early Oligocene between MP 20 and 21). A second dipodid, *Heterosminthus gansus*, comes from the late Miocene of Mongolia. A longitudinal section exposing the buccal and the lingual side shows well-developed lamellar enamel on both sides, which is overlain by a layer of radial enamel. The upper part of the tooth crown is formed by radial enamel, too (Fig. 3b). This combination is a typical example for the C-type schmelzmuster, which was found in several other dipodids, including the extant ones (KOENIGSWALD 2004a).

The schmelzmuster of the lower incisors of *Heterosminthus gansus* is highly derived (Figs. 5a, b). In contrast to the transverse orientation in the basal stage, the uniserial HSB in the PI of *Heterosminthus* are oriented longitudinally. The IPM is arranged at

Fig. 3: Enamel microstructure of rodent molars from Mongolia. SEM images of vertical sections. – 3a. *Heosminthus minutus*, early Oligocene, Hsanda Gol Formation, Taatsiin Gol (KOE 3620). In the BRLE, the prisms decussate in uniserial horizontal layers with the IPM penetrating these layers vertically. – 3b. *Heterosminthus gansus*, late Miocene, Loh Formation, Builstyn Khudag (KOE 3217). The BRLE is best developed as an inner layer in the lower part of the molar crown. – 3c. *Pappocricetodon antiquus*, middle Eocene, Irдинmanham (KOE 3629). The earliest occurrence of a well-developed BRLE was documented in this genus from the middle Eocene. EDJ: enamel dentine junction.



an angle to the prisms but close to the margin PI to PE the IPM turns into a direction parallel to the prisms. The PE, which is formed by tangential enamel, is strongly reduced and only about 15 µm thick. This is only 15 % of the total enamel thickness. The longitudinal HSB together with the angled IPM and the reduced PE characterizes the type 7 schmelzmuster of the classification of KALTHOFF (2000). In order to avoid confusion, it should be noted that KALTHOFF (2000) described *H. gansus* under the genus name of *Lophocricetus* sp.

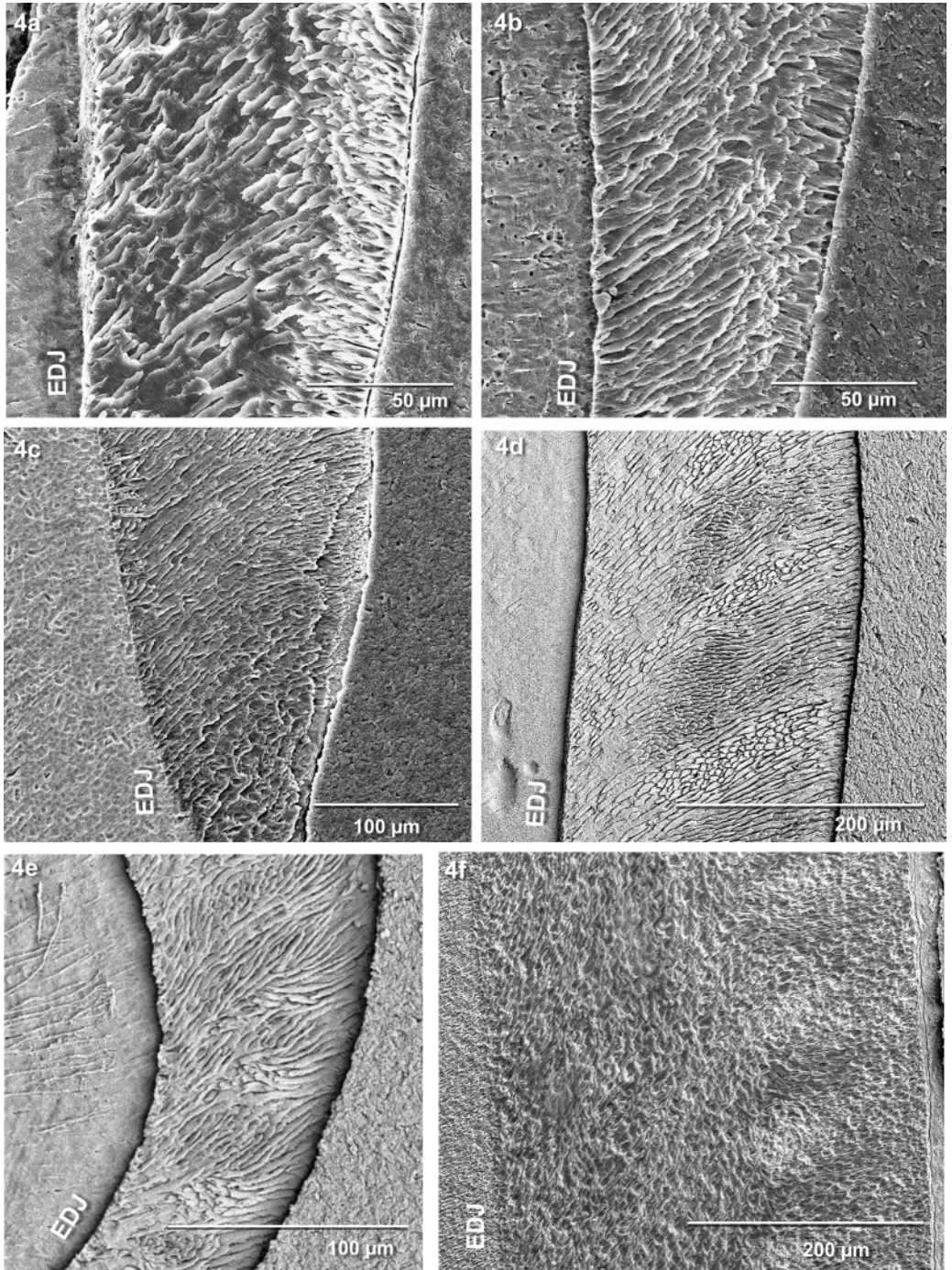
Pappocricetodontinae and Muridae

The molar schmelzmuster of the murids shows basically the C-type as in dipodids, but some murids differ. The earliest occurrence in the fossil record of the C-type schmelzmuster is from the middle Eocene of Mongolia, where it was found fully developed in *Pappocricetodon antiquus* (Fig. 3c) (KOENIGSWALD 2004a). In the classification of MCKENNA & BELL (1997, 2002), *Pappocricetodon* is listed under Myodonta in its own subfamily.

Like the molar enamel, the schmelzmuster of the lower incisors of *Pappocricetodon antiquus* is fairly derived compared to other contemporaneous taxa. The very thin enamel shows fully developed uniserial enamel and thus represents one of the earliest occurrences of this enamel type in rodent incisors (KALTHOFF 2000). The HSB are oriented transversely, and the IPM is parallel to the prisms (Fig. 5c). The PE is made up of radial enamel. The orientation of the HSB and the IPM indicates a very basal position within this kind of schmelzmuster, which is classified as a type 1a schmelzmuster by KALTHOFF (2000).

Selenomys mimicus from the early Oligocene has a unique molar morphology among rodents. MCKENNA & BELL (1997, 2002) list *Selenomys* under Muridae without indicating a specific subfamily. The schmelzmuster of the hypsodont molars has only radial enamel and thus has to be attributed to the P-type schmelzmuster. This type of schmelzmuster is unusual among murids, and occurs only in some taxa with a highly derived morphology, as in Spalacinae and Rhizomyinae. The only exceptions are some fairly basal taxa like *Cricetops*. Since the molar morphology of *Selenomys* is highly derived and unique, it is difficult to decide whether the primitive schmelzmuster was retained in his genus or secondarily modified from the C-type following the evolution of hypsodont molars (Fig. 4a).

Fig. 4: Enamel microstructure of rodent molars from Mongolia. SEM images of vertical sections. – 4a. *Selenomys mimicus*, early Oligocene, Hsanda Gol Formation, Tatal Gol (KOE 2482). The enamel of this genus is formed by radial enamel only, thus it is one of the few murids with the P-type schmelzmuster. – 4b. *Cricetops dormitor*, early Oligocene, Hsanda Gol Formation, Tatal Gol (KOE 2481). In the molars of *Cricetops* only radial enamel was found and indicates a more or less isolated systematic position within the murids. – 4c. *Tachyoryctoides kokonorensis*, transition Oligocene-Miocene, Loh Formation, Unkheltseg (KOE 3654). Only a very weakly-developed BRLE is visible. – 4d. *Ardynomys russeli*, late Eocene, Alag Tsav (KOE 3658). Thick transverse Hunter Schreger-bands characterize the molar enamel and thus the S-type schmelzmuster. – 4e. *Tataromys* sp., late Oligocene, Ulantatal (KOE 1889). Thick HSB are most prominent at the base of the molar crown. – 4f. *Tsagonomys* sp., early Oligocene, Hsanda Gol Formation (KOE 3655). The molars show an inner radial enamel and thick HSB in the outer layer, forming a modification of the S-type schmelzmuster. EDJ: enamel dentine junction.



The lower incisors of *Selenomys mimicus* show the plesiomorphic type 1a schmelzmuster, as does *Pappocricetodon* (Fig. 5d).

Cricetopidae

In the molars of *Cricetops dormitor* from the early Oligocene, a basal ring of lamellar enamel (BRLE) could not be detected, despite repeated careful investigation (Fig. 4b). This is exceptional since *Cricetops* is a typical murid, and in this family the BRLE is known since the Eocene. With radial enamel only, *Cricetops* represents the P-type and differs from most murids in this respect. It is probable that the plesiomorphic P-type is retained since the molar morphology is not modified in an unusual way.

In upper and lower incisors, *Cricetops dormitor* represents the plesiomorphic type 1a schmelzmuster. Since the schmelzmuster is generalized in molars and incisors, the enamel microstructure cannot provide additional data on the problematic systematic position of this genus as discussed by STEHLIN & SCHAUB (1951), LAVOCAT & PARENT (1985), and WANG & DAWSON (1994).

Eucricetodontini

Eucricetodon molars show a well-developed C-type schmelzmuster with a basal ring of lamellar enamel. In this feature, the Mongolian specimens are similar to other late Oligocene hamsters from Asia Minor and Central Europe like *Kerosinia*, *Trakymys*, or *Adelomyarion* (KOENIGSWALD 2004a).

Unfortunately, no in situ incisors of *Eucricetodon* were preserved in the Mongolian material, and the identification of isolated lower incisors was not possible. The schmelzmuster of both lower and upper incisors of the genus is already known from Central European species (KALTHOFF 2000, 2006), but a comparison of material from these palaeogeographically very distant areas would have been interesting. Lower incisors of *Eucricetodon* show the genus-specific type 4 schmelzmuster with mostly transversely oriented HSB with perpendicular IPM. An apomorphic feature is a greatly reduced PE. Upper incisors have a less derived schmelzmuster with transversely oriented HSB in the PI and radial enamel in the PE. The IPM in the PI may either run entirely parallel to the prisms (type 1a schmelzmuster, early Oligocene) or is perpendicular to the prisms at a thin layer close to the EDJ (type 2a schmelzmuster, late Oligocene).

Tachyoryctoidinae

The molar enamel of *Tachyoryctoides kokonorensis* predominantly consists of radial enamel. Nevertheless, some sections show patches of lamellar enamel close to the crown base (Fig. 4c). It seems that the basal ring of lamellar enamel (BRLE) is incompletely developed in this genus. This leads to the idea that the molar enamel of *Tachyoryctoides* may represent the transition from a type P into a type C schmelzmuster. If these results are true, they are further a hint that the type C schmelzmuster had evolved in parallel in different lineages within Muridae.

The lower incisor enamel of *Tachyoryctoides* sp. shows mostly transversely oriented HSB with a high-angled IPM (type 3a schmelzmuster). Towards the lateral sides of the enamel band, the HSB become somewhat oblique in orientation, and the angle of the

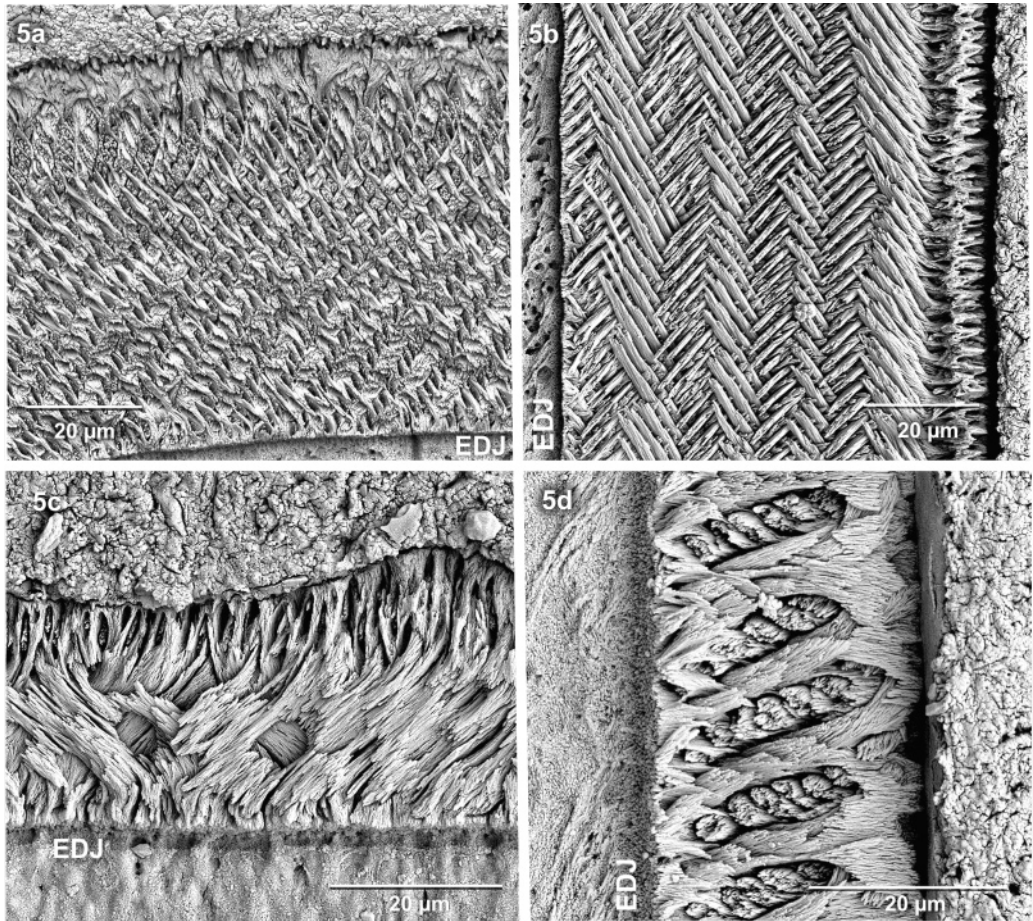


Fig. 5: Incisor enamel microstructure of dipodid and murid rodents of Mongolia. All SEM images. – 5a, b. *Heterosminthus gansus*, late Miocene, Loh Formation, Builstyn Khudag (KOE 3217); type 7 schmelzmuster. Among the analyzed Mongolian rodents, *Heterosminthus* shows the most derived schmelzmuster with longitudinally oriented HSB. a. Transverse section. b. Longitudinal section. – 5c. *Pappocricetodon antiquus*, middle Eocene, IVPP V11018.611 - Loc. 93006 (KOE 1842); type 1a schmelzmuster. The transverse section shows very thin (25 µm) enamel with transversely oriented HSB with prism-parallel IPM in the PI. The PE consists of radial enamel. The outer enamel surface is ornamented with several longitudinal ridges. – 5d. *Selenomys mimicus*, early Oligocene, Hsanda Gol Formation (KOE 2482); type 1a schmelzmuster. The longitudinal section shows slightly inclined, transversely oriented HSB with prism-parallel IPM. The PE is made up of radial enamel. The incisor tip points towards the upper margin of the image. EDJ: enamel dentine junction.

IPM in respect to the prisms becomes increasingly lower until both may run in parallel in some places. The PE is made up of an unusually thick layer of radial enamel, which takes about 60 % of the thickness of the enamel band (Fig. 6a).

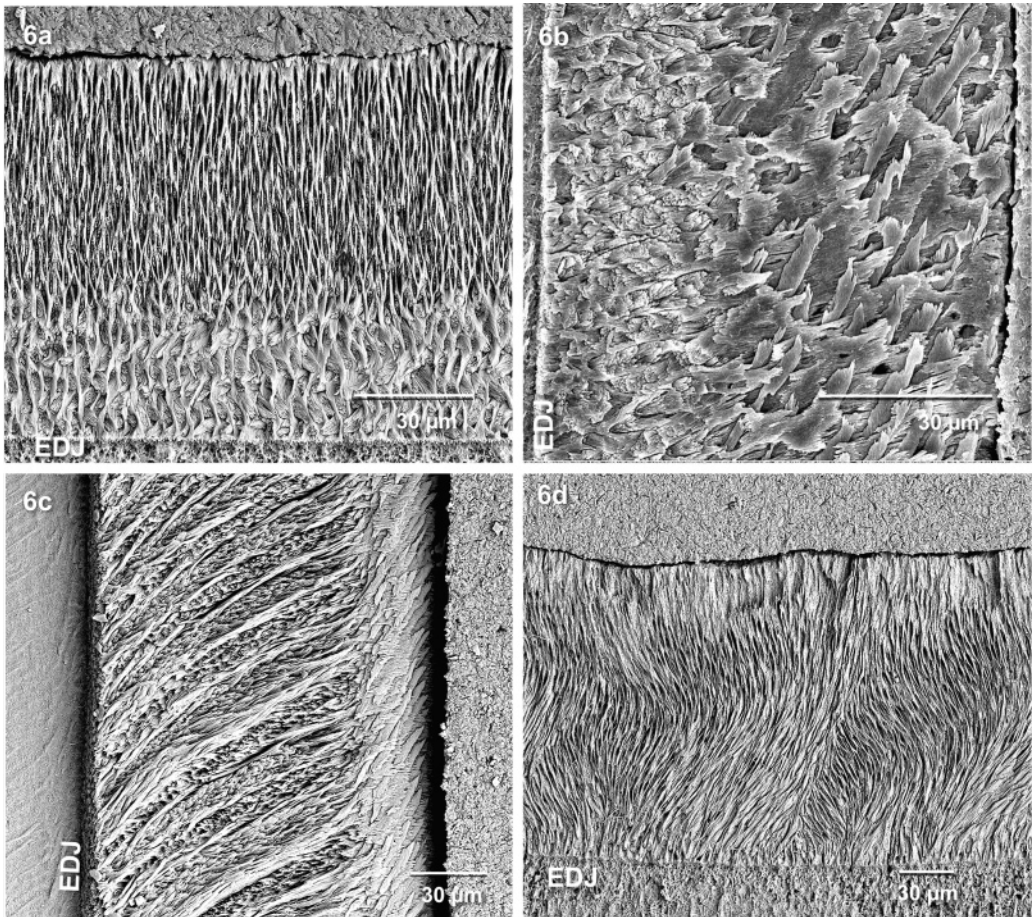


Fig. 6: Incisor enamel microstructure of tachyoryctoidine, some sciuravid, and some hystricognathous rodents of Mongolia. All SEM images. – 6a. *Tachyoryctoides* sp., transition Oligocene-Miocene, Loh Formation, Unkheltseg (KOE 3120); type 3a schmelzmuster. The transverse section shows transversely oriented HSB with perpendicular IPM in the PI and a remarkably thick PE made up of radial enamel. The thick PE may indicate a subterranean way of life. – 6b. *Ardynomys* sp., late Eocene, Ergilin Dzo Fm. (KOE 3127); type 1 schmelzmuster. The longitudinal section features transversely oriented HSB with prism-parallel IPM, which are slightly inclined. The extremely thick PE consists of radial enamel and may reflect a subterranean lifestyle. The incisor tip points towards the upper margin of the image. – 6c. *Tataromys* sp., late Oligocene, Ulantatal (KOE 1889). The longitudinal section shows steeply inclined multiseriate HSB with acute-angled IPM in the PE and relatively thin radial enamel in the PE. The incisor tip points towards the upper margin of the image. – 6d. Tsaganomyidae indet., early Oligocene, Hsanda Gol Formation, Tatal Gol (KOE 2480). The transverse section shows the weakly inclined multiseriate HSB with the acute-angled IPM in the PI. The PE features radial enamel in which the IPM runs parallel to the prisms and is therefore of special interest. EDJ: enamel dentine junction.

An isolated lower incisor from the late Oligocene of Kazakhstan had already been described by KALTHOFF (2000) under the genus name of *Tachyoryctoides*. However,

this incisor shows a schmelzmuster completely different from the Mongolian specimen studied here, which was taken from a toothed jaw. This makes it likely that the former specimen had been misidentified.

Sciuravida

Cylindrodontinae

The molars or *Ardynomys* (Fig. 4d) from the late Eocene represent the typical S-type schmelzmuster. Very thick HSB are present in an outer layer and show broad transitional zones. The HSB are developed best in the lower part of the tooth crown.

The incisors show basically uniserial HSB in the PI, but the bands often merge into each other so that the uniserial character is not as obvious as in later forms (Fig. 6b). The IPM is parallel to the prism direction. The PE with radial enamel is very thick. Upper and lower incisors do not show distinct differences in the enamel microstructures, and both show a type 1 schmelzmuster.

MARTIN (1992) investigated the incisor enamel of *Dawsonomys* and *Mysops* from the early and middle Eocene of North America. Both genera have pauciserial enamel. *Mysops* from the late Eocene may represent the transition to uniserial enamel in cylindrodont incisors in North America.

Ctenodactylidae

The molar of *Tataromys* shows the S-type schmelzmuster since thick HSB are present (Fig. 4e). They are better developed at the base of the crown than in the upper part where they are somewhat weaker. MARTIN (1992, 1995) investigated the lower incisor and found multiserial enamel in the PI (Fig. 6c). The HSB are fairly strongly inclined, and the IPM is oriented at an acute angle to the prisms. The PE is formed by radial enamel, as usual. The schmelzmuster in molars and incisors remains more or less the same in more derived ctenodactylids (MARTIN 1992, KOENIGSWALD 2004a and b).

Hystricognatha

For this study, we used molar material from Mongolia, which was attributed to *Tsaganomys* or to the Tsaganomyidae indet. The enamel of the molars is thick and contains two layers. The inner one is formed by radial enamel with the IPM at a large angle and the outer one by thick HSB (Fig. 4f). Molars with thick enamel often show a superposition of different enamel types. HSB may be placed on the inside, in the middle, or on the outsides. They are always combined with radial enamel. Tsaganomyids show the S-type schmelzmuster.

Both lower and upper incisors of different species of *Tsaganomys* show multiserial enamel in the PI with an IPM oriented at a low angle to the prism direction (Fig. 6d). The bands are inclined only slightly (10–20°) in *Tsaganomys altaicus* and *Tsaganomys* sp., while the smaller *Tsaganomys lohensis* shows somewhat more steeply inclined HSB (30°) (MARTIN 1992). The PE is formed by radial enamel, but in contrast to most rodents, the IPM of the larger *Tsaganomys* species is oriented parallel to the prisms. This parallel orientation of the IPM in the PE is unusual, but it was found in the Bathyergidae

(MARTIN 1992) and in a few species of Spalacinae, Allactaginae, and Cricetodontinae (KALTHOFF 2000). In the smaller species *Tsaganomys lohensis* that was formerly attributed to a different genus, *Cyclomytus*, the IPM in the PE retains a slight angle to the prisms (MARTIN 1992).

Discussion

Our sample of Mongolian rodents covers very different systematic units and thus provides a comprehensive survey of various types of schmelzmuster in rodent molars and incisors (Tab. 1).

Molars. In the molar enamel all three basic types of schmelzmuster, the P-, the S- and the C-type are represented. The P-type of molar schmelzmuster was found in the Oligocene genera *Cricetops* and *Selenomys*. The P-type schmelzmuster is regarded as the least derived one, since the only enamel type present, radial enamel, is the least derived enamel of all eutherian mammals. In *Cricetops*, this primitive condition possibly is preserved. In *Selenomys*, a secondary modification of the schmelzmuster may have occurred due to the aberrant morphology of the hypsodont molars (KOENIGSWALD 2004a).

The S-type schmelzmuster occurs in the molars of the late Eocene *Ardynomys*. This schmelzmuster having thick HSB is more derived than the P-type, although it occurs stratigraphically earlier in our sample. The S-type is characteristic for the more derived Sciuravida, and more primitive ones have the P-type. The S-type is present in the Sciuromorpha including the extant genera and in Hystricognatha (e.g. southern African Bathyergidae and South American Caviida).

The C-type schmelzmuster was found in the middle Eocene genus *Pappocricetodon*. This is the first occurrence of this type of schmelzmuster in the fossil record. The C-type schmelzmuster is restricted to the Myodonta. It evolved most probably from the P-type in the Dipodidae, Muridae, Eomyidae and Geomyidae, but from the S-type in the Gliridae (KOENIGSWALD 2004a). In Europe, the C-type was present only in glirids until the Grande Coupure, but with the invasion of the Muridae after this time it became dominant.

The evolutionary sequence of the various types of molar schmelzmusters is not reflected sufficiently in their stratigraphic occurrence. The schmelzmusters developed during the Eocene, and the fossil record is so far not complete enough to represent a detailed history. The evolutionary sequence therefore was deduced from the complexity of the schmelzmuster.

Incisors. The incisors of Mongolian rodents analyzed represent two of KORVENKONTIO's main types: multiserial enamel in the Ctenodactylidae and Tsaganomyidae and uniserial enamel in the Dipodidae, Muridae, Cricetopidae, Tachyoryctoidinae, and Cylindrodontinae.

The ctenodactylid *Tataromys* shows strongly inclined HSB, which can be considered more derived than the only slightly inclined HSB of smaller and larger members of tsaganomyids (MARTIN 1992). As a particular character, tsaganomyids feature radial enamel in the PE where both prisms and IPM run in parallel in the larger species and almost parallel in the smaller species. The biomechanical significance of this modification of the radial enamel is unknown so far.

Among the Mongolian rodents with uniserial enamel there are some taxa with very primitive, transversely oriented HSB with parallel IPM (type 1 schmelzmuster). These are the early hamsters *Pappocricetodon antiquus*, *Selenomys mimicus*, and *Cricetops dormitor* as well as the sciuravid *Ardynomys*. While *Pappocricetodon antiquus* is one of the stratigraphically oldest examples of uniserial HSB and therefore of importance, *Selenomys mimicus* is an example of convergence with the genus *Melissiodon* of the European Oligocene, which also shows a highly derived and complicated molar morphology in contrast to a primitive incisor enamel microstructure (KALTHOFF 2000, 2006). Additionally, the incisor enamel band of both genera is extraordinarily thin and measures only between 20 to 35 μm . Unfortunately neither the schmelzmuster of the molars nor that of the incisors provides new evidence for the phylogenetic relationship of the enigmatic *Selenomys* (WANG & DAWSON 1994).

Some systematic conclusions can be drawn from the schmelzmuster analysis. The results for *Cricetops dormitor* allow some comments on the genus *Enginia* from the early Miocene of Turkey. This genus was provisionally attributed to the Cricetopidae due to a similar molar morphology (BRUIJN & KOENIGSWALD 1994, MCKENNA & BELL 1997, 2002). But in contrast to *Cricetops*, the molar enamel of *Enginia* shows a well-developed BRLE and thus belongs to the C-type. The lower incisors of *Enginia* represent the highly derived type 10 schmelzmuster characterized by longitudinally arranged HSB with a "central syncline" (BRUIJN & KOENIGSWALD 1994, KOENIGSWALD 1997b, KALTHOFF 2000). Since *Enginia* is highly derived in the molar and the incisor enamel, it is very different from the distinctly less derived *Cricetops*. Although an evolutionary lineage from the early Oligocene *Cricetops* to the early Miocene *Enginia* cannot be totally excluded, a possible relationship has to be reconsidered due to the major differences in the enamel microstructure.

In *Ardynomys*, the thick PE with radial enamel is worth mentioning (MARTIN 1992). Since radial enamel is known for its biomechanical resistance to abrasion (RENSBERGER & KOENIGSWALD 1980), a thick PE may support a subterranean way of life for the Cylindrodontinae as assumed by WOOD (1980). A thick PE also occurs in other genera of the subfamily. With transversely oriented HSB and IPM at right angles, *Tachyoryctoides* has a more highly derived lower incisor microstructure than the taxa discussed above. But like in *Ardynomys*, the PE consists of extremely thick radial enamel, which also accounts for about 60 % of the enamel band. The thick radial enamel may indicate that *Tachyoryctoides* was a subterranean rodent too, using his incisors to some extent as digging tools (see discussion in KALTHOFF 2000: 169ff).

Among the analyzed rodents from Mongolia, the dipodid *Heterosminthus* shows the most derived incisor schmelzmuster. The PI is made up of longitudinally oriented HSB with the IPM almost entirely at right angles except for a thin layer with prism-parallel IPM close to the PI/PE boundary. The PE consists of tangential enamel. In the above-described characters, *H. gansus* agrees well with the genus *Plesiosminthus* from Europe and North America, which ranges from the Oligocene to the middle Miocene. However, *Plesiosminthus* is classified in MCKENNA & BELL (2002) as a member of the tribe Sicistini. In contrast to the type 7 schmelzmuster in *Plesiosminthus* and *Heterosminthus*, *Sicista* as the name giving taxon to this tribe has the type 6a schmelzmuster. To our present knowledge, this somewhat less derived type with diagonally oriented HSB is

restricted to *Sicista* (KALTHOFF 2000). Thus the schmelzmuster indicates that the genera currently attributed to the tribe Sicistini may not form a natural group.

TURNBULL (1991) postulated that *Protoptychus* from the Oligocene of Wyoming is an early member of the dipodids based on similar postcranial skeleton adaptations. The schmelzmuster of *Protoptychus* shows the S-type, in contrast to all investigated dipodids, which show the C-type. In the incisor enamel, *Protoptychus* has pauciserial enamel – again in contrast to all known dipodids (MARTIN 1992, KOENIGSWALD 2004b). Thus, based on our results it seems unlikely that dipodids arose from *Protoptychus*.

Conclusions

This review of the enamel of the Mongolian rodents proofs repeatedly that there is no close relationship between the schmelzmusters of incisors and molars (KOENIGSWALD 1997a). Therefore we have to assume that the genetic information for the enamel formation is specific for the different tooth categories.

Mongolia is very important for the early diversification of the Glires and especially of the Rodentia (DAWSON 2003, ASHER et al. 2005). The material studied here concentrates on the Oligocene and Miocene und thus does not include the earliest forms. Although our sample of Mongolian rodents is far from being complete, it reflects the great diversity of the molar enamel diversification among rodents. On the other hand, the observed diversity of the incisor schmelzmusters is fairly low. The real diversity is expected to be higher despite the fact that representatives of most major systematic groups were studied. The main problem is the limited material of confidently identified incisors. The hamsters, for instance, which have been proven to be remarkably diverse in the Oligocene and Miocene of Central Europe (KALTHOFF 2000, 2006), could not be included in this study.

The enamel of the Mongolian rodents contributed to the knowledge of the evolution of enamel microstructures in this group. Since the origin of rodents might be located in the Mongolian region (DAWSON 2003), the detected structures are highly specific and important for a comparison to material from North America, Asia Minor and Central Europe.

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