THE EVOLUTION OF THE SCHMELZMUSTER IN LAGURINI (ARVICOLINAE, RODENTIA)

BY

WIGHART V. KOENIGSWALD and ALEXEJ TESAKOV^{*)}

With 18 text-figures

Zusammenfassung

Die Evolution des Schmelzmusters in den Molaren der Lagurini (Graulemminge) zeigt zwei Phasen. In der ersten Phase, in der die Molaren noch bewurzelt sind, wird das Schmelzmuster differenziert. In der zweiten Phase, in der die Molaren wurzellos sind, treten Reduktionen auf der Leeseite der Dentindreiecke auf. Das asymmetrische Schmelzmuster, das in der ersten Phase entwickelt wird, ähnelt sehr dem der *Mimomys*-Gruppe, aber die Lagurini haben nie die gleiche Qualität in der Ausbildung der Schmelztypen erreicht. Auch stratigraphisch erreicht die *Mimomys*-Gruppe die volle Ausbildung des Schmelzmusters erheblich früher. Während der zweiten Phase, die durch Reduktionen gekennzeichnet ist, sind die Lagurini in allen Gattungen progressiver als die *Mimomys*-Gruppe. *Kalymnomys*, ein fossiler Lagurine aus dem östlichen Mittelmeerraum, besitzt im Gegensatz zu den anderen Lagurini ein symmetrisches Schmelzmuster, was auf eine sehr frühe Abspaltung von den anderen Lagurini schließen läßt.

Schlüsselwörter: Schmelzmuster - Lagurini - Arvicolinae - Rodentia.

Summary

The evolution of the schmelzmuster in lagurine molars shows two phases roughly related to rooted and rootless molars, respectively. In the first phase the schmelzmuster is differentiated and in the second phase partially reduced. Various species of *Borsodia* represent the first phase. The asymmetrical schmelzmuster is very similar to that in the arvicoline *Mimomys* lineage but never reached the same quality of enamel types. Stratigraphically the evolution is not synchronous in both lineages. During the second phase the lagurines represented by various genera are somewhat more progressive than *Microtus* and *Arvicola* from the *Mimomys*-group. *Kalymnomys*, a fossil lagurine from the Mediterranean shows a symmetrical schmelzmuster indicating a very early separation of the lineages within the Lagurini. The schmelzmuster analysis proves to be a very useful additional tool to investigate phylogenetic relationships.

Key words: Schmelzmuster - Lagurini - Arvicolinae - Rodentia.

Introduction

Arvicoline rodents underwent an extensive radiation during the Pliocene and Pleistocene. They achieved hypsodonty, rootless molars, and a highly derived schmelzmuster in various lineages. It seems that the ability to form the unusual differentiation of the schmelzmuster was a prerequisite for this radiation. The schmelzmuster of arvicoline molars has been proven as a useful tool for systematics and phylogeny in arvicoline rodents (KOE-NIGSWALD 1980, RABEDER 1981). The evolution of the schmelzmuster could be studied for the *Mimomys* lineage in detail (KOENIGSWALD 1980, 1982a). The lagurine lineage studied here follows partially similar trends but shows severe differences, both in morphology as well as in the chronology. From the comparison some general trends in the evolution of the schmelzmuster obvious.

The interpretation of the phylogeny of the Lagurini s.l. proceeded very much during the last decade (ZAZHIGIN 1980, RABEDER 1980, CHALINE 1985, TESAKOV 1993, REKOVETS 1994) and allows now to test some of the previous hypotheses against the evolution of the schmelzmuster in this group.

^{*)} Addresses of the authors: Prof. Dr. W. v. KOENIGSWALD, Institut für Paläontologie der Universität Bonn, Nußallee 8, D-53115 Bonn, Germany. – Dr. A. TESAKOV, Geological Institute of the Russian Academy of Sciences, Pyzhevsky 7, 109017 Moscow, Russia.



Fig. 1. Phylogenetic scheme of the evolution within Lagurini according to TESAKOV (1993) and REKOVETS (1994). The following evolutionary steps are indicated: 1* Development of tangential enamel. 2* Fully developed schmelzmuster. 3* Achievement of rootless molars. 4* Reduced thickness in the trailing enamel band.

Abb. 1. Schema zur Phylogenie der Lagurinen (Graulemminge) nach TESAKOV (1993) und REKOVETS (1994). Die folgenden evolutiven Schritte sind ihrem zeitlichen Auftreten angezeigt: 1* Ausbildung des tangentialen Schmelzes. 2* Voll entwickeltes Schmelzmuster. 3* Erwerb von wurzellosen Molaren. 4* Reduzierung der Schmelzdicke auf der Leeseite der Dentindreiecke.

Phylogeny of the Lagurini

Voles were regarded as a separate family the Arvicolidae by KRETZOI (1962) and most students in arvicolid systematics especially paleontologists followed him. Zoologists however regarded them as a subfamily of the Cricetidae (GROMOV et POLJAKOV 1977). In contrast to the first edition (HONACKI et al. 1982) the second edition of "Mammal species of the world" by WILSON & REEDER (1992) arvicolids are regarded as the subfamily

Arvicolinae of the Muridae. If voles are ranked as a subfamily steppe lemmings have the rank of a tribe: Lagurini **Kretzoi** 1955.

Even if the lagurines are a relatively small group their taxonomy is very complicated because of the many genera and species described. This paper does not intend to solve the taxonomic problems. Therefore only a short outline of the phylogenetic position of the species studied in this paper is given here (Fig. 1), as interpreted by Tesakov (1993).

The earliest lagurine genus is Borsodia JANOSSY & V.D. MEULEN 1974, occurring in the late Pliocene (MN 16). As an apomorph character Borsodia has no Mimomys-islet in the lower M1. It retains the plesiomorphic characters of rooted molars without cement and a Mimomys-ridge in the M1. In the M3 the posterior islet is present.

From the western subgenus B. (Borsodia) we studied B. steklovi, B. novoazovica, B. praehungarica. In this lineage which is recorded from the MN 16 to MN 17 the hypsodonty increases continuously. From the eastern subgenus Shamaromys three species (B. (S.) eleonorae, B. (S.) chinensis, and B. (S.) laguriformes) were studied. The morphology changes in the same direction as in the nominal subgenus Borsodia, but in the M³ the underived confluent pattern is persisting (ZAZHIGIN 1980, 1989).

In the late Villanyian Borsodia praehungarica gave rise to two independent lineages differentiated by the morphology of the M₁. One line retains the conspicuous *Mimomys*-ridge and is represented in our sample by Borsodia arankoides and Lagurodon arankae. At the transition from B. arankoides to L. arankae the molars become rootless.

In the second lineage the *Mimomys*-ridge of the M_1 is reduced. Rootless molars are achieved almost at the some time as in the other lineage. This lineage continues to the extant Lagurus lagurus. Besides that species we studied B. fejervaryi and Prolagurus pannonicus. In contrast RABEDER (1981) did not accept two parallel lineages postulated here and therefore included L. arankae as well as Prolagurus pannonicus into the genus Lagurus.

So far there are no reliable data on the origin of the extant lagurine genus *Eolagurus* which is known since the late Early Pleistocene. E. argyropuloi and the extant E. luteus were studied for schmelzmuster and compared with the mediterranean lagurine Kalymnomys.

Jordanomys pusillus HAAS 1966 from Israel was shown to be a younger synonym of Lagurodon arankae (KOENIGSWALD, FEJFAR & TCHERNOV 1991). "Jordanomys" KUSS & STORCH 1978 from the eastern Mediterranean does not belong to Lagurodon but was regarded as new genus Kalymnomys KOENIGSWALD, FEJFAR & TCHERNOV 1992.

Lemmiscus curtatus from North America was formerly regarded as a species of Lagurus. Even if there is no relationship to lagurines but to *Microtus*, the schmelzmuster of *Lemmiscus* is difficult to distinguish from extant lagurines since both groups show far reaching and similar reductions in the trailing edges.

Description of the schmelzmuster

Borsodia steklovi (ZAZHIGIN, 1980) Fig. 2

Material studied for schmelzmuster: several molars from Biteke Fauna, Northern Khazakhstan, MN 16, Lower Villanyian [KOE 214, 1751].

The enamel shows an uniform thickness without any interruptions by dentine tracks. In the leading edges a distinct layer of inner radial enamel is visible, followed by a second layer of the primitive discrete lamellar enamel. Both layers make about 1/2 of the enamel thickness. The outer layer is formed by radial enamel. These layers continue slightly into the trailing edges at the tips of the anticlines. In the anterior lobe the leading edge of the anterior cap shows discrete lamellar enamel. Both sides of the Mimomys-ridge are formed like leading edges. In trailing edges we find more than half of the thickness formed by radial enamel, which turns into primitive tangential enamel. That means, the prisms are not quite parallel to the occlusal surface.

In the closing enamel of the posterior lobe the pattern is similar to the trailing edges, but the tangential enamel seems to be somewhat better developed with prisms almost parallel to the occlusal surface.

The schmelzmuster of this earliest lagurine resembles a fairly primitive stage of the development of the Mimomys-schmelzmuster but at a much earlier stratigraphic position. It is striking that the contemporary Mimomys polonicus shows already the fully developed schmelzmuster.



Fig. 2. SEM micrographs and diagrammatical schmelzmuster of *Borsodia steklovi*, Pliocene MN 16. Shown is the 2LgA of a left M₁. (KOE 473, photos 24687–24694). Unlabled scale-bars equal 0.5 mm.

Abb. 2. Schema des Schmelzmusters und SEM-Mosaik von *Borsodia steklovi*, Pliozän MN 16. Dargestellt ist hier das Dentindreieck 2LgA des M1 als SEM-Mosaik. Die Symbole entsprechen KOENIGSWALD 1980 und RABEDER 1981.

Borsodia novoazovica (TOPACHEVSKY & SCORIK, 1977) Fig. 3

Material studied for schmelzmuster: one lower M2 from Selety suite, Biteke River, Northern Khazakhstan, MN 16, Lower Villanyian [KOE 1750].

The fairly young specimen shows uniformly thick enamel and with anterior enamel interruption only. In the leading edges a thin layer of discrete lamellar enamel is situated between an innermost thin radial enamel and thick outer radial enamel layers. Layers of lamellar enamel and inner radial enamel form nearly half of the thickness of the enamel band. In the trailing edges more than half of the band thickness is formed by radial enamel, an outer layer of primitive tangential enamel was registered in the central and lateral parts of the trailing edge. The closing enamel of the posterior lobe is two layered with a thick inner radial enamel and a rather thick tangential enamel. This layer is composed of well developed tangential enamel with prisms parallel to the occlusal surface. This layer is interrupted by radial enamel in the central part of the enamel band.



Fig. 3 and 4. Diagrammatical schmelzmuster of molars from members of the *Borsodia*-lineage showing tangential enamel in trailing edges and the full development of lamellar enamel in the leading edges. Unlabled scale-bars equal 0.5 mm.

Fig. 3. Borsodia novoazovica, Pliocene MN 16, right M2.

Fig. 4. Borsodia praehungarica, Pliocene MN 17, left M¹. The drawing is upside down to have the leading edges and trailing edges like in lower molars.

Abb. 3 und 4. Schemazeichnungen des Schmelzmusters der *Borsodia*-Linie, in der tangentialer Schmelz auf der Leeseite der Dentindreiecke und Lamellenschmelz auf der Luvseite weiter ausgebaut werden.

Borsodia praehungarica (SCHEVSCHENKO, 1965) Fig. 4

Material studied for schmelzmuster: several molars from Kryzhanovka fauna, bone beds 1 and 3, Odessa region, Ukraine, MN 17, early Late Villanyian [KOE 1748, 1749].

The various teeth studied show no significant differences. The M^1 studied from Kryzhanovka 3 bed has almost uniformly thick enamel and some thinner parts in the depth of synclines. However, leading edges can be slightly thicker than trailing ones. The leading edges show thin layer of inner radial enamel, a middle layer of discrete lamellar enamel, and very thick outer radial enamel layer. The lamellar enamel is somewhat better developed than in *Borsodia steklovi* and *B. novoazovica*. It is thicker and prisms are more parallel to the occlusal surface, though still not completely.

Trailing edges display an inner layer of radial enamel and outer layer of primitive tangential enamel, with prisms oriented not quite parallel to occlusal surface. The thickness of the outer layer is less than half of the entire thickness of the enamel band.

Closing enamel of anterior loop is formed by two enamel layers, an inner one of radial enamel and an outer one of primitive tangential enamel. It is interrupted in the middle by radial enamel. The layer of tangential enamel occupies more than a half of the enamel band thickness. Thus *Borsodia praehungarica* is distinct from more primitive species *Borsodia steklovi* and *Borsodia novoazovica* in better developed lamellar enamel and slightly differentiated in thickness enamel band. Tangential enamel remains poorly differentiated, especially in the trailing edges.

Borsodia (Shamaromys) eleonorae Erbajeva, 1975

Fig. 5

Material studied for schmelzmuster: 1 M¹ from Beregovaya fauna, Transbaical, Russia, MN 16, Early Villanyian [KOE 470].



Fig. 5-7. Diagrammatical schmelzmuster of molars from members of the early Borsodia (Shamaromys)-lineage in which the lamellar enamel is not fully developed when the reduction of the tangential enamel in the trailing edges starts. Unlabled scale-bars equal 0.5 mm. Fig. 5. Borsodia (Shamaromys) eleonorae, Pliocene MN 16, left M1. Fig. 6. Borsodia (Shamaromys) cf. chinensis, Pliocene MN 17, left M1.

Fig. 7. Borsodia (Shamaromys) laguriformes, Lower Pleistocene, right M².

Abb. 5-7. Schema der Schmelzmuster in den Molaren der Borsodia (Shamaromys)-Linie, in der zum Zeitpunkt der beginnenden Reduktion in der Leeseite, der Lamellenschmelz auf der Luvseite nur unvollständig ausgebildet ist.

In the M¹ the enamel is uniformly thick and with posterior interruption of enamel band only. In the leading edges three leavers of enamel were registered, a thin layer of inner radial enamel, a middle layer of discrete lamellar enamel curving slightly around tips of anticlines and disappearing in synclinal areas. The outer layer of leading edges is formed by radial enamel. Its thickness is usually more than half of the entire enamel band thickness. Trailing edges show inner layer of radial enamel and almost as thick a layer of well developed tangential enamel. Closing enamel of the anterior loop is composed of a very thick inner layer of radial enamel and a thinner outer layer of well developed tangential enamel.

Borsodia (Shamaromys) cf. chinensis (KORMOS, 1934) Fig. 6

Material studied for schmelzmuster: 1 M¹ from Shamar fauna, Northern Mongolia, MN 17, Late Villanyian [KOE 211].

The M¹ studied belongs to a young animal. Dentine tracts do not interrupt the enamel band yet. Thickness of enamel band is uniform. Leading edges show a distinct inner layer of radial enamel, middle layer of discrete lamellar enamel slightly curving around tips of triangles into trailing edges, and a thickest outer layer of radial enamel. Trailing edges are composed of inner layer of radial enamel and an outer layer of primitive tangential enamel. This layer is, however, present in outer sides of lingual triangles and was not found in buccal triangles. Closing enamel of the anterior lobe is built of inner radial enamel layer and an outer layer of poorly developed tangential enamel. Each layer makes up about a half of the entire thickness of the enamel band.



Fig. 8-9. Diagrammatical schmelzmuster of molars in the Borsodia-Lagurodon lineage with an intensifying of the lamellar enamel in the leading edges. Scale-bars equal 0.5 mm.

Fig. 8. Borsodia arankoides, Pliocene/Pleistocene boundary, left M1.

Fig. 9. Lagurodon arankae, Lower Pleistocene, right M¹.

Abb. 8-9. Schema der Schmelzmuster in den Molaren der Borsodia-Lagurodon-Linie, in der der Lamellenschmelz verbessert wird.

Borsodia (Shamaromys) laguriformes (ERBAJEVA, 1973) Fig. 7

Material studied for schmelzmuster: One M² from Dodogol fauna, Transbaical, Russia, Early Biharian [KOE 473].

The M² shows interruption of an enamel band by dentine tracts. Enamel band is distinctly differentiated into thicker leading edges and thinner trailing edges. Leading edges show a very thin inner layer of radial enamel turning into well developed thick layer of lamellar enamel, and an outer layer of radial enamel. Inner radial and lamellar layers make up about half of the enamel band thickness. Lamellar enamel distinctly penetrates trailing edges around tips of anticlines.

Trailing edges display an inner layer of radial enamel and very thin, almost disappearing outer layer of poorly developed tangential enamel close to the inner sides of trailing edges. Closing enamel of the anterior lobe are mostly built of radial enamel with two lateral areas of thin primitive tangential enamel.

Borsodia arankoides (ALEXANDROVA, 1976)

Fig. 8

Material studied for schmelzmuster: 1 M1 from Kryzhanovka section, bone bed 4, Odessa region, Ukraine, Latest Villanyian or lowermost Biharian [KOE 1763]. This lower M_1 is of an adult individual with well developed roots and interrupted dentine tracts. Leading edges are distinctly thicker than trailing ones. Leading edges display a very thin, almost disappearing inner layer of radial enamel, then a layer of well developed lamellar enamel distinctly entering trailing edges, and finally an outer layer of normal radial enamel. Trailing edges are composed of the inner layer of radial enamel and outer layer of fairly well developed tangential enamel. Closing enamel of the posterior loop displays an inner layer of radial enamel and a thin layer of tangential enamel. Prisms in this thin layer are rather flat, but in the outer side turn into a thin outer layer of radial enamel.

The enamel band on the lingual side of the anterior lobe is composed of radial enamel with a thin middle lamellar layer in the leading edge of the 5LgA (= LSA5) and a short interval of outer tangential enamel in the trailing edge of this anticline. A short buccal enamel portion between the *Mimomys*-ridge and anterior loop is composed of radial enamel with two tiny areas of tangential enamel at the ends of this portion. Thus the enamel of the anterior loop in *Borsodia arankoides* shows the beginning of differentiation in normal leading and trailing edges pattern. The differentiation predates the formation of additional triangles in the anteroconid complex.

Lagurodon arankae KRETZOI, 1954

Fig. 9

Material studied for schmelzmuster: 1 M1 and 1 M¹ from Tizdar fauna, Taman peninsula, Russia, Early Biharian [KOE 1753]; several molars from 'Ubeidiya fauna, Israel, Early Biharian [KOE 920].

The upper M^1 from the first fauna displays clearly differentiated thickness of enamel band with the leading edges and the outermost parts of trailing edges being thicker. Leading edges are built by an inner layer of well developed lamellar enamel and by an equally thick outer layer of radial enamel. There is no inner radial enamel layer left. Lamellar enamel curves into the outer portions of the trailing edges causing thickening of the enamel band here. Trailing edges are composed of an inner layer of radial enamel and an outer layer of primitive tangential enamel turning into an outer layer of radial enamel. The thickness of two outer layers is close to that of the inner radial enamel layer. Closing enamel of the posterior loop comprises two layers. The inner one is built by radial enamel and occupies more than half of the entire band thickness. The outer one is a layer of tangential enamel with the prisms oriented not completely parallel to the occlusal surface. The layer has an interruption by radial enamel in the middle of the enamel band length. The fragment of a lower M_1 from the same fauna with only the anteroconid preserved shows the similar schmelzmuster. An exception is the absence of tangential enamel in trailing edges in the enamel of the anterior lobe. A lower M_1 from the 'Ubeidiya fauna also shows only radial enamel in trailing edges and closing enamel of the posterior loop and prefectly developed lamellar enamel in leading edges.

Tangential enamel is present only in the upper molars but was not found in lower ones from Tizdar and 'Ubeidiya.

Borsodia fejervaryi (KORMOS, 1934) Fig. 10 and 11

Material studied for schmelzmuster: 1 M1 from Kryzhanovka fauna, bone bed 4, Odessa region, Ukraine, Latest Villanyian or Early Biharian [KOE 1755].

The M_1 is of an old individual with well developed roots, interrupted dentine tracts, and enamel band distinctly differentiated into thicker leading and thinner trailing edges. Leading edges are built by thin layer of inner radial enamel already turning into a layer of perfect lamellar enamel and an outer zone of radial enamel. Lamellar enamel curves into outer portion of trailing edges. Trailing edges are composed of inner layer of radial enamel and a thin layer of tangential enamel with prisms not quite parallel to the occlusal surface. Tangential enamel is present only in central and outer parts of trailing edge. Closing enamel of the posterior loop display a thick inner radial enamel and a thinner layer of somewhat primitive tangential enamel.

Enamel of the anterior lobe of anteroconid though still without conspicuous additional triangles is built similar to *Borsodia arankoides* with initial differentiation into leading and trailing enamel. This is indicated by tiny areas of outer tangential enamel and inner lamellar enamel within radial enamel band on both sides of the anterior lobe.



Fig. 10-12. SEM-micrographs and diagrammatical schmelzmuster of molars in the Borsodia-Lagurus lineage with an intensifying of the lamellar enamel in the leading edges and a reduction of the thickness in the trailing edges. Unlabled scale-bars equal 0.5 mm. Fig. 10. Borsodia fejervaryi, Plio-Pleistocene boundary, dentine triangle (2LgA) of M_1 in SEM micrographs (KOE 1755, photos 27891-27895).

Fig. 11. Borsodia fejervaryi, Plio-Pleistocene boundary, right M1.

Fig. 12. Prolagurus pannonicus, late Early-Pleistocene, M1.

Abb. 10-12. SEM-Mosaik und Schema der Schmelzmuster in den Molaren der Borsodia-Lagurus-Linie, in der der Lamellenschmelz verbessert wird und das leeseitige Schmelzband stark ausdünnt.

Prolagurus pannonicus (Kormos, 1930)

Fig. 12

Material studied for schmelzmuster: several molars Cherevichnoe fauna, Odessa region, Ukraine, Late Early Pleistocene, Early Biharian [KOE 1754]; Razdolie fauna, Western Siberia, Russia, Late Early Pleistocene, Early Biharian [KOE 212]; Zirany fauna, Czech Republic, Late Early Pleistocene, Early Biharian [KOE 108].

A lower M₁ from an adult animal shows a distinct differentiation in thickness of the enamel band. The enamel band is interrupted by distinct tracts in the anterior lobe as well as the posterior lobe. Leading edges are composed of inner layer of thick perfect lamellar enamel and distinctly thinner layer of radial enamel. Lamellar enamel curves into trailing edges. Trailing edges are normally built with only radial enamel. The outer portion of the trailing enamel, however, still displays slight flattening of prisms. This can indicate a disappearing layer of tangential enamel. More distinct tangential enamel was encountered in trailing edges of the anterior loop. Closing enamel of



Fig. 13 and 14. Diagrammatical schmelzmuster and SEM-micrographs of Lagurus lagurus, Recent. Unlabled scale-bars equal 0.5 mm. Fig. 13. Lagurus lagurus, Recent, right M₂.

Fig. 14. Dentine triangle (2LgA) of M1 in SEM micrographs (KOE 190, photos 27902-906).

Abb. 13 und 14. Schema des Schmelzmusters und SEM-Mosaik des rezenten Lagurus lagurus.



Fig. 15–17. SEM-micrographs and diagrammatical schmelzmuster in the *Eolagurus* lineage with lamellar enamel reaching far into the trailing edges.

Fig. 15. Eolagurus luteus, Recent, dentine triangle (2LgA) of right M² in SEM micrographs (KOE 197, photos 27896–8901). Unlabled scalebars equal 0.5 mm.

Fig. 16. Eolagurus luteus, Recent, of M2.

Fig. 17. Eolagurus argyropuloi, Lower Pleistocene, right M2.

Abb. 15-17. SEM-Mosaik und Schema der Schmelzmuster in den Molaren der Eolagurus-Linie, wo der Lamellenschmelz weit auf die Luvseite umgreift.

the posterior loop shows an inner radial enamel layer and an outer layer of poorly developed tangential enamel. The tangential enamel layer is interrupted by radial enamel in the middle of posterior enamel band. M2 studied from Razdolie and Zirany faunas show completely the same schmelzmuster.

Lagurus lagurus (PALLAS, 1773) Fig. 13

Material studied for schmelzmuster: several recent molars from the Voronezh region, Russia; and Khakassia, Siberia, Russia [KOE 190, 196].

We studied several molars belonging to adult animals. A lower M₂ from the Voronezh region displays normal advanced schmelzmuster described by KOENIGSWALD (1980). Enamel band shows perfect differentiation into thicker leading and very thin trailing edges. Leading edges are composed of inner layer of thick perfect lamellar enamel that penetrates the outer parts of trailing edges as well, and the outer layer of radial enamel. Trailing edges are built by a very thin layer of only radial enamel. Closing enamel of posterior loop is composed of only radial enamel.

Eolagurus argyropuloi argyropuloi GROMOV & PARFENOVA, 1951 Fig. 17

Material studied for schmelzmuster: 1 M2 from Cherevichnoe 1 fauna, Lusanowka, Odessa region, Ukraine, middle Biharian (Nagyharsanhegy), [KOE 1757, KOE 2168].

Eolagurus argyropuloi adventus Rekovets, 1994

Material studied for schmelzmuster: left lower M1, Kairy, Ukraine, (middle Biharian, Betfia) [KOE 2169].

All molars studied belong to adult animals with enamel band distinctly differentiated into thicker leading and thinner trailing edges. Normal interruptions of enamel band by dentine tracts are present. Leading edges are built by an inner layer of thick perfect lamellar enamel with a very thin layer of inner radial enamel. The outer layer of radial enamel is almost as thick as the lamellar enamel. Lamellar enamel curves into trailing edges near tips of triangles causing distinct thickening of enamel band here. Trailing edges are very thin and consist in most triangles only of radial enamel. However, in few cases for instance in the anterior lobe of *Eolagurus argyropuloi adventus* small areas of tangential enamel are to be found. Closing enamel of the posterior loop in *Eolagurus* from Cherevichnoe [KOE 1757] is built of a rather thin radial enamel. Only in the labial tip of the enamel band we registered a slight flattening of prisms in the outer portion of enamel band. This indicates last relicts of tangential enamel.

> Eolagurus luteus (Eversmann, 1840) Fig. 15 and 16

Material studied for schmelzmuster: several recent molars from Khazakhstan. [KOE 197, 478].

The lower M_2 described here is of an adult animal. The enamel band displays normal thickness differentiation and interruptions by dentine tracts. Leading edges are built with an inner layer of thick and well developed lamellar enamel and a thinner outer layer of radial enamel. Trailing edges are distinctly thinner than leading edges and built mostly of radial enamel. However in contrast to *Borsodia* or *Lagurus* a thin layer of lamellar enamel is found to penetrate the entire length of the trailing edges. The lamellar enamel is more distinct near the bends around the tips of the anticlines and synclines. In the closing enamel most molars show distinct lamellar enamel as an inner layer on both the lateral and the lingual side, while the center is filled with radial enamel. No tangential enamel was observed.

Eolagurus luteus gromovi TOPACHEVSKY, 1963

Material studied for schmelzmuster: left lower M1, Morosovka 2, (Upper Templomhegy-Phase), Ukraine, L. Rekovetz, [KOE 2170].

In *Eolagurus luteus gromovi* [KOE 2170], the earliest subspecies of this species from Morosovka 2, shows the typical schmelzmuster, and lamellar enamel is reaching very deeply into the closing enamel of the posterior loop. No signs of tangential enamel are visible (any more).



Fig. 18. SEM-micrographs and diagrammatical schmelzmuster of *Kalymnomys major*, Early Pleistocene, dentine triangle (2LgA) of right M₁ in SEM micrographs (KOE 246, photos 05184-05194).

Abb. 18. SEM-Mosaik und Schema des Schmelzmusters von Kalymnomys major, Alt-Pleistozän, Kalymnos Chi, Dentindreieck 2LgA des rechten M₁.

Kalymnomys major (Kuss & Storch 1978) Fig. 18

Material studied for schmelzmuster: Fragments of several molars from Kalymnos-Xi fauna, Kalymnos island, Greece, Early Pleistocene [KOE 246, 1077].

The unique symmetrical and well differentiated schmelzmuster of this form was recently described (KOENIGSWALD, FEJFAR & TCHERNOV 1991). Both leading and trailing edges of the enamel band are composed of inner layer of lamellar enamel and outer layer of radial enamel.

Discussion

The species in the various lineages of the lagurines show significant differences in their schmelzmuster. We can exclude that these differences are due to individual variability since where we studied several teeth from the same levels we found them to be very similar in the limits of the description given here. We got the impression that in some cases lower molars are more derived in the schmelzmuster than uppers for instance in the reduction of

tangential enamel in Lagurodon arankae. That would fit to other observations indicating that the teeth of the lower jaw are somewhat more progressive than those of the upper (KOENIGSWALD 1993, KOENIGSWALD et al. 1994).

Lagurini (with exception of *Kalymnomys*) process an asymmetrical schmelzmuster in their molars, i.e. the leading edges and the trailing edges consist of different enamel types (KOENIGSWALD 1980). *Kalymnomys* has a symmetrical schmelzmuster in which leading and trailing edges of each dentine triangle are built in the same way. Asymmetrical and symmetrical schmelzmusters evolved from undifferentiated schmelzmuster in separate lineages independently.

The asymmetrical schmelzmuster of the Lagurini demonstrates a continuous change throughout time, indicating distinct evolutionary trends followed up in the various lineages independently. The stratigraphical occurrence and the well established phylogeny allows to separate two distinct phases of the schmelzmuster evolution. During a first phase the schmelzmuster differentiates. This phase is roughly correlated to rooted molars with increasing hypsodonty. The second phase starts when molars become rootless. This phase is characterized by some reductions in the schmelzmuster.

The first phase of schmelzmuster evolution

During the first phase we observed a continuous increase of the quality and the quantity of the lamellar enamel in the leading edge. The increase in quality is marked by a change of the angle between the lamellae and the occlusal surface. In the primitive status the bands are rising apically. Therefore the bands intersect the occlusal surface. This is typical for primitive or "discrete lamellar enamel". In the most derived state the bands are almost parallel to the occlusal surface and therefore individual lamellae are seen over much larger areas in sections parallel to the occlusal surface.

The increase in quantity follows from two ways. On one hand, the lamellar enamel occurring first near the anticline of the dentine triangle only can be traced during evolution more and more towards the longitudinal tooth axis. On the other hand, the lamellar enamel expands from a central layer towards the EDJ forming an inner layer in an advanced state. By this expansion a layer of inner radial enamel is suppressed. The inner layer is present in the early forms like *Borsodia steklovi, Borsodia novoazovica* as well as in the Central Asian *Borsodia (Shamaromys) eleonorae.* The fully developed lamellar enamel was found in the latest species of *Borsodia arankoides,* and *Borsodia (Shamaromys) laguriformes).*

The trailing edges depict an other evolutionary trend. The tangential enamel increases in quantity and to some degree in quality as well. In the typical and most derived state of the tangential enamel the prisms are oriented almost parallel to the occlusal surface. Since tangential enamel derived from radial enamel with steeply rising prisms in radial direction without any lateral deviation, many intermediate orientations can be observed. For the description of primitive species of *Mimomys* KOENIGSWALD (1980) defined the "primitive tangential enamel" for an oblique prism orientation of about 45°, as found in early *"Mimomys" occitanus*.

In the earliest species of *Borsodia (B. steklovi* and *B. (S.) eleonorae)* the tangential enamel has its prisms not quite parallel to the occlusal surface but is a fairly well developed tangential enamel. This is found in the trailing edges and especially in the closing enamel of the posterior lobe in lower molars and the anterior in upper molars, respectively. In the younger species of *Borsodia* there is a general trend of a reduction of the tangential enamel in the trailing edges of the triangles. But a striking variability in the amount and the quality of this enamel type can be observed. In the length of the trailing edges the better tangential enamel is found in the middle part, which normally is most convex. But it does not seem to be related to the strength of the curvature since the closing enamel normally is less curved, but more conservative in preserving a better tangential enamel.

The second phase of schmelzmuster evolution

Lagurines achieve rootless molars in several lineages. This happens when the schmelzmuster was differentiated to the highest degree during the first phase. The achievement of rootless molars allows to increase the eruption rate of the molars and therefore more tooth material is available for abrasion per time unit (KOENIGS- WALD & GOLENISHEV 1979). That allows to reduce the length of the cutting edges (KOENIGSWALD 1982b). Under these circumstances the enamel thickness is reduced in the trailing edge.

The first slight reduction of the trailing edge in Lagurines can be observed in Borsodia praehungarica and B. chinensis but it becomes more obvious in the evolutionary level of B. fejervaryi. The drastic reduction occurs after the transition to rootless molars. The reduction of thickness effects mainly the outer tangential enamel while the inner radial enamel remains the same. The reduction of the tangential enamel is not only due to the reduced thickness of the outer layer but also to a reduction of the angle between the prisms in the radial and the tangential enamel. Since the angle is reduced during the reduction of the tangential enamel the type "primitive tangential enamel" reoccurs at a later phylogenetic level again. In the fully hypsodont, rootless molars of Prolagurus pannonicus and Lagurodon arankae traces of tangential enamel are still present in the closing enamel and sometimes in the triangles. In Lagurus lagurus no tangential enamel was found.

Eolagurus occurs for the first time in the Early Pleistocene and is characterized by rootless molars. The trailing edges are already reduced in thickness and only minor traces of a tangential enamel were found in the molars of the most ancient sites Kairy and Cherevichnoe of the Ukraine. All later specimen of *Eolagurus argyropuloi* and *Eolagurus luteus* studied here, showed only radial enamel and no traces of tangential enamel. The slight traces of tangential enamel indicate that the early history of *Eolagurus* passed to similar stages like the *Borsodia-Lagurus* lineage with tangential enamel in the trailing edges. Even the extension of lamellar enamel deep into the trailing edges and the closing enamel of the posterior lobe does not exclude the former presence of tangential enamel. The lineage of *Eolagurus* as represented in the fossil record, documents only the very late part of this schmelzmuster evolution. Already in *Eolagurus argyropuloi adventus* the reduction phase is almost completed.

Comparison of the schmelzmuster evolution with the Mimomys-group

The comparison of the development in the Lagurini and the one in the Mimomys-group is of special interest since there are fundamental similarities. The Mimomys-group comprises the genus Mimomys which occurred in the Pliocene and extended into the Pleistocene. Mimomys is assumed having given rise to the supergenus Microtus including Allophaiomys occurring stratigraphically at the base of the Pleistocene. While Mimomys has rooted molars Microtus is characterized by rootless molars. Later Mimomys gave rise to a second genus with rootless molars, Arvicola, occurring early in the Middle Pleistocene. The schmelzmuster of the Mimomys-group was studied in detail by KOENIGSWALD (1980). The Mimomys-group resembles the Lagurini in having an asymmetrical schmelzmuster and in having the two evolutionary phases described for the Lagurini as well. Despite the similarity of the evolution in the schmelzmuster, it was definitively developed in both lineages independently.

Nevertheless some differences have to be mentioned. In the Lagurini the lamellar enamel surrounds the apex of the dentine triangle and extends somewhat into the trailing edges. This derived pattern is not found in *Mimomys* or *Arvicola* but in derived species of *Microtus*. Lagurines never reached the quality of the enamel types found in the *Mimomys*-group. Neither the bands on the lamellar enamel nor the prisms in the tangential enamel are oriented absolutely parallel to the occlusal surface.

More significant is the stratigraphic difference at which the various levels in the schmelzmuster evolution were reached.

Stratigraphically the first phase containing the full differentiation of the schmelzmuster occurs somewhat earlier in the *Mimomys*-lineage than in the lagurines. The fully differentiated schmelzmuster is found in early Villanyian in *Mimomys polonicus* in Rembielice (MN 16) (KOENIGSWALD 1980). At that time *Borsodia steklovi* or *B. novoazovica* have mainly discrete lamellar enamel which is fading away towards the deeper parts of the synclines. *Villanyia* from Rebielice shares the fairly primitive schmelzmuster with the early species of *Borsodia* (KOENIGSWALD 1980). Even in the following zone MN 17 the schmelzmuster of *Borsodia praehungarica* is distinctly more primitive in retaining an inner radial enamel in the leading edge and less developed lamellar and tangential enamel.

The transition to rootless molars occurred roughly simultaneously in the *Mimomys-Microtus* lineage and in Lagurini. Therefore in respect to the schmelzmuster the second phase with increasing reductions starts almost at the same time too. The amount of reduction varies among the species of *Microtus*. While some tangential enamel is preserved in *M. oeconomus* and *Microtus (Terricola) subterraneus* other species like *M. arvalis* lack almost all tangential enamel. The closing enamel is often somewhat more conservative. In terms of reduction of the tan-

gential enamel Lagurus lagurus proceeded much quicker and went further than most Microtus species. In the Mimomys-group rootless molars were achieved in a second lineage at the transition from Mimomys savini to Arvicola cantianus much later during the early middle Pleistocene. In this lineage the reduction of the trailing edge can be observed as well, but did not proceed to an entire reduction of the tangential enamel yet.

The isolated position of Kalymnomys

Kalymnomys, primarily described from the eastern Mediterranean as Jordanomys major by KUSS & STORCH (1978), is characterized by rootless molars without cement and shares distinct morphological characters with the lagurines in the molar morphology. Therefore it belongs to that tribe without any doubt. But the schmelzmuster of Kalymnomys is fundamentally different. The schmelzmuster is primarily symmetrical (KOENIGSWALD 1980, KOENIGSWALD et al. 1992) and has a well developed lamellar enamel overlain by radial enamel in the entire length of the enamel band including leading and trailing edges. Despite the rootless molars Kalymnomys does not show any differentiation of the enamel thickness. The evolutionary history of the schmelzmuster of Kalymnomys is unknown and cannot be reconstructed from the history in related genera.

When KOENIGSWALD (1980) delivered the first survey of arvicoline schmelzmuster he assumed that the schmelzmuster of the lagurines was initially symmetrical, based on the observation in the lagurine Kalymnomys (= Jordanomys). This assumption is falsified by the evolutionary history of the schmelzmuster now documented for the Borsodia-Lagurus lineage. RABEDER (1981) defined the schmelzmuster of Lagurus as "leptokneme" and derived it from a "proleptokneme" condition. As proleptokneme he postulated a schmelzmuster with tangential enamel restricted to the closing enamel of the posterior lobe only. For the trailing edges of the triangles he postulated radial enamel only. He saw in this schmelzmuster an alternative to the reduction of the tangential enamel as accepted for the Mimomys-group. The presence of tangential enamel in Borsodia indicates that (most) early lagurines had a primarily asymmetrical schmelzmuster and did not develop from a "proleptokneme" condition.

Final remarks

The investigation of the schmelzmuster can be used for the reconstruction of phylogenetic relationships. However, it is mostly to exclude taxa, since parallel evolution occurs quite frequently. Further more, the enamel investigation allows to recognize evolutionary trends. The Arvicolinae are a very reasonable study object since the diversity of the enamel is larger than in any other taxon. Very distinct evolutionary trends can be seen and correlated to morphological changes. This allows to compare similar or identical evolutionary trends in independent evolutionary lineages. Not only Lagurini and Arvicolini show similarities. *Clethrionomys* can be added since it evolved the same asymmetrical schmelzmuster. However, *Clethrionomys* is restricted to phase one since the molars retain their roots. The thinning of the trailing edges is paralleled in some Lemmini and in Dicrostonychini.

Acknowledgements

We are indebted to the colleagues who gave samples of lagurine and other arvicoline molars for enamel investigation. From the many we want to thank especially Margarita Erbajeva from Uland-Ude, Kazimierz Kowalski from Kraków, and Leonid Rekovets from Kiew, who contributed very valuable material especially to this project. The authors thank further the Deutsche Forschungsgemeinschaft (DFG) for the possibility for one of us (A.T.) to spend two month at the Institute of Paleontology in Bonn, where this study was carried out. We thank G. Oleschinski, A. Gossmann and D. Kranz for their valuable assistance in preparation of the illustrations. Special thanks are due to Dr. C. Gee and Dr. M. Sander for improving the English.

References

CHALINE, J. (1985): Evolutionary data on steppe lemmings (Arvicolidae, Rodentia). – In: LUCKETT, W. P. and HARTENBERGER, J.-L. (eds.): Evolutionary Relationships among Rodents. Multidisciplinary Analysis. – pp. 631–641; New York/London (Plenum). GROMOV, I. M. & POLJAKOV, I. J. (1977): Voles (Microtinae). – Fauna of the USSR, Mammals, 3/8: 1–504; Leningrad (NAUKA). HONACKI, J. H., KINMAN, K. E. & KOEPPL, J. W. (1982): Mammal species of the world. - 694 pp.; Lawrence (Allen Press).

- JANOSSY, D. & VAN DER MEULEN, A. (1974): On *Mimomys* (Rodentia) from the Ostramos-3. North Hungary. Proc. Nederlandse Akad. Wetens., B., 782: 3812–3912; Amsterdam.
- KOENIGSWALD, W. v. (1977): Mimomys cf. reidi aus der villafranchischen Spaltenfüllung Schambach bei Treuchtlingen. Mitt. Bayer. Staatssamml. Paläont. hist. Geol., 17: 197–212; München.
- -,- (1980): Schmelzmuster und Morphologie in den Molaren der Arvicolidae (Rodentia). Abh. Senckenberg naturforsch. Ges., 539: 1– 129; Frankfurt a. M.
- -,- (1982a): Enamel structure in molars of Arvicolidae (Rodentia) a key to functional morphology and phylogeny. In: KURTEN, B.: Teeth: Form, Function & Evolution. – pp. 109–122, Fig. 9.1.–9.7; Columbia Univ. Press, New York.
- -,- (1982b): Zum Verständnis der Morphologie der Wühlmausmolaren (Arvicolidae, Rodentia, Mammalia). Z. geol. Wiss., 10: 951–962; Berlin.
- -,- (1993): Die Schmelzmuster in den Schneidezähnen der Gliroidea (Gliridae und Seleviniidae, Rodentia, Mammalia) und ihre systematische Bedeutung. Z. Säugetierkd., 58: 92–115; Hamburg.
- KOENIGSWALD, W.V. & GOLENISHEV, F.N. (1979): A method for determining growth rates in continuously growing teeth. J. Mammalogy, 60/2: 397-400; Lawrence.
- KOENIGSWALD, W. v., FEJFAR, O. & TCHERNOV, E. (1991): Revision einiger alt- und mittelpleistozäner Arvicoliden (Rodentia, Mammalia) aus dem östlichen Mittelmeergebiet ('Ubeidiya, Jerusalem und Kalymnos-Xi). – N.Jb. Geol. Paläont. Abh., 184: 1–23; Stuttgart.
- KOENIGSWALD, W. V., SANDER, M., LEITE, M., MÖRS, T. & SANTEL, W. (1994): Functional symmetries in the schmelzmuster and morphology in rootless rodent molars. - J. Linnean Society, 110: 141-179, 23 figs.; London.
- KRETZOI, M. (1962): Arvicolidae oder Microtidae? Vertebrata Hungarica, 4: 171-175; Budapest.
- Kuss, S. E. & Storch, G. (1978): Eine Säugetierfauna (Mammalia: Artiodactyla, Rodentia) des älteren Pleistozäns von der Insel Kalymnos (Dodekanés, Griechenland). – N. Jb. Geol. Paläont. Mh., 1978: 206–227; Stuttgart.
- RABEDER, G. (1981): Die Arvicoliden (Rodentia, Mammalia) aus dem Pliozän und dem älteren Pleistozän von Niederösterreich. Beitr. Paläont. Österr., 8: 1–373; Wien.
- REKOVETS, L. (1994): Small mammals of the Anthropogene in the south of Eastern Europe. 370 pp., Nauka Dumka; Kiev. [Russ.]
- TESAKOV, A. (1993): Evolution of *Borsodia* (Arvicolidae, Mammalia) in the Villanyian and the Early Biharian. Quart. Internat., 19: 41–45, 6 Fig.; Oxford.
- WILSON, D. E. & REEDER, D. M. (1992): Mammal species of the world. Second edition. 1206 pp.; Washington & London (Smithsonian). ZAZHIGIN, V. S. (1980): Late Pliocene and anthropogene rodents of the south of Western Siberia. - 155 pp., Nauka; Moscow.
- -,- (1989): Upper Pliocene reference sections and their biostratigraphic characteristic (based on mammals). In: DEVYATKIN, E. V. (ed.): Late Cenozoic of Mongolia (stratigraphy and paleogeography). - pp. 10-24, Nauka, Moscow.