

## EVOLUTION OF INCISOR ENAMEL MICROSTRUCTURE IN LAGOMORPHA

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**ABSTRACT**—A single layer of radial enamel in the incisors represents the plesiomorphic condition for stem-lineage representatives of Glires (Lagomorpha and Rodentia). A single layer of radial enamel is detected in the incisors of the zalambdalestid *Barunlestes butleri* and the pseudictopid *Pseudictops lophiodon* as well as the eurymylid *Eurymylus laticeps*. The eurymylid *Matutinia nitidulus* exhibits a more derived, double-layered schmelzmuster with Hunter-Schreger bands (HSB) in the portio interna (PI) and radial enamel in the portio externa (PE). Mimotonids are characterized by a schmelzmuster with HSB: *Anatolimys rozhdestvenskii* has double-layered enamel (PI with HSB, PE with radial enamel) and two undetermined mimotonids from Mongolia exhibit a single-layered enamel. An incisor of an undetermined leporid (*Strenulagus* or *Aktashmys*) from the early Eocene of Kyrgyzstan, one of the geologically oldest studied, has double-layered schmelzmuster with HSB in the PI and radial enamel in the PE, whereas all other leporids have single-layered enamel with HSB. This is evidence that the single-layered leporid incisor schmelzmuster is derived from a double-layered condition. The presence of multilayered schmelzmuster in upper and lower incisors of Ochotonidae with modified radial enamel, HSB, and tangential enamel is corroborated. All three species of the supposed ochotonid *Desmatolagus* (*D. gobiensis*, *D. robustus*, and *D. vetustus*) exhibit a single-layered schmelzmuster with HSB and therefore are transferred to the Leporidae. Ochotonid schmelzmuster was derived by a different pathway than leporid schmelzmuster and possibly originated from that of yet poorly known early Paleogene Gliriformes such as *Decipomys mongoliensis*. This indicates that the ochotonid-leporid divergence is much older than previously believed.

### INTRODUCTION

There is a long-standing debate on the interrelationships of Lagomorpha and Rodentia. From a morphological viewpoint, Glires (Rodentia and Lagomorpha) is one of the best established supraordinal monophyletic groups within Eutheria (Novacek, 1985, 1996; Luckett, 1985; Novacek and Wyss, 1986; Luckett and Hartenberger, 1993; Shoshani and McKenna, 1998; Meng and Wyss, 2001). Support for Glires from molecular studies has been equivocal, although is now stronger (Czelusniak et al., 1990; Graur et al., 1996; Huchon et al., 1999; Madsen et al., 2001; Murphy et al., 2001a, b).

In the discussion on the interrelationships of Lagomorpha and Rodentia, incisor enamel microstructure plays an important role. Lagomorpha have generally been characterized as having single-layered incisor enamel in contrast to double-layered incisor enamel in Rodentia (Tomes, 1850; Korvenkontio, 1934; Li et al., 1987), a view which entered some textbooks (e.g., Carroll, 1988). Koenigswald (1995, 1996) demonstrated that this approach is too simplistic, because within Lagomorpha only Leporidae (hares and rabbits) have single-layered incisor enamel whereas Ochotonidae (pikas) exhibit multilayered incisor enamel. A simple counting of enamel layers proved insufficient, and it is necessary to consider the enamel types that form the incisor schmelzmuster (Koenigswald, 1995, 1996). Since the classic works of Tomes (1850) and Korvenkontio (1934), incisor enamel microstructure of a number of fossil and modern lagomorphs has been investigated. But there has not been a comprehensive study of lagomorph incisor enamel microstructure that also includes stem-lineage representatives of both lagomorph and rodent and important Cretaceous and early Paleogene outgroup taxa. To elucidate the origin and early evolution of lagomorph and rodent incisor schmelzmuster and to clarify character polarity of enamel microstructure within glir-

iform mammals, the zalambdalestid *Barunlestes butleri* and the pseudictopid *Pseudictops lophiodon* were included in this study. The urgent need for a clarification of character polarity in the incisor enamel microstructure of gliriforms is demonstrated by contradictory discussions on this topic (e.g., Flynn et al., 1987; Koenigswald, 1995, 1996; McKenna and Meng, 2001; Meng et al., 1994; Meng and Wyss, 1994, 2001; Martin 1997, 1999a). Enamel microstructure can be studied equally in extant and fossil organisms. It therefore provides a character complex that can be traced from plesiomorphic stem-lineage representatives to the living crown groups. Thus, it has a great potential in providing important information on the evolutionary history of mammalian higher taxa.

**Institutional Abbreviations**—AMNH, American Museum of Natural History, New York; **IVPP**, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing; **MA**, enamel collection of T. Martin, currently housed at the Institut für Geologische Wissenschaften, Fachrichtung Paläontologie, Freie Universität, Berlin; **MAE**, Mongolian-American Museum of Natural History Expedition; **MgM**, suffix for mammalian specimens from Mongolia in the collections of ZPAL (Mg, Mongolia, M, Mammalia); **ZIN**, Zoological Institute, Russian Academy of Sciences, St. Petersburg; **ZPAL**, Institute for Paleobiology, Polska Akademia Nauk, Warsaw.

**Enamel Microstructure Abbreviations**—**EDJ**, enamel-dentine junction; **HSB**, Hunter-Schreger bands; **IPM**, interprismatic matrix; **OES**, outer enamel surface; **P**, prism; **PE**, portio externa; **PI**, portio interna; **PLEX**, prismless external layer.

### MATERIAL AND METHODS

#### Specimens Studied

**Zalambdalestidae**—*Barunlestes butleri*, MgM-I/135, right lower incisor taken from mandible with p3–4 and m1–3; Barun Goyot Formation, Late Cretaceous; MA 178.

**Pseudictopidae**—*Pseudictops lophiodon*, MgM-II/11, left lower incisor (i2) associated with isolated ?dc, p1, p2, p3, m1, m2; Naran Bulak, Paleocene, Sulimski, 1968; MA 257. *Pseu-*

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*dictops lophiodon*, MgM-II/24, isolated left upper incisor (I2); Naran Bulak, Paleocene, 1964; MA 258.

**Eurymylidae**—*Eurymylus laticeps*, MgM-II/61, right lower incisor taken from mandible with p4–m3 (Sych, 1971:pls. 25, 27–28); Naran Bulak, Nemegt Basin, late Paleocene; MA 256. *Matutinia nitidulus*, IVPP V-7444, left upper and right lower incisors taken from skull fragment with mandible; Lingcha Formation, Hengyang Basin, China, early Eocene; MA 172. *Matutinia nitidulus*, IVPP V-7449, left upper and right lower incisors taken from skull with lower jaw; Lingcha Formation, Hengyang Basin, China, early Eocene; MA 173.

**Mimotonidae**—*Anatolimys rozhdestvenskii*, ZIN 79158, left lower incisor taken from mandible with p4 and m2–3; Andarak 2, Kyrgyzstan, early Eocene (*Anatolimys* Shevyreva 1994 has priority over *Anatolimys* Averianov 1994; Averianov and Godinot, 1998); identified by A. O. Averianov; MA 180. cf. *Anatolimys rozhdestvenskii*, ZIN-An-5, ?upper isolated incisor; Andarak 2, Kyrgyzstan, early Eocene; according to A. O. Averianov (pers. comm., July, 2003) *Anatolimys rozhdestvenskii* is the only species of that genus present at Andarak; MA 181. Mimotonidae gen. et sp. indet., MAE-56-97-5112, right upper incisor taken from anterior skull fragment with I2–3 and cheek teeth; above base of Bumban Member, early Eocene; identified by M. C. McKenna; MA 204. Mimotonidae gen. et sp. indet., MN 50a, left upper and lower incisors taken from skull with I2–3 and mandible with i2 plus complete cheek dentition; Bumban Beds, Naran Bulak, early Eocene; identified by M. C. McKenna; MA 206.

**Ochotonidae**—*Sinologomys* sp. indet., AMNH 56648, left lower incisor taken from mandible with i, p3–m1; Hsanda Gol Formation, Tsagan Nor Basin, Mongolia, Oligocene; MA 186. *Desmatolagus vetustus*, AMNH 26093, left lower incisor taken from mandible with i, p3–m3, Ulan Gochu Formation, Shara Murun region, early Oligocene; MA 189. *Desmatolagus gobiensis*, AMNH 84851, right lower incisor taken from mandible with i, p3–m2; Hsanda Gol Formation, Tsagan Nor Basin, Mongolia, Oligocene; MA 187. *Desmatolagus robustus*, AMNH 83856, right lower incisor taken from mandible with i, p3–p4; Hsanda Gol Formation, Tasagan Nor Basin, Mongolia, Oligocene; MA 188. *Australogomys simpsoni*, AMNH 22528b, right lower incisor taken from mandible with p3–p4 (paratype); S. of Lüderitz Bay, Namibia, S.W. Africa, Miocene; MA 252. *Belatona forsythmajori*, AMNH 26238 (805), right lower incisor taken from mandible with i, p3–m3; Tung Gur beds, Tairum Nor Basin, middle Miocene; MA 202. *Ochotonoides complicidens*, AMNH 141011, left upper and lower incisors taken from skull with associated mandible; Hsi Chuang, Shou Yang, China, Pliocene; MA 249.

**Leporidae**—Leporidae gen. et sp. indet. (*Aktashmys* or *Strenulagus*), ZIN-An-1, isolated right upper incisor; Andarak 2, Kyrgyzstan, early Eocene; MA 185. According to A. O. Averianov (pers. comm., July, 2003), two lagomorphs are present in Andarak, *Aktashmys montealbus* Averianov 1994 (= "*Valerilagus reshetovi*" Shevyreva 1995) and a new species of *Strenulagus* Tong and Lei 1987; although the latter is slightly larger, identification of isolated incisors is not possible. Leporidae gen. et sp. indet. (*Aktashmys* or *Strenulagus*), ZIN-An-6, isolated left upper incisor; Andarak 2, Kyrgyzstan, early Eocene; identified by A. O. Averianov; MA 285. *Litolagus molidens*, AMNH 105999, left lower incisor taken from mandible with p2–m2; Niobrara County, Wyoming, late Eocene (Chadronian); MA 194. *Shamolagus medius*, AMNH 26144, piece of right lower incisor taken from mandible with p3–m1 (holotype); Shara Murun Formation, near Baron Sog, Inner Mongolia, China, late Eocene; MA 253. *Chadrolagus emryi*, AMNH 99121, right lower incisor taken from mandible with p3–m1; Natrona County, Wyoming, late Eocene (Chadronian); MA 195. *Palaeolagus temnodon*, AMNH 99137, right lower incisor taken from mandible with p3–m3; Natrona County, Wyoming, late

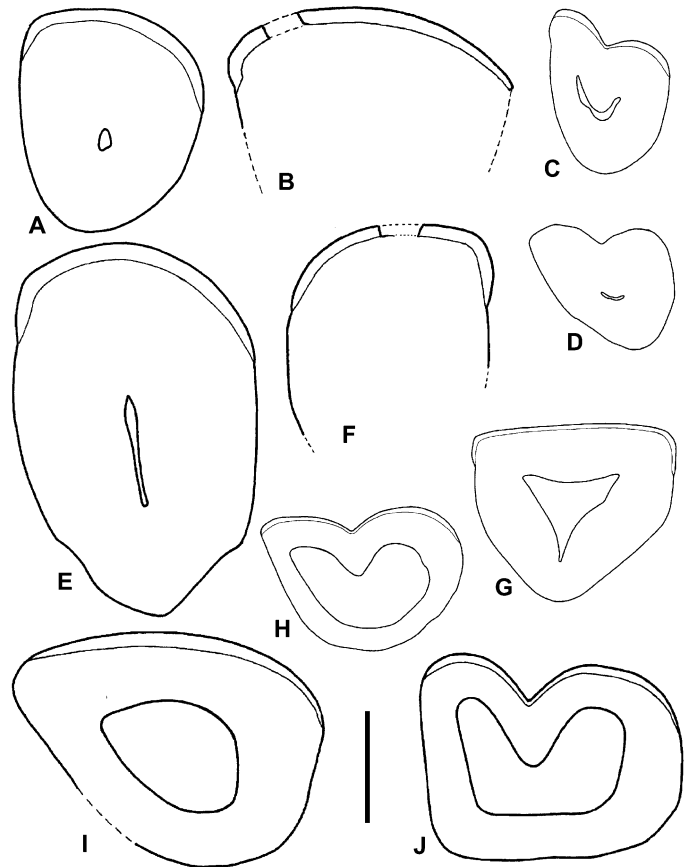


FIGURE 1. Incisor cross sections of various Eurymylidae and Lagomorpha. Scale bar equals 1 mm. A, *Matutinia nitidulus*, right lower incisor (MA 172). B, *Matutinia nitidulus*, left upper incisor (MA 172). C, Leporidae, gen. et sp. indet. (*Aktashmys* or *Strenulagus*), ZIN-An-6, left upper incisor (MA 285). D, Leporidae, gen. et sp. indet. (*Aktashmys* or *Strenulagus*), ZIN-An-1, right upper incisor, enamel layer missing in this part of tooth due to corrosion (MA 185). E, Mimotonidae, gen. et sp. indet., left upper incisor (MA 206). F, Mimotonidae, gen. et sp. indet., right upper incisor (MA 204). G, *Eurymylus laticeps*, right lower incisor (MA 256). H, *Palaeolagus temnodon*, left upper incisor (MA 203). I, *Ochotonoides complicidens*, left lower incisor (MA 249). J, *Megalagus turgidus*, left upper incisor (MA 193).

Eocene (Chadronian); MA 191. *Palaeolagus temnodon*, AMNH 99130, left upper incisor taken from skull with I, dP2–3, P3–M2 (right), P2–M2 (left); Natrona County, Wyoming, late Eocene; MA 203. *Palaeolagus burkei*, AMNH 106367, left upper incisor taken from anterior skull portion with teeth; Washington County, South Dakota, early Oligocene; MA 198. *Palaeolagus haydeni*, AMNH 105835, upper and left lower incisors taken from skull with lower jaw; S. Heart, South Dakota, early Oligocene; MA 200. *Palaeolagus intermedius*, AMNH 141013, left lower incisor taken from mandible with i, p3–m2; 7 mi. south of S. Heart, South Dakota, early Oligocene; MA 201. *Megalagus turgidus*, AMNH 545, left lower incisor taken from mandible with p3–4; White River, Logan County, Colorado, early Oligocene; MA 192. *Megalagus turgidus*, AMNH 141012, left upper incisor taken from anterior skull fragment with teeth; 4 miles SE of Douglas, Wyoming, early Oligocene; MA 193. *Gobiolagus andrewsi*, AMNH 26097, right lower incisor taken from mandible with p4–m2; Ulan Gochu Formation, Shara Murun region, early Oligocene; MA 190. *Archaeolagus macrocephalus*, AMNH 141010, right lower incisor taken from mandible with i, p3–m3 (left) and i, p3–m2 (right); Royal Valley, late Oligocene/early Miocene; MA 196. *Archaeolagus* cf.



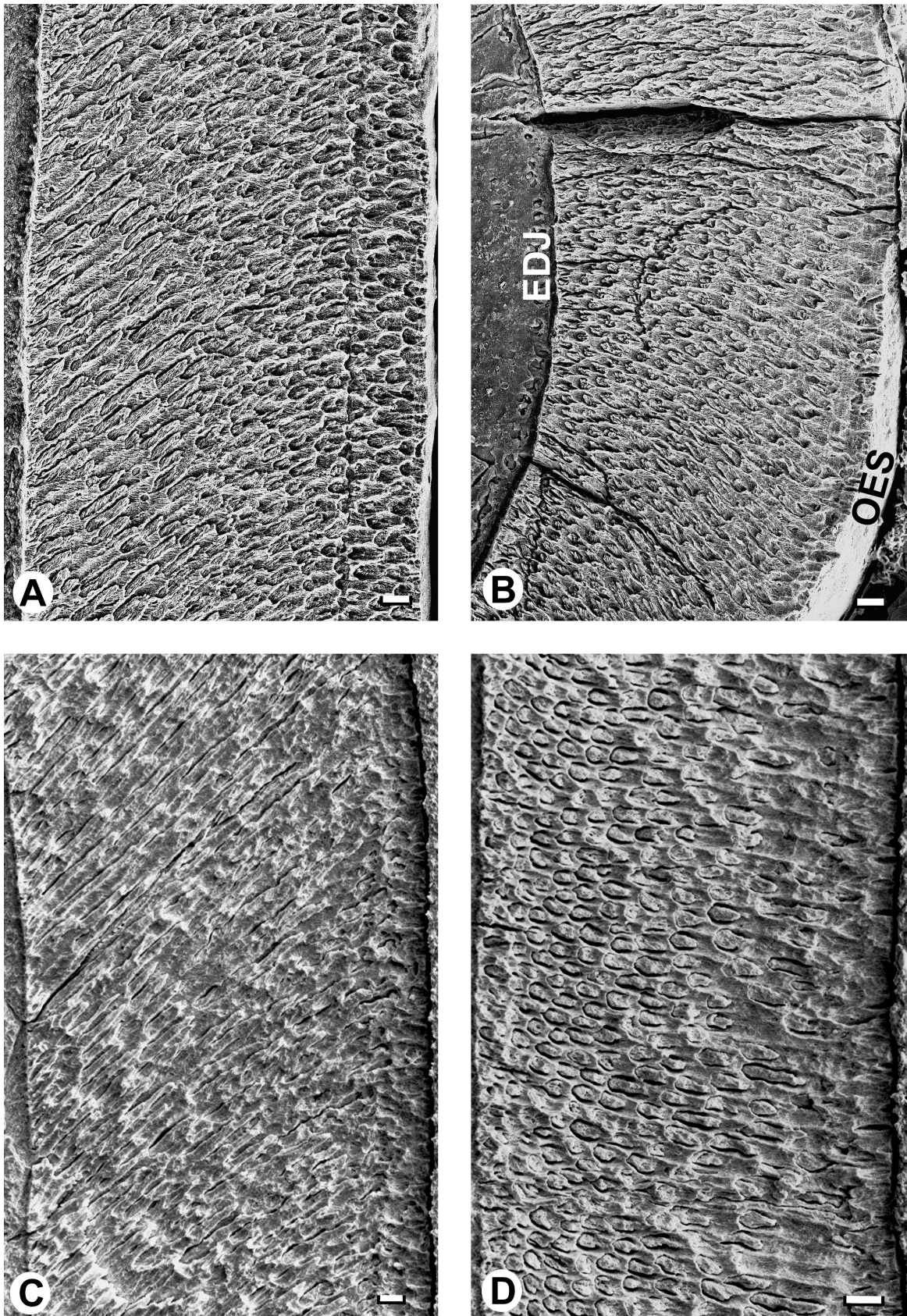


FIGURE 2. Scanning electron micrographs of incisor enamel sections of Zalambdalestidae and Pseudictopidae. **A** and **C**, longitudinal sections; **B** and **D**, cross sections. In all sections, EDJ is to the left and in the longitudinal sections, the tip of the incisor is to the top. Scale bar equals 10  $\mu\text{m}$ . **A** and **B**, *Barunlestes butleri*, Late Cretaceous, MA 178. Lower incisor enamel with a single layer of radial enamel. As evident from the longitudinal section, prisms are inclined  $40^\circ$  apically near the EDJ and turn horizontally towards the OES. **C** and **D**, *Pseudictops lophiodon*, Paleocene, MA 258. Upper incisor enamel with a single layer of radial enamel. Prisms are slightly bent antapically and thick IPM surrounds the prisms.



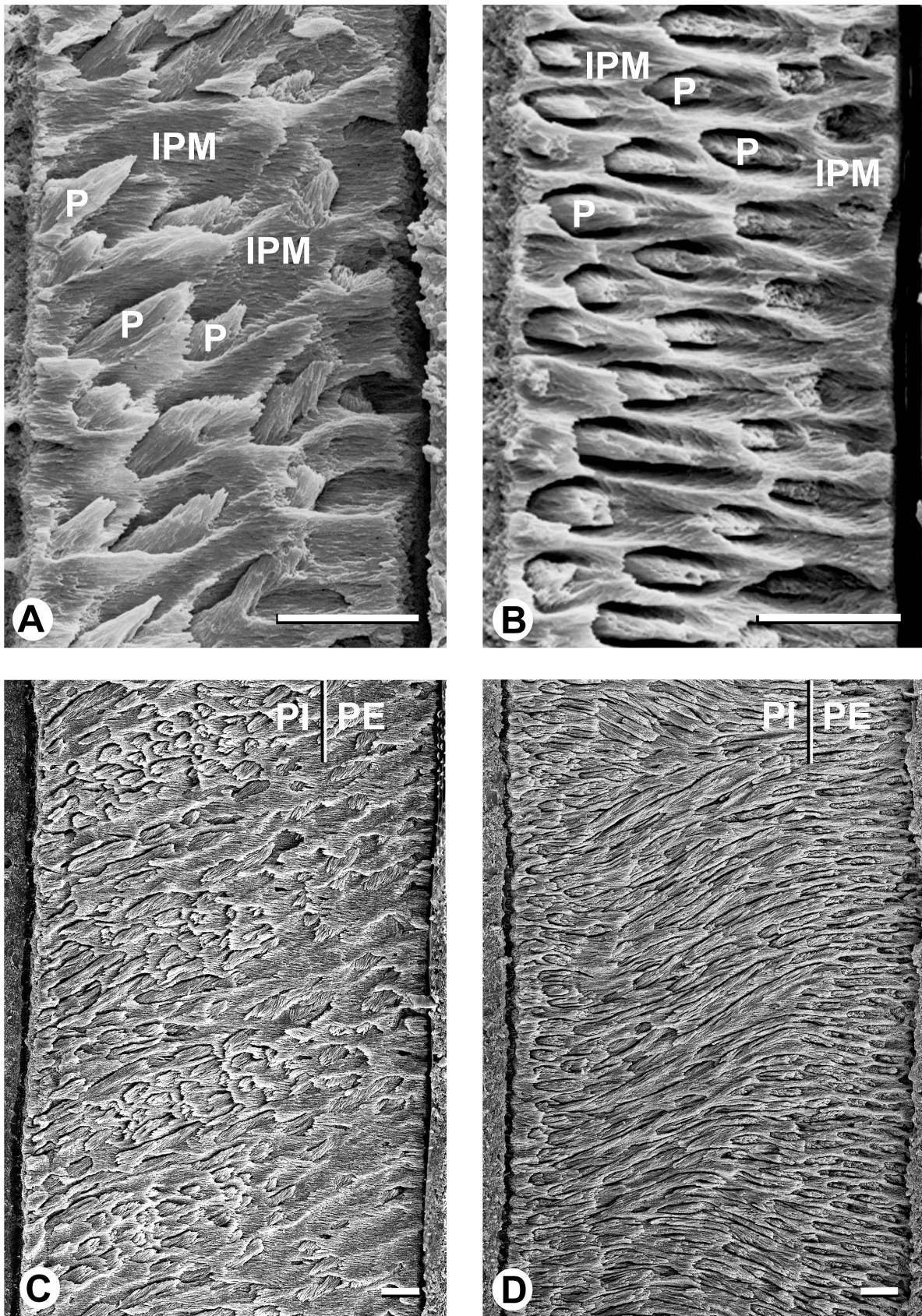


FIGURE 3. Scanning electron micrographs of incisor enamel sections of Eurymylidae. **A** and **C**, longitudinal sections; **B** and **D**, cross sections. In all sections, EDJ is to the left and in the longitudinal sections the tip of the incisor is to the top. Scale bar equals 10  $\mu\text{m}$ . **A** and **B**, *Eurymylus laticeps*, late Paleocene, MA 256. Lower incisor enamel with a single layer of radial enamel. Prisms (**P**) run straight from the EDJ to the OES and the enamel layer is very thin. Thick interprismatic matrix (**IPM**) surrounds the prisms. **C** and **D**, *Matutinia nitidulus*, early Eocene. **C**, lower incisor longitudinal section (MA 172) with double-layered enamel. Portio externa (**PE**) with radial enamel is much thinner than portio interna (**PI**) with HSB. **D**, upper incisor cross section (MA 173) with double layered enamel. In the PE, prism cross sections are strongly laterally flattened.



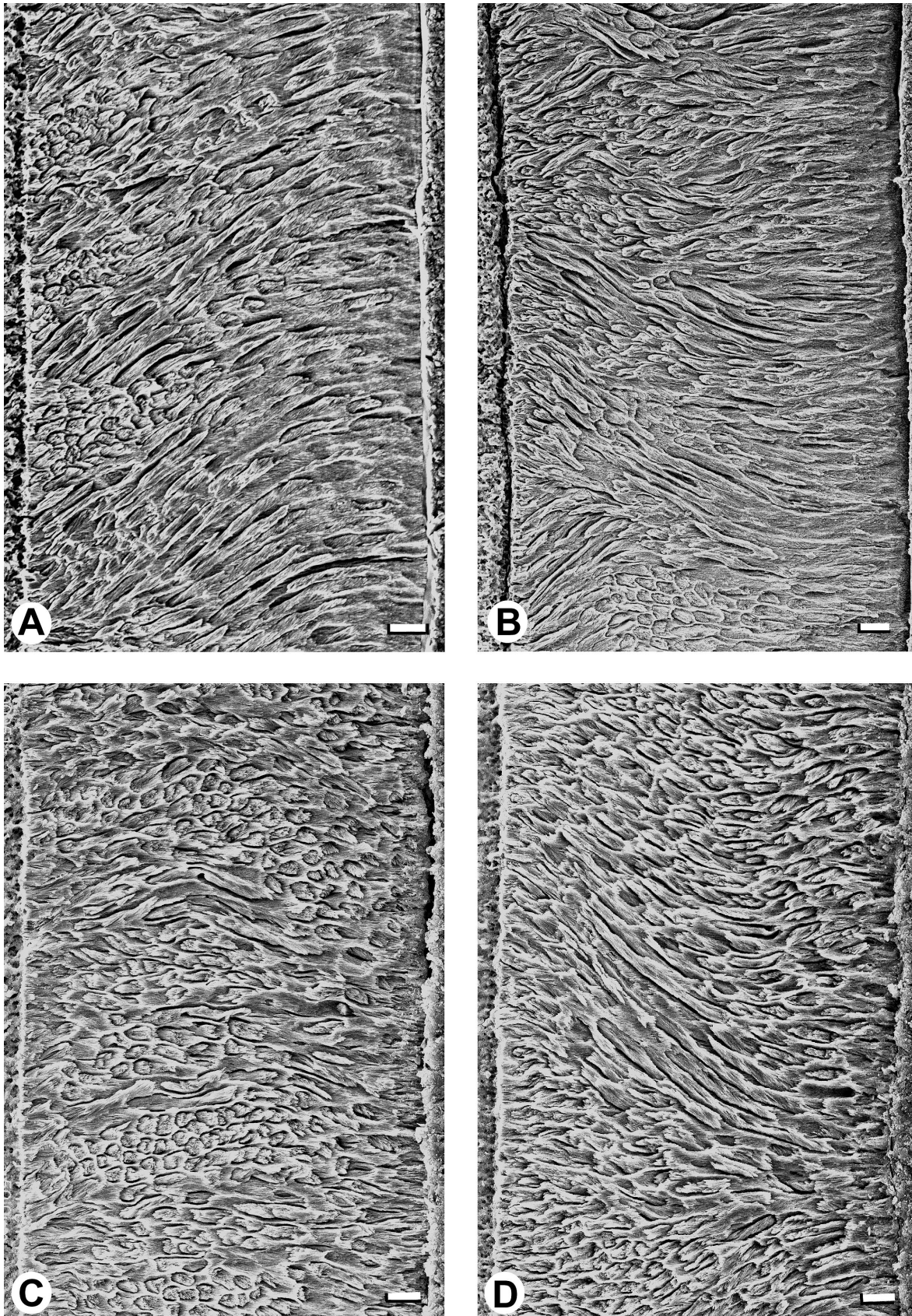


FIGURE 4. Scanning electron micrographs of lower incisor enamel of early Eocene Mimotonidae. **A** and **C**, longitudinal sections; **B** and **D**, cross sections. In all sections, EDJ is to the left and in the longitudinal sections, the tip of the incisor is to the top. Scale bar equals 10  $\mu\text{m}$ . **A** and **B**, *Anatolimys rozhdestvenskii*, MA 180. The incisor enamel is double layered with HSB in the PI and radial enamel in the PE. Prism inclination is  $0^\circ$  in the PE, therefore prisms are cut longitudinally in the longitudinal and cross section. **C** and **D**, *Mimotonidae*, gen. et sp. indet., MA 206. The incisor enamel consists of a single layer with HSB. Towards the OES, HSB become somewhat indistinct, because the angle of decussation decreases.



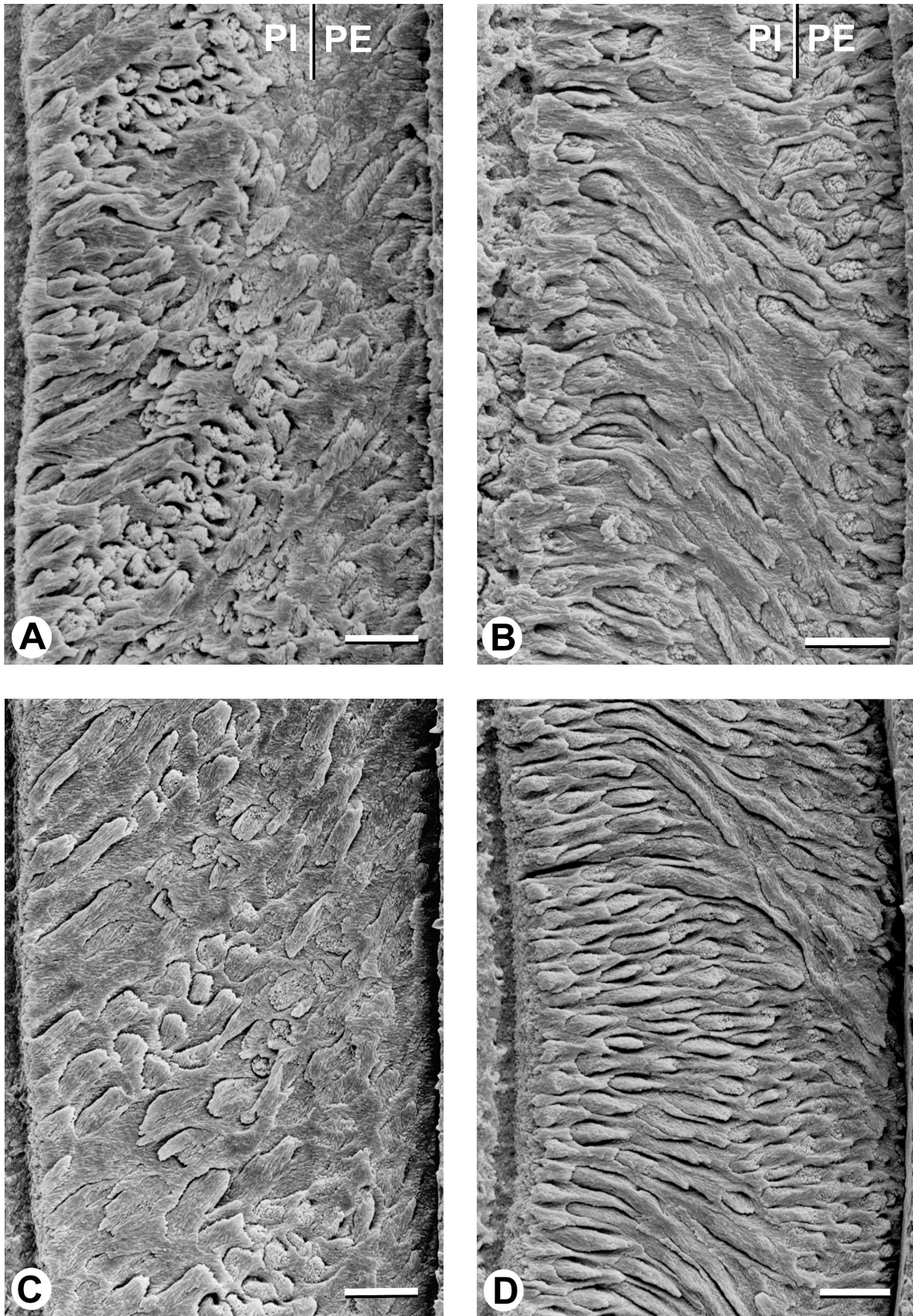


FIGURE 5. Scanning electron micrographs of upper incisor enamel sections of early Eocene Leporidae. **A** and **C**, longitudinal sections; **B** and **D**, cross sections. In all sections, EDJ is to the left and in the longitudinal sections, the tip of the incisor is to the top. Scale bar equals 10  $\mu\text{m}$ . **A** and **B**, Leporidae, gen. et. sp. indet. (*Aktashmys* or *Strenulagus*), MA 185. The incisor enamel is double layered with HSB in the PI and radial enamel in the PE. The border between PI and PE is not very distinct, but the presence of a PE is clearly evident from the cross section. Prism cross sections in the PE are irregularly rounded. **C** and **D**, Lagomorpha, gen. et. sp. indet. (*Aktashmys* or *Strenulagus*), MA 285. In this specimen



*macrocephalus*, AMNH 22288, upper incisors (I2 and I3) taken from maxillary fragment, associated broken lower jaw with dentition; Sandoval County, New Mexico, late Oligocene/early Miocene; MA 199. *Alilepus* sp. indet., AMNH F:AM 116221, left upper incisor taken from skull; T' a Tsun, China, late Miocene; MA 248.

### Preparation Techniques

Pieces a few millimeters long were cut off the incisors using a minidrill diamond-coated disk. Specimens were embedded in polyester resin and cut transversely and longitudinally. Embedded specimens were ground smooth and etched for 2–4 seconds with 2N HCl to make morphological details visible. After ultrasonic cleansing and rinsing with distilled water, the specimens were dried, mounted on SEM stubs, and sputtercoated with gold (6 min). The specimens were studied by SEM at magnifications from 500 to 2,000X. Following general convention, schmelzmuster descriptions refer to the zone which is close to the sagittal plane of the incisor (Flynn and Wahlert, 1978:fig. 2). Laterally, the enamel usually becomes thinner and its microstructure may be simplified (e.g., in two layered enamel the PI with HSB may become obsolete so that only the PE with radial enamel remains). In lagomorph upper incisors that are characterized by a median groove, either the enamel of the sagittal plane of the mesial or lateral lobe is described (Fig. 1). A slight difference in enamel thickness between both lobes has been observed, but there is no structural difference in the schmelzmuster. If not otherwise indicated, “upper incisor” refers to dI2 in Lagomorpha. Systematics follows McKenna and Bell (1997); enamel terminology follows Koenigswald and Sander (1997) and Martin (1999a, b).

### Orientation of IPM

The orientation of the IPM crystallites plays an important role in the distinction of enamel types. Plesiomorphic is a thick IPM where the IPM crystallites are oriented parallel to the prism long axes. This is the case in early prismatic enamel, the (primitive) radial enamel, where prisms and IPM crystallites are oriented perpendicularly to the EDJ. If a certain inclination of the prisms occurs, the IPM crystallites (which remain perpendicular to the EDJ) are at an acute angle to the long axes of the prisms. Both types of IPM orientation are found in radial enamel. An IPM is called “surrounding” if it is thick (at least half a prism diameter) and it surrounds each individual prism. This applies also for HSB, where the orientation of IPM crystallites may be parallel or acute to the prism long axes (depending on the inclination of HSB).

If the IPM is thin (less than half a prism diameter), it usually does not surround each individual prism, but it anastomoses between the prisms or groups of prisms (anastomosing IPM). Orientation of IPM crystallites may be parallel, but in most cases it is acute angular or even rectangular to the prism long axes. IPM may form plates between the prism rows, which do not anastomose (interrow sheets, only in rectangular IPM). This enamel type is called modified radial enamel and is highly derived according to biomechanical constraints (Pretzschner 1988, 1994). In this case, IPM crystallites are no longer perpendicular to the EDJ, but oriented about 45° in antapical direction; the angle between IPM crystallites and prism long axes is about 90°. Parallel/acute anastomosing and rectangular IPM (interrow sheets) also occurs in HSB; it is an important character for the distinction of HSB types.

The terms “multiserial” and “pauciserial” are avoided in the description of lagomorph enamel, because Korvenkontio (1934: 97, 130) originally referred these exclusively to enamel of Rodentia. Lagomorph incisor schmelzmuster was called “lagodont” by Korvenkontio (1934:48), a term which never came in common use. HSB in lagomorph incisors are generally thicker than in those of rodents (except for very large taxa such as *Hydrochaeris* and some fossil giant forms). In early Gliriformes, HSB are structurally similar to the pauciserial condition (e.g., IPM surrounds each individual prism and runs parallel to prism long axes), and in lagomorphs they resemble the multiserial condition (IPM at an acute or right angle to prism long axes). From the early Gliriform condition, the pauciserial HSB of rodents evolved by reduction of HSB thickness, whereas greater HSB thickness was retained in lagomorphs. For the description of early gliriform and lagomorph HSB, the term “multilayered” is used.

## RESULTS

### Outgroup Representatives

**Zalambdalestidae**—The lower incisor enamel of *Barunlestes butleri* is single-layered and consists of radial enamel with no prism decussation (Fig. 2A, B). In the inner part of the enamel, prisms are inclined 45° apically; after having reached the middle of the enamel layer, prisms turn simultaneously in a horizontal direction (inclination = 0°). IPM surrounds the prisms and IPM crystallites are oriented perpendicularly to the EDJ. Therefore, they run at an angle of about 40° to the prism long axes in the inner part of the enamel and parallel to the prisms in the outer part. Prism cross sections are rounded ovals. Enamel thickness is 145 μm. A PLEX of 5–10 μm is present.

**Pseudictopidae**—The upper and lower incisor enamel of *Pseudictops lophiodon* is single-layered and consists of radial enamel (Fig. 2C, D). Prisms run parallel to each other and no prism decussation occurs. Prisms perform a slight antapical bending in the upper incisor. In the inner part of the enamel, near the EDJ, they are inclined 40° apically. Towards the OES, prism inclination slightly decreases (about 30° near the OES). In the lower incisor, prisms run straight (without bending) from the EDJ to the OES and are inclined 30° apically. IPM surrounds the prisms and IPM crystallites are oriented at an acute angle to the prism long axes. Enamel thickness is 100–150 μm in the upper incisor depending on the area of the tooth crown; in the lower incisor it is 50 μm. A PLEX of 10–15 μm is present.

### Early Simplicidentata

**Eurymylidae**—The lower incisor enamel of *Eurymylus laticeps* has a single layer of radial enamel (Fig. 3A, B). Prisms run straight from the EDJ to the OES without bending and are inclined 30° apically. Thick IPM surrounds the prisms and IPM crystallites are oriented at an acute angle to the prism long axes. Prism cross sections are oval. Enamel thickness is 25–30 μm and a PLEX is present.

The upper and lower incisor enamel of *Matutinia nitidulus* is double-layered with an inner portion with HSB and a thin outer portion of radial enamel (Fig. 3C, D). In the upper incisors, HSB are 4–5 prism layers wide and are inclined 15–25° apically. Enamel thickness is 115–125 μm and the PE comprises 25–30% of the total enamel thickness. In the lower incisor enamel, HSB are 3 to 4 prism layers wide and are inclined

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the enamel is single layered. Towards the OES, HSB become indistinct (decrease of decussation). From the cross sections it is evident that no PE with radial enamel is present and that HSB run from the EDJ to the OES.



TABLE 1. Summary of schmelzmuster of studied taxa. ?? indicates not measured.

Taxon	Age	Incisor	Number of layers	Enamel types
<i>Barunlestes butleri</i>	Late Cretaceous	lower	1	radial
<i>Pseudictops lophiodon</i>	Paleocene	upper	1	radial
<i>Pseudictops lophiodon</i>	Paleocene	lower	1	radial
<i>Eurymylus laticeps</i>	late Paleocene	lower	1	radial
<i>Matutinia nitidulus</i> MA 172	early Eocene	upper	2	HSB, radial
<i>Matutinia nitidulus</i> MA 172	early Eocene	lower	2	HSB, radial
<i>Matutinia nitidulus</i> MA 173	early Eocene	upper	2	HSB, radial
<i>Matutinia nitidulus</i> MA 173	early Eocene	lower	2	HSB, radial
<i>Anatolimys rozhdestvenskii</i>	early Eocene	lower	2	HSB, radial
cf. <i>Anatolimys rozhdestvenskii</i>	early Eocene	?upper	2	HSB, radial
Mimotonidae sp. indet. MA 204	early Eocene	upper	1	HSB
Mimotonidae sp. indet. MA 206	early Eocene	upper	1	HSB
Mimotonidae sp. indet. MA 206	early Eocene	lower	1	HSB
<i>Sinolagomys</i> sp. indet.	Oligocene	lower	2	modified radial, HSB
<i>Austrolagomys simpsoni</i>	Miocene	lower	2	modified radial, HSB
<i>Bellatona forsythmajori</i>	Miocene	lower	2	modified radial, HSB
<i>Ochotonoides complicidens</i>	Pliocene	upper	2	modified radial, HSB
<i>Ochotonoides complicidens</i>	Pliocene	lower	3	modified radial, HSB, tangential
Leporidae gen. et sp. indet.	early Eocene	upper	2	HSB, radial
Leporidae gen. et sp. indet.	early Eocene	upper	1	HSB
<i>Shamolagus medius</i>	late Eocene	lower	1	HSB
<i>Litolagus molidens</i>	late Eocene	lower	1	HSB
<i>Chadrolagus emryi</i>	late Eocene	lower	1	HSB
<i>Palaeolagus temnodon</i>	late Eocene	lower	1	HSB
<i>Palaeolagus temnodon</i>	late Eocene	upper	1	HSB
<i>Palaeolagus haydeni</i>	early Oligocene	upper	1	HSB
<i>Palaeolagus haydeni</i>	early Oligocene	lower	1	HSB
<i>Palaeolagus haydeni</i>	early Oligocene	(I3)	1	radial
<i>Palaeolagus burkei</i>	early Oligocene	(I3)	1	radial
<i>Palaeolagus intermedius</i>	early Oligocene	lower	1	HSB
<i>Megalagus turgidus</i>	early Oligocene	lower	1	HSB
<i>Megalagus turgidus</i>	early Oligocene	upper	1	HSB
<i>Gobiolagus andrewsi</i>	early Oligocene	lower	1	HSB
<i>Desmatolagus vetustus</i>	early Oligocene	lower	1	HSB
<i>Desmatolagus gobiensis</i>	Oligocene	lower	1	HSB
<i>Desmatolagus robustus</i>	Oligocene	lower	1	HSB
<i>Archaeolagus macrocephalus</i>	late Olig./early Mioc.	lower	1	HSB
<i>Archaeolagus</i> cf. <i>macrocephalus</i>	late Olig./early Mioc.	upper	1	HSB
<i>Archaeolagus</i> cf. <i>macrocephalus</i>	late Olig./early Mioc.	(I3)	1	HSB
<i>Alilepus</i> sp. indet.	late Miocene	upper	1	HSB

25–30° apically. Enamel thickness is 100–110 µm and the PE comprises about 25–30% of the total enamel thickness. In upper and lower incisors, IPM surrounds the prisms and IPM crystallites are oriented at an acute angle to the prism long axes. Prism cross sections are oval in the PI and laterally flattened in the PE; in most specimens a thin PLEX is present.

### Early Duplicidentata

**Mimotonidae**—The lower incisor (di2; according to Averianov, 1994 and pers. comm. July, 2003, *Anatolimys* has two pairs of lower incisors) of *Anatolimys rozhdestvenskii* has a double-layered schmelzmuster with a PI of HSB and a PE of radial enamel (Fig. 4A, B). There is no clear boundary between HSB and radial enamel, and single bands may extend into the outer layer of radial enamel. The PI is about two-thirds of total enamel thickness. HSB are 3–5 prism layers thick and are inclined 30° apically; between HSB transition zones occur. In the PE, prisms are not inclined, but are oriented perpendicular to the EDJ (inclination = 0°). IPM is thin. In the PI and PE, IPM crystallites run parallel to the prism long axes and IPM anastomoses between the prisms. Prism cross sections are rounded ovals. Enamel thickness is 135 µm and a thin PLEX is present. The ?upper incisor enamel of cf. *Anatolimys rozhdestvenskii* is also double-layered with HSB in the PI and radial enamel in the PE. As in the lower incisor, the boundary between inner and outer portions is not sharp and the PI is about two thirds of total enamel thickness. HSB are 4–6 prism layers thick and

between the HSB transition zones are visible. HSB inclination varies from almost 0° to 30°. IPM is thin. In the PI, IPM crystallites run parallel to the prism long axes and IPM anastomoses between the prisms. In the PE, IPM crystallites run at an acute angle to the prism long axes; prisms are inclined with 45° apically. Enamel thickness is 150 µm and a thin PLEX is present.

The upper and lower incisor enamel of two undetermined mimotonid specimens from Mongolia (MA 204 and MA 206) have single-layered schmelzmuster with HSB that become indistinct towards the OES (Fig. 4C, D). This phenomenon is caused by the fact that the angle of decussation of adjacent HSB decreases in the outer part of the enamel layer. HSB thickness varies between 4–6 prism layers and HSB inclination is low to moderate (0–35°). Between HSB, transition zones are present. IPM is thin and IPM crystallites run parallel or at an acute angle to the prism long axes and anastomose regularly. Prism cross sections are oval in the PI and laterally flattened in the PE. Enamel thickness is 120–135 µm and a PLEX is missing.

### Lagomorpha

**Leporidae**—Except for one of the earliest representatives, the incisor schmelzmuster of Leporidae is very uniform and consists of a single layer with HSB. In contrast to all other leporids studied, the upper incisor schmelzmuster of an undetermined leporid (*Aktashmys* or *Strenulagus*) from the early Eocene of Andarak is double-layered with HSB in the PI and radial enamel in the PE (Fig. 5A, B). The PE comprises up to



TABLE 1. (Extended.)

Prism inclination (deg)	Prism bending	HSB inclination (deg)	HSB thickness (prisms)	IPM in HSB	IPM in radial enamel	Enamel thickness (μm)	% PE
40–0	antapical	—	—	—	acute surrounding	145	—
40–30	antapical	—	—	—	acute surrounding	100–150	—
30	straight	—	—	—	acute surrounding	50	—
30	straight	—	—	—	acute surrounding	25–30	—
30 (PE)	—	15–20	4–5	parallel surrounding	acute	125	30
30 (PE)	—	30	3–4	acute surrounding	acute	110	30
25 (PE)	—	25	4–5	parallel surrounding	acute	115	25
30 (PE)	—	25	3–4	acute surrounding	acute	105	25
0 (PE)	—	30	3–5	parallel	parallel	135	30
45 (PE)	—	0–30	4–6	parallel	acute	150	30
—	—	35	4–6	parallel to acute	—	125	—
—	—	25	3–5	parallel to acute	—	135	—
—	—	0–5	3–4	parallel to acute	—	120	—
45 (PI)	straight	50	3–4	rectangular	rectangular	70	40
55 (PI)	straight	45	5	rectangular	rectangular	70	40–50
45 (PI)	straight	45	2–3	rectangular	rectangular	120	40
45 (PI)	straight	45	4–6	rectangular	rectangular	65	70
45	straight	45	3–5	rectangular	rectangular	140	—
60 (PE)	straight	40	3–4	acute	acute	50	30
—	—	35	3–4	parallel surrounding	—	55	—
—	—	40	3–4	acute	—	35	20
—	—	50	3–5	rectangular	—	70	—
—	—	55	3–4	rectangular	—	50	—
—	—	55	3	rectangular	—	50	—
—	—	55	4–5	rectangular	—	45	—
—	—	??	3–6	rectangular	—	45–50	—
—	—	40	3–4	rectangular	—	70	—
30	straight	—	—	—	rectangular	40	—
Not measured	straight	—	—	—	rectangular	45–55	—
—	—	0	5–6	rectangular	—	70	—
—	—	35	3–5	rectangular	—	75	—
—	—	35	5–6	rectangular	—	55–60	—
—	—	45–50	4–5	acute	—	75	—
—	—	45	3	acute	—	30	—
—	—	45	3	rectangular	—	50	—
—	—	45	3–4	rectangular	—	45	—
—	—	30	3–5	rectangular	—	90	—
—	—	30	2–3	rectangular	—	35	—
—	—	45	3	rectangular	—	35	—
—	—	50	5	rectangular	—	40	—

30% of the total enamel thickness. Prism cross sections are oval and a PLEX is missing. The enamel of a second undetermined leporid upper incisor from Andarak (*Aktashmys* or *Strenulagus*) exhibits a single-layered schmelzmuster with HSB (Fig. 5C, D). Towards the OES, HSB become indistinct because the angle of decussation is decreasing. However, a few HSB in this specimen reach the OES and a separate PE with radial enamel cannot be distinguished. IPM surrounds and runs parallel to the prisms.

The lower incisor enamel of *Shamolagus medius* is very thin (35 μm) and formed by a single layer with HSB (Fig. 6A). As in the undetermined leporid (ZIN-An-6) from Andarak, HSB become indistinct towards the OES, but a separate PE with radial enamel is not discernible. IPM anastomoses between the prisms and IPM crystallites are oriented at an acute angle to the prism long axes. Prism cross sections are oval, and a very thin PLEX is present. The schmelzmuster of all other leporids (e.g., Fig. 6B, D) studied is single-layered with HSB. Slight differences occur in the thickness and inclination of HSB, in IPM orientation, and in enamel thickness (Table 1). IPM may form interrow sheets (rectangular) or run at an acute angle to the prism long axes. HSB thickness varies between 3 and 6 prisms and enamel thickness between 35 and 90 μm. Prism cross sections are oval to lancet shaped and a thin PLEX (about 5 μm) may be present.

The enamel of the third upper incisor (I3) of *Archaeolagus* cf. *macrocephalus* resembles that of di2/DI2 and consists of a single layer with HSB with rectangular IPM. The enamel of the I3 of *Palaeolagus haydeni* and *Palaeolagus burkei* does not

contain HSB, but has a single layer of radial enamel. Such a reduction of HSB is typical for vestigial teeth. IPM runs at a right angle to the prism long axes, a condition that is a remnant of the HSB.

**Ochotonidae**—The lower incisor schmelzmuster of the ochotonids *Sinolagomys* sp. indet. (Fig. 7A, B), *Austrolagomys simpsoni* (Fig. 7C, D), and *Bellatona forsythmajori* is double-layered with modified radial enamel in the PI and HSB in the PE. In modified radial enamel, IPM crystallites are perpendicular to the prism long axes and IPM forms interrow sheets between prism rows which do not anastomose (Pfretzschner 1988, 1994). The HSB in *Sinolagomys* sp. indet. are weakly developed because the prism layers decussate at an acute angle. Due to the low angle of decussation, HSB are not very distinct in the longitudinal section, and in the cross section they appear only as slight undulation of prism cross sections. In the PE, IPM is at a right angle to the prism long axes and anastomoses. In the PI and PE, IPM is much thinner than the prism cross sections. A thin PLEX is present. Near the medial overlap of the enamel cover of the incisor, the PE is formed by tangential enamel with interrow sheets; HSB are not developed in this area. The tangential enamel here is 55–60% of the total enamel thickness.

The lower incisor enamel of *Austrolagomys simpsoni* closely resembles that of *Sinolagomys* sp. indet., but HSB are more distinct (higher angle of decussation). IPM is comparatively thin and forms interrow sheets in the PI; in the PE, IPM crystallite orientation is also rectangular to the prism long axes, but



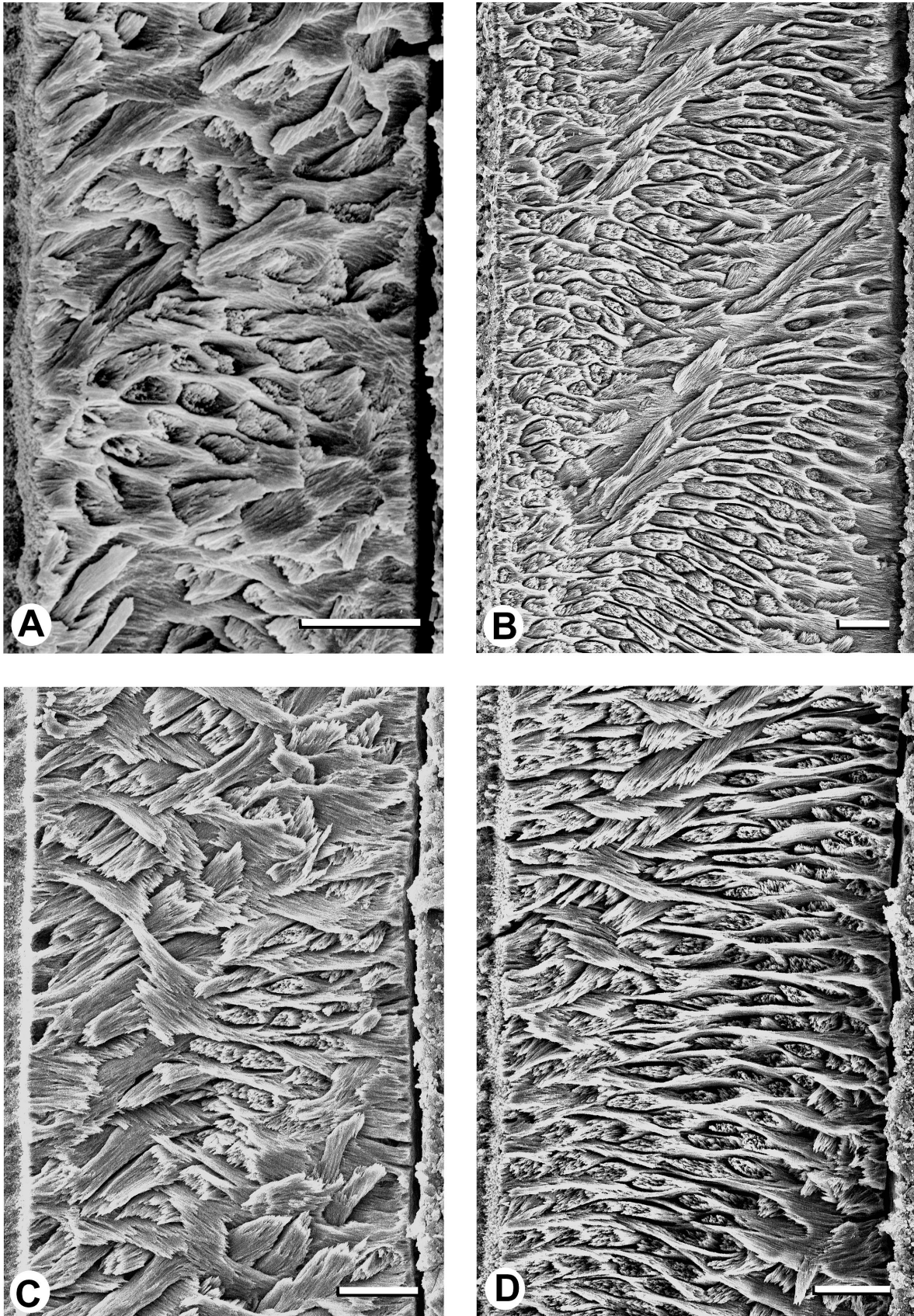


FIGURE 6. Scanning electron micrographs of lower incisor enamel sections of Leporidae. **A**, **B**, and **C**, longitudinal sections; **D**, cross section. In all sections, EDJ is to the left and in the longitudinal sections, the tip of the incisor is to the top. Scale bar equals 10  $\mu\text{m}$ . **A**, *Shamolagus medius*, early Eocene, MA 253. The enamel of *Shamolagus* is very thin. As typical for Leporidae, it is single layered with HSB. IPM runs at an acute angle to the prism long axes and anastomoses regularly. Towards the OES, HSB become indistinct. **B**, *Gobiolagus andrewsi*, early Oligocene, MA 190. The enamel of *Gobiolagus* is comparatively thick and consists of a single layer with thick HSB. IPM runs at an acute angle to the



IPM anastomoses regularly. Prism cross sections are oval and laterally flattened in the PI and PE. A PLEX is missing.

The schmelzmuster of *Bellatona forsythmajori* resembles that of *Sinolagomys* sp. indet. but the enamel is much thicker. The border between PI and PE is not clear and HSB are not very distinct (low decussation angle); in the incisor cross section they are indicated only by a slight undulation of prism rows. A thin PLEX is present.

The lower incisor schmelzmuster of *Ochotonoides complicidens* is three-layered with an inner layer of modified radial enamel, a middle layer with HSB, and an outer layer with tangential enamel. This schmelzmuster closely resembles that of the extant *Ochotona princeps*. The inner radial enamel comprises about 35% of the total enamel thickness, the middle part with HSB 50%, and the outer part with tangential enamel 15%, respectively. The border between modified radial enamel and HSB is not sharp, because decussation of prisms begins very weakly and increases towards OES. IPM crystallites are perpendicular to the prism long axes in the inner and middle part of the enamel, forming interrow sheets. In the outer tangential enamel, IPM anastomoses between the prisms. Prism cross sections are oval and laterally flattened. A PLEX is present. The lower incisor enamel of *Ochotonoides complicidens* is double-layered with modified radial enamel in the inner layer and HSB in the outer layer. A thick PLEX (10  $\mu\text{m}$ ) is present.

## DISCUSSION

### The Plesiomorphic Therian Incisor Schmelzmuster

The single layer of radial enamel in the incisors of *Barunlestes butleri* and *Pseudictops lophiodon* (Fig. 2) represents the plesiomorphic therian condition. In plesiomorphic radial enamel, the IPM surrounds the prisms and IPM crystallites are oriented parallel to the prism long axes. Prisms are oriented parallel to each other and run straight or slightly bent from the EDJ to the OES. A single layer of radial enamel has been found in the molars of the holotherian *Dryolestes leiriensis* from the Late Jurassic (Martin, 1999c), in a lower incisor of the multituberculate *Taeniolabis taoensis* (Carlson and Krause, 1985), and in incisors and molars of many early Paleogene mammals such as *Heterohyus europaeus* (Apatotheria), *Conacodon* sp. (Condylarthra), and most Paleogene to Recent lipotyphlans and marsupials (Koenigswald et al., 1987; Koenigswald, 1988, 1994). Plesiomorphic radial enamel has also been observed in the incisors of the extant macroscelidid *Petrodromus tetradactylus* (Martin, 1999a). Character polarity is also indicated by biomechanical aspects. A single layer of plesiomorphic radial enamel is much less resistant to failure than a schmelzmuster with HSB because it does not provide any crack-stopping mechanism (Koenigswald et al., 1987; Koenigswald and Pfretzschner, 1991; Pfretzschner, 1988, 1994). HSB evolved in the molars of many small mammals to cope with increased chewing stress (Koenigswald et al., 1987). In contrast to plesiomorphic radial enamel, modified radial enamel with a plate-like IPM that forms thick interrow sheets is derived, as evidenced from biomechanics (Pfretzschner, 1988, 1994). In this enamel type, the crystallites of the thick IPM-plates are oriented perpendicularly to the prisms and both prisms and IPM-plates form a decussating pattern analogous to HSB.

### Incisor Schmelzmuster of Early Simplicidentata

*Eurymylus laticeps* (Fig. 3A, B) retained the plesiomorphic condition with a single layer of plesiomorphic radial enamel. A

similar schmelzmuster is present in the lower incisors of cf. *Eomylus* from the late Paleocene of Mongolia and the upper incisor of the recently described *Sinomylus zhaii* McKenna and Meng 2001 from the late Paleocene of Anhui Province, China (Martin, 1999a). The occurrence of a single layer of radial enamel in *Barunlestes butleri* and *Pseudictops lophiodon* is evidence that this character state represents the plesiomorphic condition for Glires. A single layer of plesiomorphic radial enamel is also present in the upper incisors of *Tribosphenomys minutus* (Rodentiaformes), a sister taxon of Rodentia (Meng and Wyss, 1994; Meng et al., 1994; Wyss and Meng, 1996). A reversal from enamel with HSB to plesiomorphic radial enamel never has been observed except in teeth where the enamel is becoming vestigial (e.g., teeth of extant odontocetes; Sahni and Koenigswald, 1997). Plesiomorphic radial enamel is not to be confused with the highly derived modified radial enamel that is found in ochotonid incisors, for example. In the incisors of gliriform mammals, which are subject to high stresses during gnawing, a reversal from HSB to plesiomorphic radial enamel can be excluded; therefore the interpretation of the single layer of radial enamel as a possible autapomorphic character of *Tribosphenomys minutus* (Meng and Wyss, 1994; McKenna and Meng, 2001:568) is very unlikely. More probably, *Tribosphenomys* has retained the plesiomorphic therian condition.

The schmelzmuster of the eurymylid *Matutinia nitidulus* (Fig. 3C, D) is more derived. The studied specimens of *Matutinia* (now considered a valid taxon following Ting et al., 2002; contra McKenna and Bell, 1997) have double-layered enamel in upper and lower incisors with HSB in the PI and radial enamel in the PE. The presence of HSB is a derived character (Koenigswald and Pfretzschner, 1987, 1991; Pfretzschner, 1988, 1994). According to the phylogenetic position of *Matutinia* as member of the sistergroup of *Tribosphenomys* plus Rodentia (Meng et al., 2003:fig. 74) it must be assumed that HSB evolved convergently in Eurymylidae and Rodentia.

A schmelzmuster with HSB is also present in the incisors of *Gomphos* sp. indet., *Rhombomylus* sp. indet. (Martin, 1999a) and *Zagmys insolitus* (Flynn et al., 1987). The schmelzmuster of *Gomphos* sp. indet. is double-layered with an outer portion of radial enamel; *Zagmys insolitus* originally was interpreted as having only a single layer with HSB, but reinterpretation of the SEM images of Flynn et al. (1987) made the presence of an outer layer with radial enamel probable (Martin, 1999a). The schmelzmuster of *Rhombomylus* sp. indet. was first described as single-layered (Martin, 1992) in a specimen from the early Eocene of Hubei Province in China (IVPP V 5257), but later Martin (1999a) observed a double-layered schmelzmuster in a specimen (cf. *Rhombomylus*) from Mongolia (PSS-MAE-914). The outer layer of radial enamel of *Rhombomylus* sp. indet. and *Zagmys insolitus* is not very obvious because it is rather thin and the boundary between PI and PE is somewhat irregular. The number of enamel layers in PSS-MAE-914 could suggest that it represents a different species or even genus. These observations demonstrate, that double-layered and derived single-layered schmelzmuster with HSB occur in both stem-lineages of Lagomorpha and Rodentia.

### Incisor Schmelzmuster of Early Duplicidentata

In basal Duplicidentata, double-layered and single-layered schmelzmuster with HSB were detected. *Anatolimys rozhdestvenskii* (Fig. 4A, B) has double layered schmelzmuster with HSB in the PI and radial enamel in the PE in upper and lower incisors. Upper and lower incisors of two "mimotonids" (MA

←

prism long axes and anastomoses frequently. C and D, *Desmatolagus gobiensis*, Oligocene, MA 187. The enamel is single layered with HSB (typical leporid schmelzmuster). IPM runs rectangular to the prism long axes and anastomoses frequently.



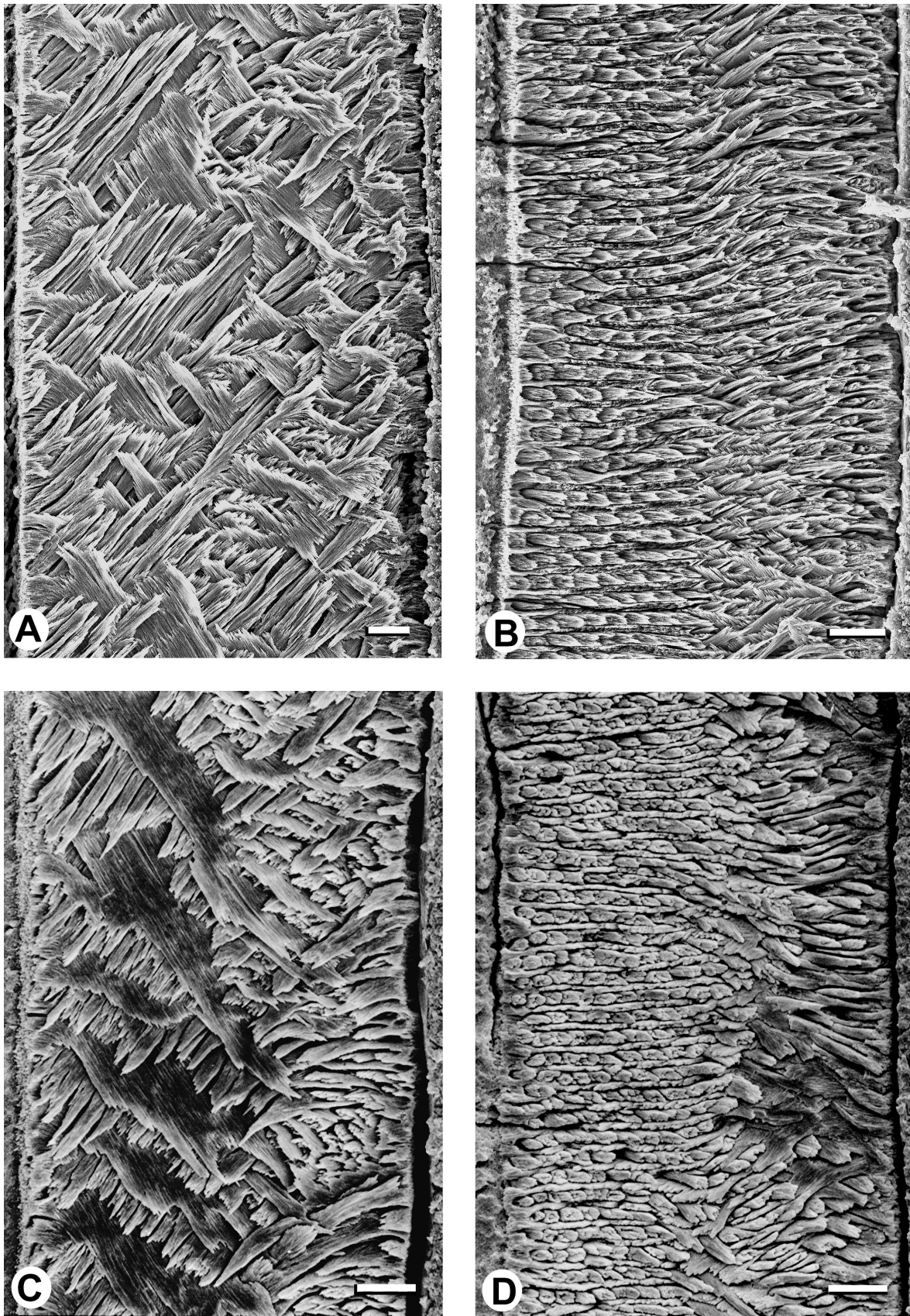


FIGURE 7. Scanning electron micrographs of lower incisor enamel sections of Ochotonidae. **A** and **C**, longitudinal sections; **B** and **D**, cross sections. In all sections, EDJ is to the left and in the longitudinal sections, the tip of the incisor is to the top. **A** and **B**, *Sinolagomys* sp. indet., Oligocene, MA 186. The enamel is double-layered with modified radial enamel in the PI and weakly developed HSB in the PE. As is typical for modified radial enamel, IPM forms plates between the prism rows. **C** and **D**, *Austrolagomys simpsoni*, Miocene, MA 252. The schmelzmuster of *Austrolagomys* is similar to that of *Sinolagomys*, but HSB are more clearly developed (higher angle of decussation). Plate-like interrow sheets are clearly visible.



204 and MA 206; not yet identified at the specific and generic level) collected by the MAE in Mongolia have single-layered schmelzmuster. In the outer part of the enamel layer, HSB become less distinct due to decreasing angle of prism decussation. This supports the interpretation that HSB originated in the inner part of the formerly single layer of radial enamel and expanded towards the OES (Koenigswald, 1985). An upper incisor of another undetermined mimotomid specimen from Mongolia (MA 130) has double-layered enamel with HSB in the PI and radial enamel in the PE (Martin 1999a:262, fig. 3A, B). Studied basal Duplicidentata represent different transitional stages from a double-layered towards a single-layered schmelzmuster, as is to be expected from stem-lineage representatives of leporids. Therefore, the earlier hypothesis that single-layered incisor enamel with HSB in Glires is derived from a double-layered condition with HSB in the PI and radial enamel in the PE is reconfirmed here (Martin, 1999a). The lower incisor enamel of *Decipomys mongoliensis* (unclear attribution of order) differs from all other studied Gliiriformes (sensu Meng and Wyss, 2001) (Martin, 1993, 1999a; Dashzeveg et al., 1998). It lacks HSB and has an inner layer of (derived) tangential enamel with interrow sheets and an outer layer of radial enamel. At the moment it is not clear, how widely this schmelzmuster was distributed among Gliiriformes of which many taxa are known only by very fragmentary remains; it would make a good structural predecessor of the ochotonid schmelzmuster with an inner layer of modified radial enamel and only weakly developed HSB in the lower incisor and an upper incisor enamel without HSB.

### Incisor Schmelzmuster of Lagomorpha

**Leporidae**—Undetermined leporids (Fig. 5A, B) from the early Eocene (Ypresian) of Anarak, Kyrgyzstan are the geologically oldest representatives of Lagomorpha of which the incisor enamel has been studied. The upper incisor of ZIN-An-1 has two-layered schmelzmuster with HSB in the PI and radial enamel in the PE. This is direct evidence that two-layered schmelzmuster is the plesiomorphic condition in Leporidae. This schmelzmuster can easily be derived from the condition present in some stem-group Duplicidentata (e.g., *Anatolimys rozhdvestvenskii*, Fig. 4A, B). A second, undetermined leporid upper incisor from Anarak (ZIN-An-6) has single-layered schmelzmuster with HSB; towards the OES, HSB become indistinct due to a decrease of the decussation angle. This can be interpreted as a transitional stage from the condition found in ZIN-An-1 and later leporids.

All other undoubted members of the Leporidae which have been studied (e.g., Fig. 6) have a very uniform, single-layered schmelzmuster with HSB in upper and lower incisors. The two-layered enamel with radial enamel in the PE of the leporids from the early Eocene of Anarak represents an ideal predecessor for the leporid schmelzmuster, which easily can be derived by reduction of the PE with radial enamel or an extension of HSB to the OES. The enamel of the small I3 is very thin and consists of radial enamel, as is typical for extremely thin, almost vestigial enamel.

**Ochotonidae**—The ochotonid incisor schmelzmuster differs clearly from that of leporids and is two- to three-layered in the sagittal plane of the enamel cover; laterally and medially it can be reduced to a single layer where the enamel is thin (Koenigswald, 1995, 1996; Martin, 1999a). The studied ochotonids have two-layered enamel in upper incisors with an inner layer of (derived) modified radial enamel with interrow-sheets and an outer layer of tangential enamel. Koenigswald (1995) observed a one- to three-layered schmelzmuster (tangential enamel and/or modified radial enamel in variable arrangements) in cross sections of the upper incisor of *Prolagus sardus* depending on the topographic position within the enamel cover; as in *Ochotona princeps*, HSB do not occur in upper incisor enamel. This

does not imply a reversal of enamel evolution from derived (HSB) to plesiomorphic enamel, because the upper incisor schmelzmuster of ochotonids is formed by highly derived enamel types. If the ochotonid schmelzmuster evolved from a structural predecessor similar to that of *Decipomys mongoliensis*, it possibly never went through a stage with fully developed HSB. The lower incisors of ochotonids have two- to three-layered enamel with an inner layer of modified radial enamel, a middle layer of weakly developed HSB, and a thin outer layer of tangential enamel. The outer layer of tangential enamel was detected in various species of *Ochotona*, in the early Miocene *Piezodus* sp. indet. and *Titanomys* sp. indet. (Koenigswald, 1995), and in *Ochotonoides complicidens*. In two species of *Prolagus* (*P. oeningensis* and *P. sardus*), Koenigswald (1995) observed a double-layered schmelzmuster where the outer layer of tangential enamel is missing; this type of schmelzmuster was also found in the lower incisors of *Sinolagomys* sp. indet. (Fig. 7A, B) and *Bellatona forsythmajori*. The much greater thickness of the enamel in *Bellatona forsythmajori* (Miocene) compared to *Sinolagomys* sp. indet. (Oligocene) cannot be explained alone by its slightly larger size, but probably represents a more derived condition. Although the schmelzmuster varies within ochotonids, it is clearly distinct from the very uniform leporid schmelzmuster with a single layer of HSB (Table 1). The presence of multilayered schmelzmuster with derived enamel types (modified radial and tangential enamel) indicates that the ochotonid schmelzmuster is highly derived despite the lack of extensive HSB. The incisor enamel of ochotonids evolved along a different pathway than those of leporids and rodents for improving the biomechanical properties of their microstructure. Extensive study of ochotonid incisor enamel indicates that they never went through a stage with strongly developed HSB.

### Systematic Position of *Desmatolagus*

The lower incisor enamel of three species of *Desmatolagus* (*D. gobiensis*, *D. robustus*, and *D. vetustus*) is consistently single-layered with HSB (Fig. 6C, D), the autapomorphic condition for Leporidae. In the original description, Matthew and Granger (1923:10) placed *Desmatolagus* provisionally within Leporidae, although they stated that "... the genus undoubtedly is related to the Ochotonidae and may be considered ancestral to some of the genera. . . ." McKenna (1982) put *Desmatolagus* on the stem-lineage of Ochotonidae and Leporidae based on dental characters, while McKenna and Bell (1997:108) listed the genus *Desmatolagus* within Ochotonidae and stated in a footnote that "Some species assigned to *Desmatolagus* may be leporids." The occurrence of a single-layered schmelzmuster with HSB in the lower incisors of *D. gobiensis*, *D. robustus*, and *D. vetustus* shows that these species do not belong to the Ochotonidae and are indeed members of the Leporidae.

### Relationship of Ochotonid and Leporid Incisor Schmelzmuster

Koenigswald (1995) interpreted the single-layered incisor schmelzmuster of Leporidae as more derived than the multilayered schmelzmuster of Ochotonidae. The results from the present study suggest that both schmelzmusters are derived, but by different pathways. The single-layered schmelzmuster of Leporidae can be derived directly from "mimotomid" schmelzmuster of double-layered enamel with thin PE (e.g., *Anatolimys rozhdvestvenskii*) or even a single-layered enamel with HSB (undetermined mimotomid from Mongolia). One of the earliest leporids studied still has double-layered enamel with a thin PE; in all other (younger) leporids investigated, the enamel is single-layered with HSB.

The inner layer of the ochotonid schmelzmuster consists of modified radial or tangential (upper incisor of *Prolagus sardus*)



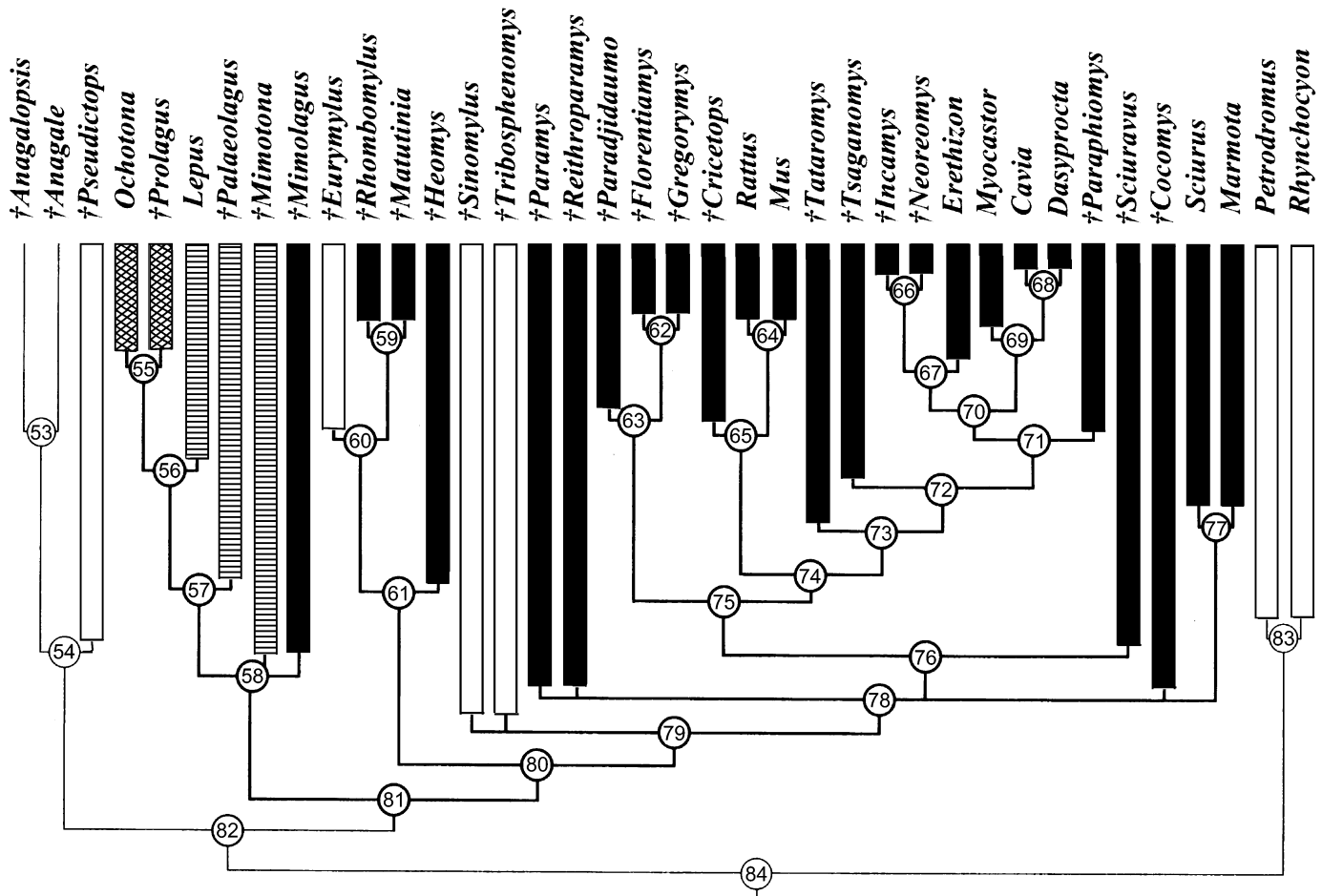


FIGURE 8. Incisor schmelzmuster mapped on a cladogram of Gliriformes presented by Meng et al. (2003:fig. 74). Numbers indicate the nodes discussed by Meng et al. (2003); branches below node 84 are cut off. The cladogram covers only a small selection of the taxa studied here and several basal Glires (1985) after figures based on light-microscopic images. Other enamel information derives from Korvenkontio (1934), Wahlert (1983), Wahlert and Koenigswald (1985), Koenigswald (1988, 1990, 1996, 1997), Martin (1992, 1993, 1999a), Meng and Wyss (1994), and Kalthoff (2000). White bars, single layer of plesiomorphic radial enamel; black bars, two-layered enamel with HSB in the PI and radial enamel in the PE (PI may be subdivided, e.g., in *Paradjidaumo*); horizontally hatched bars, single layer with HSB; and cross-hatched bars, two- to three-layered enamel with modified radial or tangential enamel in the inner layer; middle and outer layer formed in varying arrangement by weakly developed HSB, radial or tangential enamel.

enamel. In contrast to the plesiomorphic radial enamel which is found for example in marsupials, many lipotyphlans, and *Tribosphenomys*, modified radial (and tangential) enamel is a highly derived enamel type characterized by IPM plates (inter-row sheets) between the prisms rows (Pfretzschner, 1994). Crystallite orientation of the IPM plates is rectangular to the prism long axes, an adaptation to strengthen the enamel (the "plywood effect"; Pfretzschner, 1988, 1994; Koenigswald and Pfretzschner, 1991). Therefore, it is very unlikely that this enamel type is a predecessor for HSB which usually start with an IPM that is running parallel to or at a very low angle to the prism long axes. This indicates that leporid and ochotonid schmelzmusters are equally derived.

#### Cladistic Analysis and Schmelzmuster Distribution in Gliriformes

According to the cladogram presented by Meng et al. (2003: fig. 74; Fig. 8), at least three clades of Gliriformes independently evolved a double layered schmelzmuster with HSB in the PE and radial enamel in the PE from the primitive condition with a single layer of plesiomorphic radial enamel: in Dupli-

cidantata (node 58), in the clade formed by *Rhombomylus* and *Matutinia* (node 59), and in Rodentia (node 78) (Fig. 8). In Lagomorpha, the outer layer with radial enamel was subsequently reduced in the Leporidae, whereas a multilayered schmelzmuster formed mainly by derived modified radial enamel and tangential enamel evolved in the Ochotonidae. The position of Ochotonidae (here represented by *Ochotona* and *Prolagus*) as the sister taxon of *Lepus* (Meng et al., 2003:fig. 74) poses a problem, because this would imply evolution of the multilayered ochotonid schmelzmuster that largely lacks HSB from the single layered schmelzmuster with HSB of *Lepus* and its allies (Leporidae). On the other hand, the schmelzmuster without HSB of the early gliriform *Decipomys mongoliensis* represents a possible structural predecessor for the ochotonid schmelzmuster. Due to its fragmentary nature (only partial mandibles are known), *Decipomys* does not occur in the cladogram. The strong differences between the ochotonid and leporid schmelzmuster suggest a more basal divergence of Ochontidae from early Paleogene stem-lineage lagomorphs than suggested in the cladogram of Meng et al. (2003:fig. 74).

Within Eurymylidae, *Eurymylus* has retained the plesio-



morphic condition with a single layer of radial enamel, whereas *Rhombomylus* and *Matutinia* evolved a double layered schmelzmuster with HSB in the PI and (retained) radial enamel in the PE. In Rodentiaformes (node 79), *Sinomylus* and *Tribosphenomys* retained the plesiomorphic pre-Glires schmelzmuster with a single layer of radial enamel. Rodentia (node 78) evolved a double-layered schmelzmuster with HSB in the PI and retained radial enamel in the PE. All unquestioned early Paleogene Rodentia examined so far exhibit a double-layered schmelzmuster with HSB and radial enamel. Flynn et al. (1987) thought some early rodents lacked PE, but this was disproved by Martin (1999a). The PE was later reduced in very few rodent clades (e.g., *Heterocephalus jaegeri*; Martin, 1992), and, in some groups with uniserial incisor enamel (e.g., Eomyidae), the PI may be subdivided.

### CONCLUSIONS

A single layer of radial enamel in the incisors represents the plesiomorphic condition for Gliiriformes, corroborated by investigation of early representatives as well as by outgroup comparison. From this stage, a two-layered schmelzmuster evolved with HSB in the PI and radial enamel in the PE. Development of HSB took place by the decussation of prism layers within the inner zone of the radial enamel. This double-layered stage is represented by the eurymylid *Matutinia nitidulus*, the mimotonid *Anatolimys rozhdestvenskii*, and an undetermined early leporid; it was retained in rodents. In the leporid lineage, HSB extended towards the OES and finally completely displaced the outer layer of radial enamel, resulting in a single layer of HSB. As noted by Koenigswald (1995, 1996), the schmelzmuster of ochotonids differs from that of leporids by the number of enamel layers and the enamel types involved. Contra Koenigswald (1995, 1996), the ochotonid schmelzmuster is here considered apomorphic. The multilayered ochotonid schmelzmuster with (apart from weakly developed HSB) additional derived enamel types most probably did not evolve from the double-layered stage with strongly developed HSB. Possibly it originated from the schmelzmuster of poorly known early Gliiriformes such as *Decipomys mongoliensis* that have derived enamel types other than HSB. Although rather speculative at the moment, this indicates a much longer separation of ochotonids and leporids than assumed so far. Schmelzmuster distribution in the cladogram of Gliiriformes (Meng et al., 2003:fig. 74; Fig. 8) demonstrates that incisor enamel microstructure has limited value as a synapomorphy for Glires. However, it is a powerful tool for addressing phylogenetic and systematic questions within Simplicidentata and Duplicitentata.

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