




Incisor enamel microstructure places New and Old World Eomyidae outside Geomorpha (Rodentia, Mammalia)

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Abstract

The lower incisor enamel microstructure of the fossil rodent family Eomyidae was believed to be three-layered and highly derived but rather uniform throughout the clade. Here, we describe a new four-layered schmelzmuster in Eomyidae consisting of a three-fold portio interna with longitudinal oriented, uniserial Hunter-Schreger bands and a one-fold portio externa, accounting for a unique enamel microstructure character combination in Rodentia. This new schmelzmuster type has developed early in eomyid evolution and is detectable already in the late Eocene (Chadronian) of North America. In European eomyids, it first occurs in the early Miocene (MN 3), implying that this four-layered schmelzmuster was not present in all members of the family but restricted to species included in Eomyini and some genera currently considered Eomyidae incertae sedis within Eomyidae. Additionally, our analysis recognizes three taxa with schmelzmuster divergent from all other eomyids. Incisor enamel microstructure does not advocate a close phylogenetic relationship of Eomyidae to either fossil or extant Heteromyidae and Geomyidae, nor to fossil Heliscomyidae and Florentiamyidae. Our results rather support the view that Eomyidae are placed outside Geomorpha.

KEYWORDS

Enamel microstructure, Eurasia, Neogene, North America, Paleogene, schmelzmuster

1 | INTRODUCTION

Eomyidae are an extinct, Holarctic family of myomorph rodents, often regarded as the closest relatives of extant New World Pocket Mice, Heteromyidae, and Pocket Gophers, Geomyidae (Engesser, 1999; Fahlbusch, 1985; McKenna & Bell, 1997; Wahlert, 1978; Wilson, 1949). Eomyids were small- to medium-bodied rodents that occupied warm-temperate forest environments (Engesser, 1999). The oldest records are from the middle Eocene (Bridgerian) of North America, about 47 Ma (Flynn, 2008), but according to Engesser (1999), they could have as well have originated in Central and East Asia where the oldest record dates back to the late Eocene (Emry et al., 1997). In Europe, the first eomyid immigrants arrived from Asia after the Grande Coupure in the Early Oligocene (Suevian, MP 21; Engesser, 1999). Eomyids diversified during the Eocene, Oligocene, and Miocene with a heterogenous pattern in North America and Eurasia (Engesser, 1999; Flynn, 2008; Kimura et al., 2019, 2020). In North America and East Asia, eomyids disappeared at the end of the Miocene about 5 Ma (Hemphillian, Baodean), while they persisted in Europe until the end of the Pliocene about 2 Ma (Villanyian, MN 17; Engesser, 1999). Although eomyids are very abundant elements in some small mammal assemblages, most species are exclusively known by craniodental material without associated postcrania (Engesser, 1999; Kimura et al., 2020; Maridet et al., 2010). Only two species, both from the late Oligocene (Arvernian, MP 28) Enspel locality in Germany, are known as complete skeletons even with soft part preservation. One species with a patagium was a glider, whereas the other species was a generalized terrestrial rodent (Engler & Martin, 2015; Storch et al., 1996).

Lower incisor schmelzmuster and incisor morphology of eomyids was shown to be highly derived and unlike that of other rodents (Wahlert & Koenigswald, 1985). As two distinctive characters for this clade, these authors described (1) a three-layered schmelzmuster with a two-fold portio interna showing uniserial, longitudinally oriented Hunter-Schreger bands (HSB) and a one-fold portio externa, plus (2) a lateral thickening of the enamel band, expressed as a longitudinal ‘ridge’ (Figure 1).

Since 1985, the knowledge of incisor enamel microstructures of fossil and extant Glires has considerably increased (hystricognathous rodents: Martin, 1992, Vieytes et al., 2007; Gliridae: Koenigswald, 1995a; early rodents: Martin, 1993; Glires: Koenigswald, 1995b, Martin, 1999b, 2004; Theridomyidae: Martin, 1999a; myomorph rodents: Kalthoff, 2000; Castoridae and Hystricidae: Koenigswald & Mörs, 2001; Sciuravida: Martin, 2007), offering a much more complete picture of schmelzmuster characters present.

The two-layered schmelzmuster state is plesiomorphic for all rodents. Apomorphic multi-layered schmelzmuster (i.e., more than two layers) developed repeatedly in rodent incisors with uniserial HSB, i.e., among the mouse- and squirrel related clades Supramyomorpha and Eusciurida (Banga-Kanfi et al., 2009; Flynn et al., 2019; Kalthoff, 2000, 2006; Koenigswald, 1995a; Koenigswald & Kalthoff, 2007). Four-layered schmelzmuster with uniserial HSB in a longitudinal arrangement and without central syncline is detected in a few fossil and extant rodent taxa belonging to fossil hamsters (Paracricetodontinae; schmelzmuster type 8) and some jerboas (*Allactaga*, *Pygeretmus*; schmelzmuster type 8a) (Kalthoff, 2000, 2006). This four-layered schmelzmuster consists of a two-fold portio interna (PI) and a two-fold portio externa (PE). In contrast, the here described four-layered schmelzmuster in Eomyidae consists of a three-fold portio interna and a one-fold portio externa, a unique and novel enamel microstructure character combination in Rodentia (Figure 1). In addition, multiple studies show that the development of an additional layer and the concomitant splitting of the PI into an inner and outer part (IPI and OPI) is always initiated at the enamel-dentine junction (e.g. Kalthoff, 2000, 2006; Koenigswald, 1995a). The development of an additional layer within the PI is equally unique and has never been observed in rodents before.

The lateral, longitudinal ‘ridge’ (here referred to as longitudinal edge) described by Wahlert and Koenigswald (1985) still holds up as a character in eomyids but is also present in a number of other rodents of the mouse-related clade (Kalthoff, 2000; Mörs & Kalthoff, 2004).

Our motivation for this study is (1) to describe the new four-layered schmelzmuster in Eomyidae; (2) to highlight its development and occurrence within the clade; (3) to depict eomyid taxa without clade-typical schmelzmuster; (4) to discuss paleogeographical implications of the results; and (5) to discuss their phylogenetic and systematic implications for the relation of Eomyidae to Geomorpha.

2 | MATERIAL AND METHODS

The analysed material comes from localities of Europe, Japan and North America and stretches stratigraphically from late Eocene to late Miocene (Supporting Information 1). It consists of 65 lower incisors or incisor fragments, which have been taken either from dentaries identified to the respective species or from isolated tooth material which has been—where possible—compared to confidently identified incisors in jaws. Two localities contributed with exceptional rich material, the late Oligocene (early Arikarean) Ridgeview local fauna

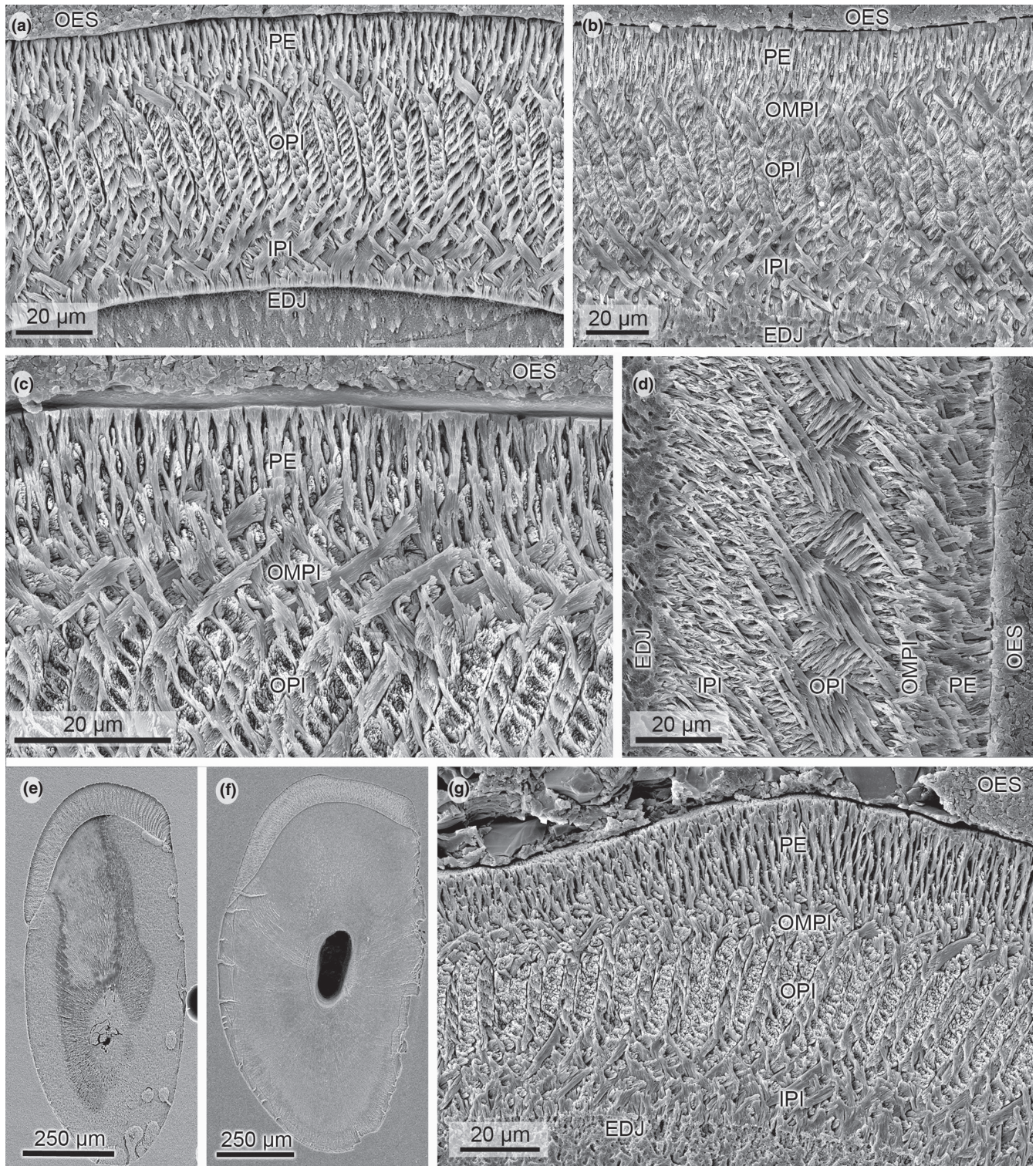


FIGURE 1 Scanning electron micrographs of lower incisor enamel microstructure in Eomyidae; all transverse sections except for d. (a) *Eomys zitteli*, KOE 3204. *Eomys* has a three-layered schmelzmuster; the interprismatic matrix turns into an acute angle to the prisms here and there at the junction OPI/PE. (b) *Paradjidaumo* sp., KOE 3581. This *Paradjidaumo* species has a four-layered schmelzmuster with a well-developed outermost portio interna (OMPI). (c, d) *Ligerimys florancei*, KOE 3554. (c) Detail of the outermost portio interna (OMPI), situated between the outer portio interna (OPI) and the portio externa (PE). (d) The four-layered schmelzmuster with a tree-fold portio interna is also obvious in the longitudinal section. (e) *Keramidomys thaleri*, KOE 4229. *Keramidomys* lacks a longitudinal edge. (f) *Eomys zitteli*, KOE 3204. *E. zitteli* has a well-developed longitudinal edge. (g) *Pseudotheridomys* aff. *parvulus*, NM Pv 12,225. Close-up of the thickening of the enamel band at the longitudinal edge and of the OMPI. Abbreviations: EDJ, enamel–dentine junction; IPI, inner portio interna; OMPI, outermost portio interna; OPI, outer portio interna; OES, outer enamel surface; PE, portio externa; PI, portio interna

in Nebraska (Bailey et al., 2005) and the early Miocene (Orleanian) Merkur-North lignite mine in Czech Republic (Fejfar, 1974; Fejfar et al., 2003). We analysed exclusively mandibular incisors to gain comparability with published results. Enamel microstructure analysis is a well-established tool regarding systematic-phylogenetic questions at the genus and higher taxonomic levels. Because enamel formation is controlled by genetic and epigenetic factors, the schmelzmuster of a taxon can be characterized with only few samples. Eomyid systematics largely follows McKenna and Bell (1997), updated by information from Flynn et al. (2008) for North American genera, and from Kimura et al. (2020) for Eurasian genera.

Character polarity in the lower incisor enamel of Eomyidae, Geomyoidea, Heliscomyidae and Florentiamyidae is as follows (from most plesiomorphic to most apomorphic condition, modified from Martin, 1999a): (1) Number of schmelzmuster layers: two–three–four; (2) Orientation of Hunter-Schreger bands (HSB): transverse–diagonal–longitudinal; (3) Orientation of interprismatic matrix (IPM) in the portio interna in respect to prism long axes: parallel–acute–perpendicular; (4) Outermost portio interna (OMPI): absent–zone of irregular appearance at the junction outer portio interna (OPI) and portio externa (PE)—present and thin—present and thick; (5) Zone of modified radial enamel close to the enamel–dentine junction (EDJ): absent–present.

Preparations for enamel microstructure analysis were executed following the methodology described in Koenigswald and Mörs (2001) and Kalthoff (2000, 2006). The resulting transverse and/or longitudinal sections were studied and documented with scanning electron microscope (SEM) technique (CamScan MV 2300, located at the Institute for Geosciences, University of Bonn; Hitachi S-4300 SEM and Quanta FEG 650, both located at the Swedish Museum of Natural History in Stockholm), at acceleration voltages of 15–20 kV and magnifications of $\times 30$ to $\times 4000$. All measurements are given in μm and were carried out on transverse sections. Denotation of schmelzmuster types follows Kalthoff (2000). Incisor cross sections were obtained directly from SEM micrographs and drawn to scale.

We attempted to quantify the longitudinal edge shape by measuring the angle of its slope. However, we abandoned this idea because of mainly two reasons: (1) its perceived angle is dependent on the angle of the prepared section in respect to the incisor long axis, which—in such small incisors—almost never hits the ideal 90° ; (2) there is no reproducible point of reference for the angular measurement. Instead, we recorded the longitudinal edge as ‘absent’, ‘weak’ and ‘well developed’.

Institutional abbreviations. **FMNH**, Fossil Mammals Collection, The Field Museum, Chicago (IL), USA. **IGPB**,

Institute of Geosciences, Section Palaeontology, University of Bonn, Germany. **KOE**, enamel collection established by Wighart von Koenigswald, housed in the IGPB. **NM**, National Museum of Prague, Czech Republic.

Anatomical Abbreviations. **EDJ**, enamel–dentine junction; **HSB**, Hunter-Schreger bands; **IPI**, inner portio interna; **IPM**, interprismatic matrix; **OMPI**, outermost portio interna; **OPI**, outer portio interna; **OES**, outer enamel surface; **PE**, portio externa; **PI**, portio interna; **PLEX**, prismless layer.

3 | RESULTS

We describe the enamel microstructure of lower incisors in a sample covering 36 taxa of Old and New World eomyid rodents (Figures 1–4, Supporting Information 1). In many rodent clades and true also for Eomyidae (Wahlert & Koenigswald, 1985), lower and upper incisors show different schmelzmuster with lower incisor always being more derived than the upper pair. Due to this fact and to maintain comparability with published results, we restrict our analysis to lower incisors.

As typical for eomyid lower incisors, HSB are of the uniserial type and longitudinally oriented, i.e., about parallel to the long axis of the incisor (Wahlert & Koenigswald, 1985). The portio interna (PI), in which the HSB occur can be two-fold or—as a new result of this paper—three-fold. The portio externa (PE) is always a single layer of radial enamel.

For a clearer overview and for keeping the descriptions short, all measurements of the enamel band and its layers are shown in Supporting Information 2; all enamel microstructure characters states are shown in Tables 1 and 2.

4 | DISCUSSION

Already late Eocene eomyids show a much derived lower incisor schmelzmuster with longitudinal oriented uniserial Hunter-Schreger bands (HSB) in a two-layered portio interna (PI), differing from each other by IPM orientation (Wahlert & Koenigswald, 1985). With more and new eomyid material available, we revisited their lower incisor schmelzmuster and found more microstructural diversity than previously known including a new, third PI layer introduced here as “outermost portio interna” (OMPI) (Figure 1c). In addition, we compared the actual and relative thickness of the enamel band and its single layers; the presence and form of a longitudinal edge; and the lower incisor cross sections (Figure 5). Schematic drawings of the three types of microstructure architecture in Eomyidae are shown in Figure 6.

TABLE 1 Summary results of the lower incisor enamel character states for North American Eomyidae (ordered stratigraphically)

Species	Collection ID	Thickness of enamel band	Number of PI layers	Thickness of OMPI	Longitudinal edge	Stratigraphic age and locality
<i>Pseudotheridomys hesperus</i>	KU 10197	Thin	3	3–4 prisms	Could not be evaluated	Hemingfordian, Quarry A LF
<i>Neoadjidaumo hemedapus</i>	KOE 3584	Thick	1	n/a	Absent	Arikareean, Ridgeview LF
Eomyidae indet.	KOE 3043	Moderate	1	n/a	Weak	Arikareean, Ridgeview LF
<i>Pentabuneomys engesseri</i>	KOE 3041	Thin	3	1–2 prisms	Weak	Arikareean, Ridgeview LF
<i>Leptodontomys douglassi</i>	KOE 3583	Thin	3	1–2 prisms	Well developed	Arikareean, Ridgeview LF
Eomyidae indet.	KOE 3525	Thin	3	1–2 prisms	Well developed	Whitneyan, Blue Ash LF
<i>Paradjidaumo minor</i> ^b	F: AM 94877	Thin	1	n/a	Could not be evaluated	Orellan, Chalky Buttes
<i>Paradjidaumo trilophus</i>	AMNH 96856	Moderate	2	n/a	Well developed	Orellan, Chalky Buttes
<i>Paradjidaumo trilophus</i>	KOE 3467	Thick	2	n/a	Well developed	Orellan, Crawford
<i>Adjidaumo</i> sp.	KOE 3480	Moderate	3	2–3 prisms	Well developed	Orellan, Mellinger loc.
<i>Adjidaumo intermedius</i>	KOE 3580	Thin	2	n/a	Well developed	Orellan, UNSM loc. Sx-14
<i>Leptodontomys douglassi</i>	KOE 3582	Thin	3	1–2 prisms	Well developed	Orellan, UNSM loc. Sx-13a
<i>Paradjidaumo</i> sp.	KOE 3581	Moderate	3	5–6 prisms	Absent	Orellan, UNSM loc. Sx-26
<i>Adjidaumo minutus</i>	KOE 3527	Thick	3	3 prisms	Well developed	Orellan, Eastman Creek
<i>Paradjidaumo</i> sp.	FMNH: PM 20518	Thick	3	1–3 prisms	Well developed	Orellan, Dry Plains LF
<i>Adjidaumo</i> sp.	FMNH: PM 46401	Thick	3	3 prisms	Well developed	Orellan, Scenic Mbr
Eomyidae indet.	KOE 3530A	Thick	2	n/a	Well developed	Chadronian/Orellan, White River Fm.
Eomyidae indet.	KOE 3530B	Thick	3	2–3 prisms	Well developed	Chadronian/Orellan, White River Fm.
<i>Zemiodontomys burket</i> ^b	KOE 3246	(Moderate/ thick)	2	n/a	Absent ^a	Chadronian, Seaman Hills
<i>Adjidaumo</i> sp.	KOE 1994	Thin	2	n/a	Weak	Chadronian, Flagstaff Rim
<i>Centimanomys major</i>	KOE 3529	Thick	3	1–2 prisms	Well developed	Chadronian, Iliff loc.
<i>Paradjidaumo</i> sp.	KOE 3464	Thick	2	n/a	Well developed	Chadronian, Cameron Springs LF
<i>Paradjidaumo</i> sp.	KOE 3473	Moderate	3	1–3 prisms	Well developed	Chadronian, Pipestone Springs

(Continues)

TABLE 1 (Continued)

Species	Collection ID	Thickness of enamel band	Number of PI layers	Thickness of OMPI	Longitudinal edge	Stratigraphic age and locality
<i>Aulolithomys bounites</i>	KOE 3474	Thick	2	n/a	Well developed	Chadronian, Pipestone Springs
Eomyidae indet.	KOE 3027	Thick	2	n/a	Well developed	Duchesnean/Chadronian, Spring Canyon
Eomyidae indet.	KOE 3028	Thick	2	n/a	Well developed	Duchesnean/Chadronian, Spring Canyon

^aAccording to Emry and Korth (1993).

^bOnly longitudinal section.

4.1 | The portio interna (PI) in Eomyidae

Just above the enamel–dentine–junction (EDJ), the IPM is oriented perpendicular to the prism long axes in the inner portio interna (IPI), in which longitudinal HSB are low to moderately inclined and rise towards the outer enamel surface (OES). The outer portio interna (OPI) is composed of non-inclined longitudinal HSB and prism-parallel oriented IPM. By the latest Eocene, a third PI layer may be present, the OMPI, in which the IPM turns and again runs at an angle in respect to prism long axes. This angle is acute (ca 45°) in the stratigraphically older taxa but becomes nearly perpendicular in the younger taxa. In the OMPI, the HSB are again low to moderately inclined and mirror the IPI in this respect.

The presence of a three-fold PI is unique within Rodentia and exclusively found in the eomyid subfamily Eomyinae, where it is most probably restricted to Eomyini and some taxa incertae sedis (we could not sample Ronquillomyini and Namatomyini). Eomyini comprise the vast majority of eomyid genera and species.

The stratigraphically oldest, here analysed lower incisors come from an undetermined eomyid (Figure 2e, f) from the upper member of the Pomerado Conglomerate of middle to late Eocene (=late Duchesnean/early Chadronian) as well as *Zemiodontomys burkei* and *Aulolithomys bounites* (late Eocene: Chadronian) (Figure 2d). These taxa share the three-layered schmelzmuster as described by Wahlert and Koenigswald (1985) for eomyids. However, at the junction OPI/PE, a zone of unordered, irregular appearance develops, in which the IPM here and there turns from a parallel into an acute-angled direction in respect to the prisms, inducing the development of a true OMPI (Figure 2e, f). In our sample, the late Eocene (Chadronian) *Centimanomys major* and *Paradjidaumo* sp. (KOE 3473; from the same fauna as *Aulolithomys bounites*) are the first to show a thin yet

continuous OMPI and thereby proving that a four-layered schmelzmuster in Eomyini is of great antiquity. Obviously, not all Eomyini have developed an OMPI at that age or even later as evidenced by three-layered schmelzmuster but with a zone of irregular appearance at the junction OPI/PE, in *Adjidaumo* sp. (KOE 1994, late Eocene: middle Chadronian), *Adjidaumo intermedius* (early Oligocene: Orellan) (Figure 2a), an undetermined eomyid from the White River Fm. (KOE 3530A, late Eocene/early Oligocene: Chadronian/Orellan), *Paradjidaumo trilophus* (early Oligocene: Orellan), *Neoadjidaumo hemedapus*, and an undetermined eomyid from the Gering Fm. (KOE 3043, late Oligocene: early Arikarean) (Figure 4a). On the other hand, an OMPI is present in an undetermined eomyid (KOE 3530B, late Eocene/early Oligocene: Chadronian/Orellan) and *Adjidaumo minutus* (early Oligocene: Orellan) from the White River Fm., in two *Adjidaumo* sp. (KOE 3480, FMNH: PM 46401, both early Oligocene: Orellan), in *Paradjidaumo* sp. (FMNH: PM 20518, early Oligocene: Orellan), in an undetermined eomyid from the early Oligocene (KOE 3525, Whitneyan), in *Leptodontomys douglassi* (Figure 2c) and *Pentabuneomys engesseri* (late Oligocene: early Arikarean) (Figure 2b), in the early/middle Miocene (Hemingfordian) *Pseudotheridomys hesperus*, and in one *Paradjidaumo* sp. (KOE 3581) from the early Oligocene (Orellan) (Figure 1b).

No OMPI can be detected in late Oligocene (Arvernian), European Eomyini. We investigated three *Eomys* species (Figures 1a, f, 3f), one (or two) *Eomyodon* species, and *Rhodanomys transiens* (Figure 3a), spanning the Mammalian Paleogene units MP 28–30. There, mirroring the schmelzmuster development in some of the Eocene North American taxa, a zone of unordered, irregular appearance is present, presumably initiating the development of a true OMPI. Although no material from the European early Oligocene could be sampled, we do not expect the presence of a three-fold PI with

TABLE 2 Summary results of the lower incisor enamel character states for Eurasian Eomyidae (ordered stratigraphically)

Species	Collection ID	Thickness of enamel band	Number of PI layers	Thickness of OMPI	Longitudinal edge	Stratigraphical age and locality
<i>Eomyops catalaunicus</i>	KOE 420	Thin	3	2 prisms	Well developed	Vallesian, Suchomasty
cf. <i>Keramidomys carpathicus</i>	KOE 2488	Thin	2	n/a	Weak	Astaracian, Neudorf Spalte
<i>Keramidomys thaleri</i>	KOE 4228	Moderate	2	n/a	Absent	Orleanian, Rothenstein 1/13
<i>Keramidomys thaleri</i>	KOE 4229	Moderate	2	n/a	Absent	Orleanian, Rothenstein 1/14
<i>Ligerimys florancei</i>	KOE 422	Moderate	3	3 prisms	Well developed	Orleanian, Erkertshofen 1
cf. <i>Ligerimys florancei</i>	KOE 3554	Moderate	3	5 prisms	Well developed	Orleanian, Dolnice 1
<i>Japaneomys yasunoi</i>	NMNS-PV 19994	Thin	3	4 prisms	Weak	Orleanian, Nakamura Formation
Eomyidae indet.	NMNS-PV 20162	Moderate	3	6–7 prisms	Well developed	Orleanian, Nakamura Formation
<i>Pseudotheridomys</i> aff. <i>parvulus</i>	KOE 3555	Moderate	3	5 prisms	Well developed	Orleanian, Merkur-North
<i>Pseudotheridomys</i> aff. <i>parvulus</i>	NM Pv 12,219	Moderate	3	5–6 prisms	Well developed	Orleanian, Merkur-North
<i>Pseudotheridomys</i> aff. <i>parvulus</i>	NM Pv 12,220	Thin	3	5–6 prisms	Well developed	Orleanian, Merkur-North
<i>Pseudotheridomys</i> aff. <i>parvulus</i>	NM Pv 12,221	Thin	3	5–6 prisms	Well developed	Orleanian, Merkur-North
<i>Pseudotheridomys</i> aff. <i>parvulus</i>	NM Pv 12,222	Thin	3	4–5 prisms	Well developed	Orleanian, Merkur-North
<i>Pseudotheridomys</i> aff. <i>parvulus</i>	NM Pv 12,223	Thin	3	4–5 prisms	Well developed	Orleanian, Merkur-North
<i>Pseudotheridomys</i> aff. <i>parvulus</i>	NM Pv 12,224	Moderate	3	4–5 prisms	Well developed	Orleanian, Merkur-North
<i>Pseudotheridomys</i> aff. <i>parvulus</i>	NM Pv 12,225	Thin	3	5–6 prisms	Well developed	Orleanian, Merkur-North
<i>Pseudotheridomys</i> aff. <i>parvulus</i>	NM Pv 12,227	Thin	3	4–5 prisms	Well developed	Orleanian, Merkur-North
<i>Pseudotheridomys</i> aff. <i>parvulus</i>	NM Pv 12,228	Thin	3	4–5 prisms	Well developed	Orleanian, Merkur-North
<i>Pseudotheridomys</i> aff. <i>parvulus</i>	NM Pv 12,229	Thin	3	4–5 prisms	Well developed	Orleanian, Merkur-North
<i>Pseudotheridomys</i> aff. <i>parvulus</i>	NM Pv 12,230	Thin	3	4–5 prisms	Well developed	Orleanian, Merkur-North
<i>Pseudotheridomys</i> aff. <i>parvulus</i>	NM Pv 12,232	Thin	3	3–4 prisms	Well developed	Orleanian, Merkur-North
cf. <i>Pentabuneomys</i> sp.	KOE 3558	Thin	3	1–3 prisms	Well developed	Orleanian, Merkur-North

(Continues)

TABLE 2 (Continued)

Species	Collection ID	Thickness of enamel band	Number of PI layers	Thickness of OMPI	Longitudinal edge	Stratigraphical age and locality
<i>Ligerimys lophidens</i>	NM Pv 12,216	Thin	3	4–5 prisms	Absent	Orleanian, Merkur-North
<i>Ligerimys lophidens</i>	NM Pv 12,218	Thin	3	4–5 prisms	Absent	Orleanian, Merkur-North
<i>Ligerimys lophidens</i>	NM Pv 12,217	Thin	3	3–4 prisms	Absent	Orleanian, Merkur-North
<i>Ligerimys lophidens</i>	NM Pv 12,215	Thin	3	4–5 prisms	Absent	Orleanian, Merkur-North
<i>Megapeomys lavocati</i>	NM Pv 12,233/74081a	Thick	1	n/a	Absent	Orleanian, Merkur-North
<i>Apeomys tuerkheimae</i>	KOE 3556	Thin	2	n/a	Well developed	Agenian, Rothenstein 10/14b
<i>Rhodanomys transiens</i> ^a	KOE 423	–	2	n/a	n/a	Avernian, Coderet
<i>Rhodanomys transiens</i>	KOE 3130	Thin	2	n/a	Weak	Avernian, Coderet
<i>Rhodanomys transiens</i>	KOE 2486	Thin	2	n/a	Weak	Avernian, Sayatón 6
<i>Eomyodon volkeri</i> ^a	KOE 1900	–	2	n/a	n/a	Avernian, Herrlingen 9
<i>Eomyodon volkeri</i> ^b	KOE 1898	Thin	2	n/a	Well developed	Avernian, Herrlingen 8
cf. <i>Eomyodon</i>	KOE 2424	Moderate	2	n/a	Well developed	Avernian, Enspel
cf. <i>Eomyodon</i>	KOE 2425	Thin	2	n/a	Well developed	Avernian, Enspel
<i>Eomys reductus</i>	KOE 1897	Thin	2	n/a	Well developed	Avernian, Herrlingen 9
<i>Eomys</i> aff. <i>huerzeleri</i>	KOE 1896	Moderate	2	n/a	Weak	Avernian, Herrlingen 10
<i>Eomys zitteli</i>	KOE 419	Thin	2	n/a	Well developed	Avernian, Gaimersheim
cf. <i>Eomys zitteli</i>	KOE 3204	Moderate	2	n/a	Well developed	Avernian, Gaimersheim

^aOnly longitudinal section.

^bOnly transverse section.

continuous OMPI at that stratigraphic level because all species belong to the genus *Eomys*, an immigrant after the Grande Coupure.

The OMPI is fully developed in our Miocene European sample, spanning the Mammalian Neogene units MN 3–10 (but see below), and for Asia in two early Miocene (Orleanian, MN 3) eomyids from Japan. The OMPI layer is with one to three prisms comparably thin in cf. *Pentabuneomys* sp. (KOE 3558, early Miocene: Orleanian, MN 3) and *Eomyops catalanicus* (late Miocene: Vallesian, MN 10; Figure 3b) but usually thick in the other taxa measuring at least three and up to seven prisms. *Ligerimys* (Figure 1c, d), *Pseudotheridomys* (Figure 1g), as well as *Japaneomys* (all early Miocene: Orleanian, MN 3) show exemplary organization of the OMPI (Kimura et al., 2019: Figure 4a).

The apeomyine *Apeomys tuerkheimae* (Figure 3d) features a somewhat archaic schmelzmuster for an early Miocene (Agenian, MN 2) eomyid. This taxon has a well-developed longitudinal edge and a proper eomyid schmelzmuster, although the PI is only two-fold and therefore plesiomorphic in comparison to other contemporaneous eomyine taxa. A possible third PI layer (the OMPI) is yet maturing at the OPI/PE junction where a zone of irregular appearance is present. Because *A. tuerkheimae* is a Miocene survivor from the Oligocene eomyid immigration event, its ancient schmelzmuster make-up is not surprising. Interestingly, the schmelzmuster of *A. tuerkheimae* shows marked differences to that of *Megapeomys lavocati* (early Miocene: Orleanian, MN 3; Figure 4b) although both taxa are

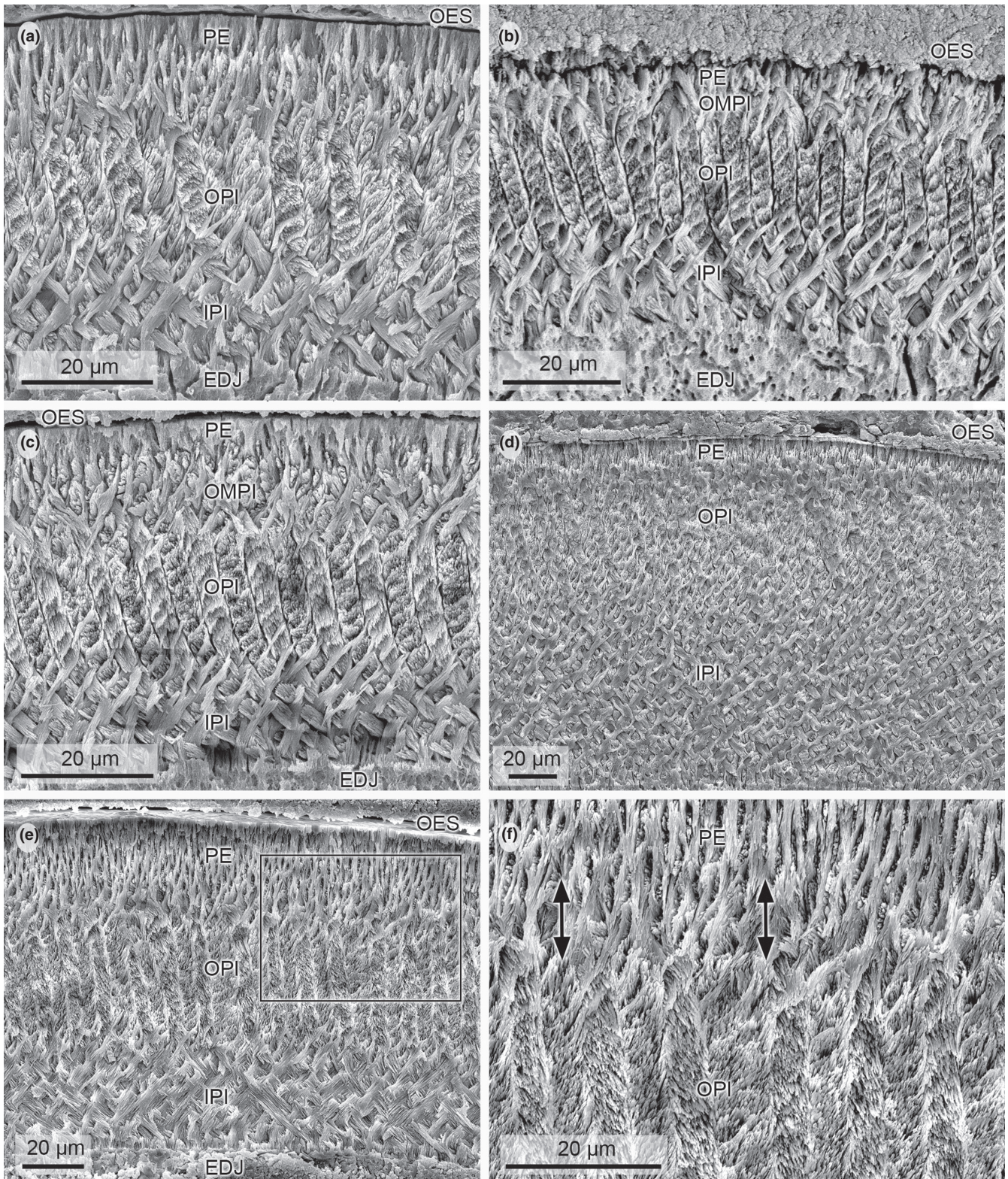


FIGURE 2 Scanning electron micrographs of lower incisor enamel microstructure in North American eomyids, all transverse sections. (a) *Adjidaumo intermedius*, KOE 3580. The Orellan *A. intermedius* shows a three-layered schmelzmuster. In places close to the OPI/PE junction, the interprismatic matrix (IPM) turns into an acute angle in respect to the prisms. (b) *Pentabuneomys engesseri*, KOE 3041. The schmelzmuster has four layers with a very thin but continuous OMPI; here, IPM runs at acute angle to the prism long axes. (c) *Leptodontomys douglassi*, KOE 3583. The schmelzmuster has four layers with a thin OMPI. (d) *Aulolithomys bounites*, KOE 3474. The schmelzmuster is three-layered with a thick IPI, a much thinner OPI, and a very thin PE. (e, f) Eomyidae indet., KOE 3028. (e) This middle to late Eocene taxon has a three-layered schmelzmuster. (f) Close-up of E (insert) shows a thin zone with an irregular prism and IPM arrangement at the junction OPI/PE (arrows). Abbreviations: EDJ, enamel–dentine junction; IPI, inner portio interna; OMPI, outermost portio interna; OPI, outer portio interna; OES, outer enamel surface; PE, portio externa; PI, portio interna

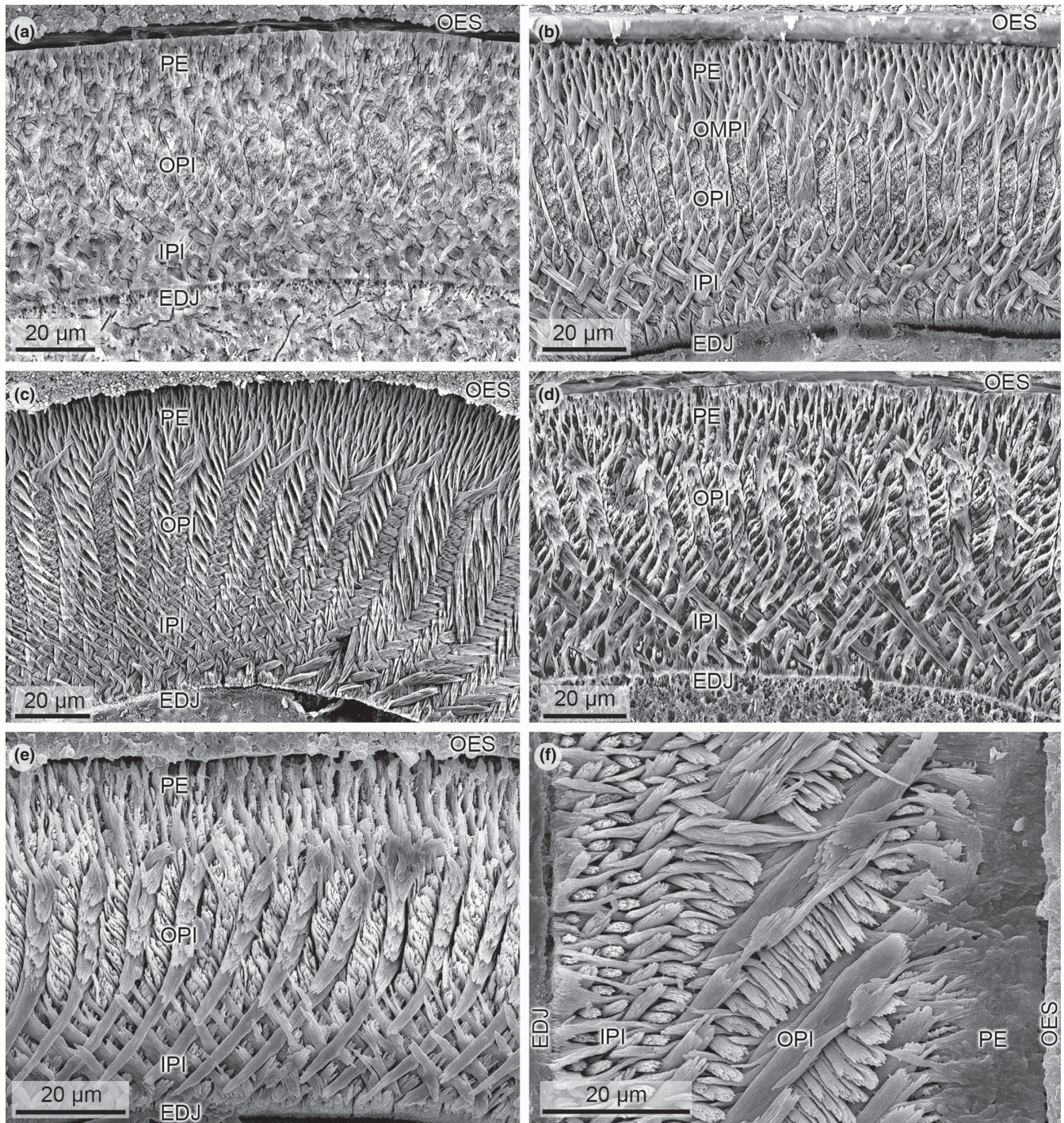


FIGURE 3 Scanning electron micrographs of lower incisor enamel microstructure in European eomyids; all transverse sections except for f. (a) *Rhodanomys transiens*, KOE 3130. The schmelzmuster is three-layered; the interprismatic matrix turns into an acute angle to the prisms at the junction OPI/PE. (b) *Eomyops catalaunicus*, KOE 420. The schmelzmuster has four layers, IPI and OPI are of equal thickness and a thin OMPI is present. (c) *Keramidomys thaleri*, KOE 4229. The schmelzmuster is three-layered and as special feature of the IPI, the interprismatic matrix largely forms an acute angle to the prisms. (d) *Apeomys tuerkheimae*, KOE 3556. The schmelzmuster is three-layered with an unordered zone at the junction PI/PE. (e, f) *Eomys reductus*, KOE 1897. In the IPI of the three-layered schmelzmuster, the interprismatic matrix turns from parallel into an acute angle to the prisms here and there at the junction PI/PE. Abbreviations: EDJ, enamel–dentine junction; IPI, inner portio interna; OMPI, outermost portio interna; OPI, outer portio interna; OES, outer enamel surface; PE, portio externa; PI, portio interna

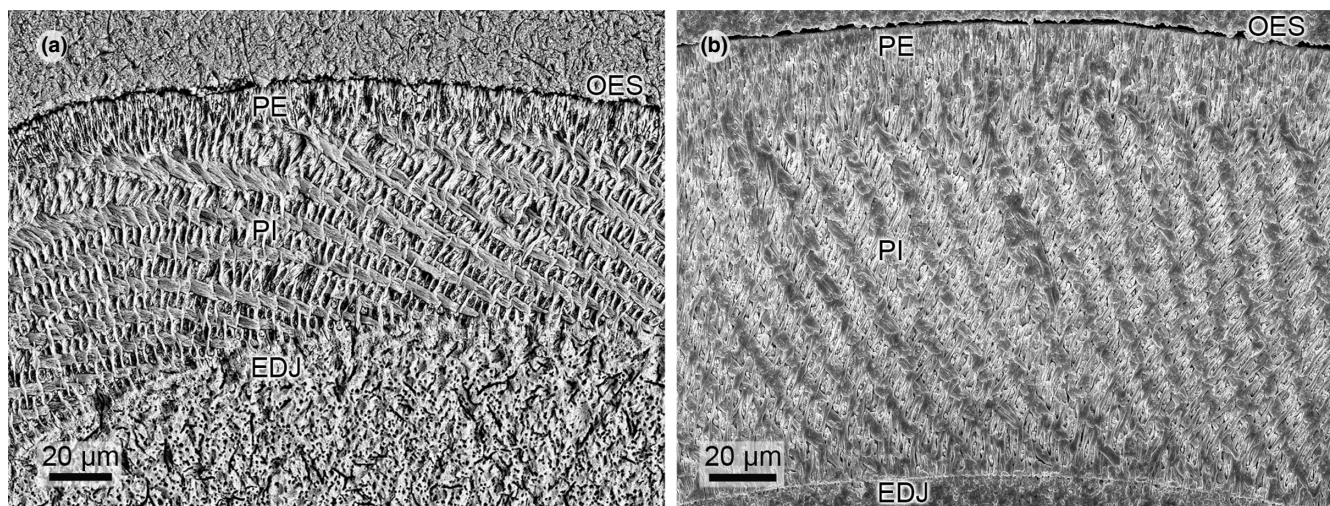


FIGURE 4 Scanning electron micrographs of lower incisor enamel microstructure in eomyid taxa without clade-typical schmelzmuster, both transverse sections. (a) Eomyidae indet., KOE 3043. The schmelzmuster is two-layered and shows diagonal oriented Hunter-Schreger bands with perpendicular interprismatic matrix. (b) *Megapeomys lavocati*, NM Pv 12,233 = 74081a in Fejfar et al. (1998). The schmelzmuster is two-layered and shows a very thick, one-fold PI with diagonal to longitudinal Hunter-Schreger bands with the interprismatic matrix being perpendicular to the prism long axes. Abbreviations: EDJ, enamel–dentine junction; OES, outer enamel surface; PE, portio externa; PI, portio interna

regarded as belonging to the tribe Apeomyini (see below).

Also, *Keramidomys* (Figure 3c) shows a plesiomorphic schmelzmuster compared to other early Miocene Eomyini: the PI is two-fold and no continuous OMPI is developed.

4.1.1 | Remark

Enamel microstructures are generally similar among species belonging to the same genus. In strong contrast, three- as well as four-layered schmelzmuster were found in material attributed to *Adjidaumo* and to *Paradjidaumo*. The unstable taxonomy of North American eomyids and species allocations might be an explanation for this discrepancy (compare Flynn, 2008; Korth, 2008).

4.2 | Eomyid taxa without clade-typical schmelzmuster

Megapeomys lavocati (early Miocene: Orleanian, MN 3) is a strong outlier for its enamel microstructure looks nothing like that of other Eomyidae. *Megapeomys* does not have a multi-layered portio interna but its PI is one-fold with diagonal to longitudinal HSB (Figure 4b). The IPM is continuously at right angle to the prisms until close to the PI/PE junction where the angle is acute; the PE is made up of radial enamel (schmelzmuster type 5 of Kalthoff, 2000).

Because the analysed tooth comes from the holotype specimen, its identification is confident.

The considerably larger body size of *Megapeomys* compared to most of other eomyid taxa might explain the observed dissimilarities. Deviations from a clade-typical schmelzmuster as observed here were already found for other rodents like the large-bodied squirrels *Marmota* (Koenigswald, 1990) and *Spermophilinus giganteus* (DCK own observation, unpublished) and large-bodied beavers (Koenigswald & Mörs, 2001). None of the other large-bodied eomyid taxa (i.e., several *Megapeomys* and the North American *Apeomyoides* and *Arikareomys*) could be sampled so future research might assess whether the observed dissimilarities are the effect of size.

Other strong outliers are *Neoadjidaumo hemedapus* and an undetermined eomyid, both from the same fauna (late Oligocene: early Arikareean). Both show the same but aberrant schmelzmuster for eomyids (Figure 4a), which moreover is strikingly similar to that of *Megapeomys lavocati*: a one-fold PI with diagonal to longitudinal HSB with perpendicular IPM and a PE with radial enamel (also schmelzmuster type 5). Here, we can exclude a size effect because *N. hemedapus* is medium-bodied and the undetermined eomyid (KOE 3043) is even smaller.

The evolution of a highly derived schmelzmuster might be another possible explanation for the deviations in *Megapeomys lavocati*, *Neoadjidaumo hemedapus*, and the undetermined eomyid similar to what has been observed in hamsters of the Oligocene genus *Pseudocricetodon* (Kalthoff, 2000, 2006). In this theoretic scenario, the more

apomorphic enamel type of the IPI became thicker during evolution, subsequently stepwise replacing the more plesiomorphic enamel type of the OPI. If more basal species of the above eomyid taxa had an OMPI in intermediate stages, the expanding IPI could have finally fused with the structurally identical OMPI, now representing a single PI layer.

4.3 | Thickness of the enamel band and of its layers

Total enamel thickness could loosely be connected to biogeography, but neither to stratigraphy or taxonomy (Supporting Information 2). Enamel band is subdivided

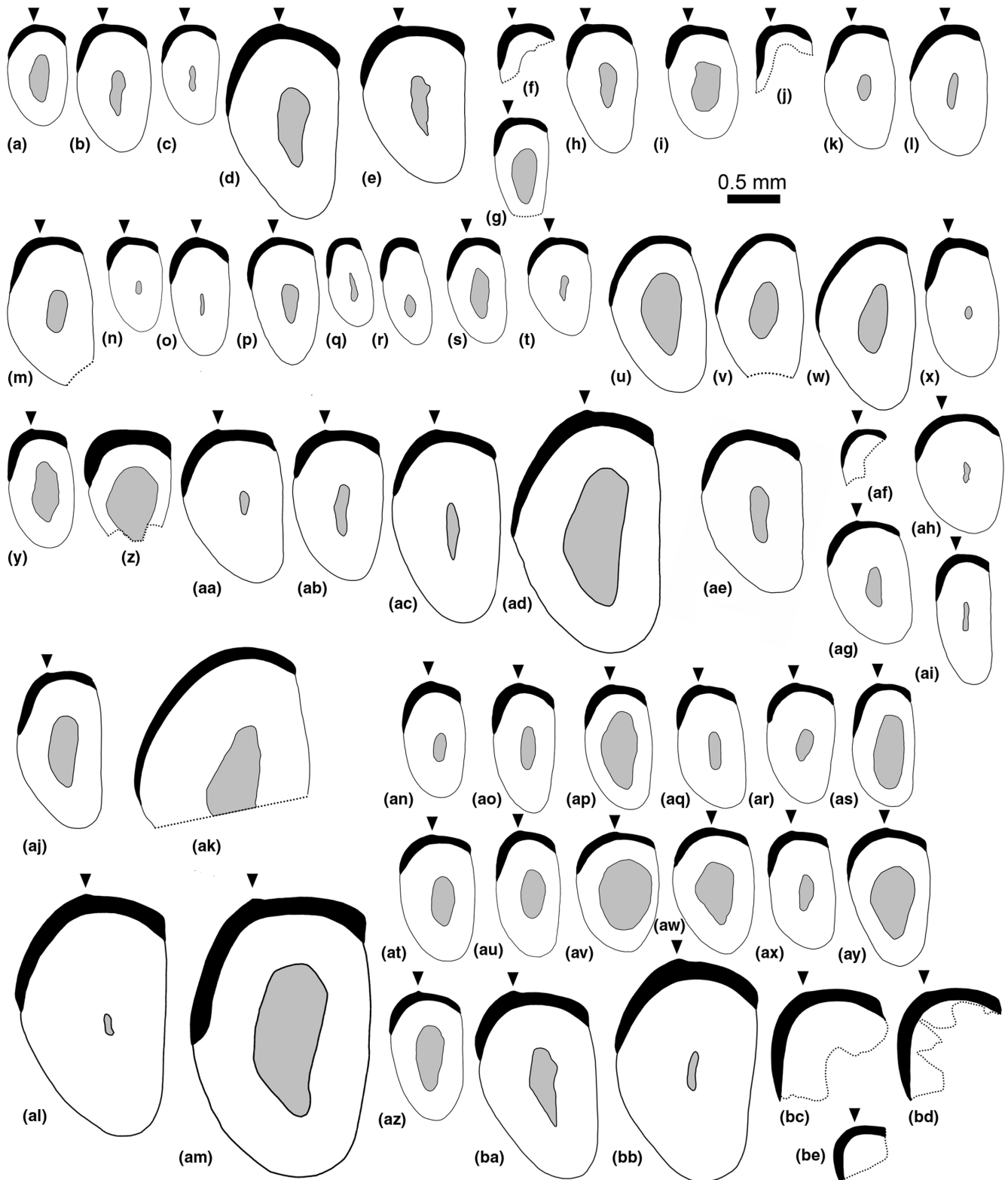
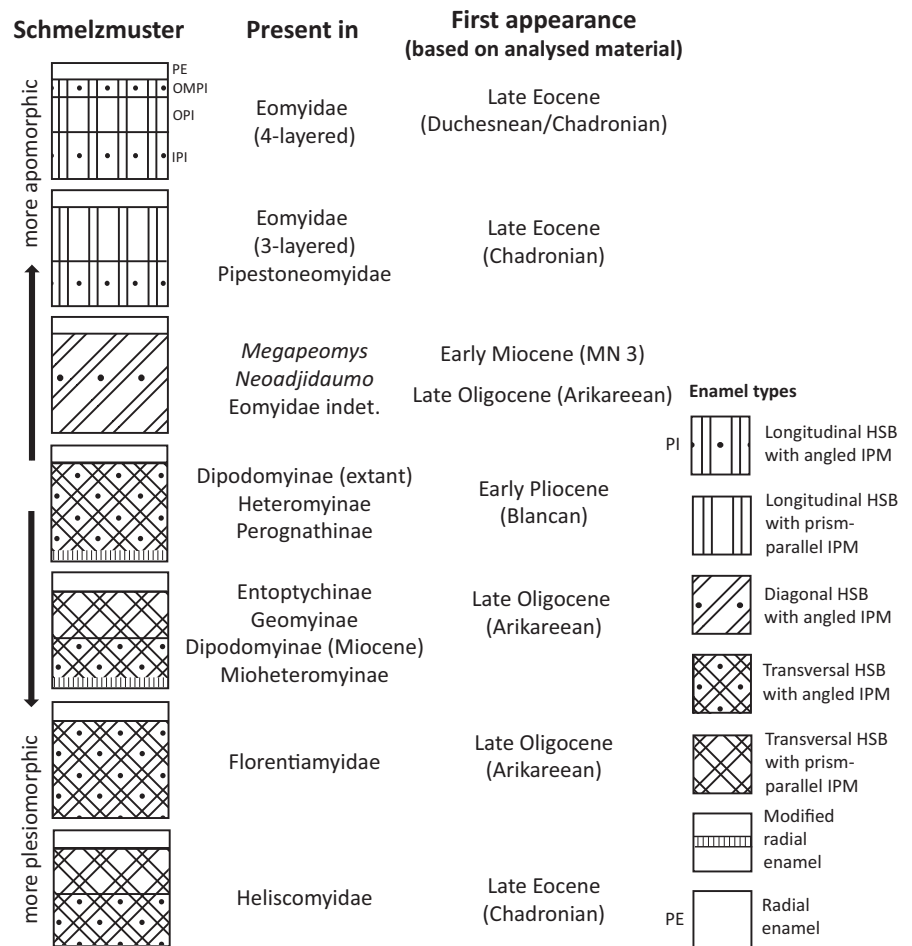


FIGURE 5 Lower incisor cross sections of the analysed Eomyidae. (a) *Adjidaumo intermedius*, KOE 3580. (b) *A. minutus*, KOE 3527. (c–e) *Adjidaumo* sp., KOE 1994, FMNH: PM 46401, KOE 3480. (f, g) *Eomyodon* sp., KOE 2424, 2425. (h) *E. volkeri*, KOE 1898. (i) *Eomyops catalaunicus*, KOE 420. (j) *Eomys zitteli*, KOE 419. (k) cf. *E. zitteli*, KOE 3204. (l) *E. aff. huerzeleri*, KOE 1896. (m) *E. reductus*, KOE 1897. (n) *Japaneomys yasunoi*, NMNS-PV 19994. (o) Eomyidae indet., NMNS-PV 20162. (p) cf. *Keramidomys carparthicus*, KOE 2488. (q, r). *K. thaleri*, KOE 4228, 4229. (s, t) *Leptodontomys douglassi*, KOE 3582, 3583. (u–w) *Ligerimys lophidens*, NM Pv 12,216, 12,217, 12,218. (x) *L. florancei*, KOE 422. (y) cf. *L. florancei*, KOE 3554. (z) *Neoadjidaumo hemedapus*, KOE 3584. (aa) *Paradjidaumo trilophus*, KOE 3467. (ab–ae) *Paradjidaumo* sp., KOE 3464, 3473, FMNH: PM 20518, KOE 3581. (af) *Pentabuneomys engesseri*, KOE 3041. (ag) cf. *Pentabuneomys* sp., KOE 3558. (ah, ai) *Rhodanomys transiens*, KOE 3130, 2486. (aj) *Apeomys tuerkheimae*, KOE 3556. (ak) *Megapeomys lavocati*, NM Pv 12,233 = 74081a in Fejfar et al. (1998). (al) *Aulolithomys bounites*, KOE 3474. (am) *Centimanomys major*, KOE 3529. (an–ay) *Pseudotheridomys* aff. *parvulus*, KOE 3555, NM Pv 12,219, 12,220, 12,222, 12,223, 12,224, 12,225, 12,227, 12,228, 12,229, 12,230, 12,232. (az–be) Eomyidae indet., KOE 3525, 3530A, 3530B, 3027, 3028, 3043. Arrow indicates longitudinal edge where present. All cross sections are shown as left side and drawn to scale

FIGURE 6 Schematic drawings of schmelzmuster present in lower incisors of Eomyidae, Pipestoneomyidae (results from Korth & Emry, 2013), Geomyoidea (results from Kalthoff & Mörs, 2021), Florentiamyidae (results from Wahlert, 1983), and Heliscomyidae (results from Kalthoff & Mörs, 2021). The schmelzmuster are ordered with regard to their evolutionary level; the stratigraphic appearance of a schmelzmuster refers to analysed material of unambiguously identified taxa of the particular clade. Eomyidae and Pipestoneomyidae are highest evolved among the included clades concerning lower incisor enamel microstructure. Enamel type symbols adapted from Kalthoff (2000) and Pfretzschner (1994)



into three classes by thickness: thin ($\leq 70 \mu\text{m}$), moderate ($71\text{--}90 \mu\text{m}$), and thick ($> 90 \mu\text{m}$). A thin enamel band is predominant in half of the analysed eomyid taxa (50%) with the largest share among the European and Japanese species (71%). A thick enamel band was measured in more than half of the North American taxa (56%) but only in *Megapeomys lavocati* among the European taxa, possibly representing an effect of its comparatively large body size.

A second aspect is the thickness of the individual layers. We expected (1) a relative thinning of the plesiomorphic OPI in favour of the apomorphic IPI with decreasing (i.e., younger) stratigraphical age; (2) a relative thinning of the PE in favour of a developing OMPI. These kinds of evolutionary changes have been described in multilayered incisor enamel of other rodents, such as hamsters (Kalthoff, 2000, 2006). However, no such pattern of change in thickness of the

individual layers is detectable through time, taxonomy, or biogeography.

4.3.1 | Remark

An explanation for varying thicknesses, even within a single species, and lack of a pattern might be the small size of eomyid incisors, making it impossible to produce perfectly perpendicular transverse sections. Consequently, measurements should be seen as guide values.

4.4 | The longitudinal edge

A lateral thickening of the enamel band, expressed as a longitudinal ridge was mentioned by Wahlert and Koenigswald (1985) as unique for Eomyidae. We found, however, that this is not the case: this outer enamel ornamentation is not present in all eomyid taxa and also occurs in other rodent taxa of the mouse-related clade (Kalthoff, 2000).

When distinctly developed, e.g., in *Eomys zitteli* (Figure 1f), *Pseudotheridomys* (Figure 1g), *Japaneomys*, and *Centimanomys*, the longitudinal edge is a character easy to detect by eye in transverse sections. Microstructurally, the longitudinal edge is mainly realized by a thickening of the IPI and the PE (contrary to Wahlert & Koenigswald, 1985 who name OPI and PE), in *Pseudotheridomys* (Figure 1g) and *Centimanomys* also by the OMPI. The thickening persists until the enamel band naturally thins out laterally. Here, we favour the term ‘longitudinal edge’ for this feature is asymmetrical with a raising slope on the lingual side and a gentle gradual decline laterally (Figure 1f, g); consequently, the shape and enamel band area effected by a longitudinal edge is broader than that of a longitudinal ridge as seen e.g., in the cricetids *Eumyarion* and *Cricetodon* (Kalthoff, 2000). In exceptional cases, however, the thickening of the enamel band is either expressed in a more ridge-like fashion (Eomyidae indet. KOE 3525) or as gradual thickening without forming an edge (*Adjidaumo* sp. KOE 1994; *Adjidaumo intermedius*; undetermined eomyid from Japan; *Ligerimys lophidens* NM Pv 12,216). Furthermore, in some taxa, even the lingual part of the enamel band is somewhat thicker than the central part but an edge is not developed and the thickness change is mild and gradual (e.g., *Eomys*, *Eomyodon*, *Eomyops*). Longitudinal edge occurrence and shape could not be correlated to either stratigraphic occurrence or taxonomy.

In sum, the longitudinal edge can no longer be regarded as an autapomorphy of Eomyidae for it is absent in a number of confidently identified eomyids in our sample, such as *Ligerimys lophidens*, *Keramidomys thaleri*,

Paradjidaumo sp. (KOE 3581), and in *Zemiodontomys burkei* (Emry & Korth, 1993). Moreover, growing detailed documentation of rodent incisor morphology showed the presence of a longitudinal edge in a number of other rodents of the mouse-related clade (Kalthoff, 2000), typified by the democricetodontid hamster *Karydomys wigharti* (Mörs & Kalthoff, 2004).

Outer enamel ornamentation in Leptodontomys/Eomyops. To separate the European *Leptodontomys* species from their North American counterparts, Engesser (1979) erected the genus *Eomyops*. He described a “crenulated lower incisor” as “the most important difference between *Leptodontomys* from North America and Europe” and figured the labial side of a fragmented lower incisor with two parallel enamel ridges from the French locality La Grive, labelled as *Eomyops* aff. *catalaunicus* (Engesser, 1979: 27 and Figure 8b). However, there is no indication that the figured lower incisor stems from a toothed mandible, meaning we consider it as an isolated tooth specimen and as such not safely identified. We assume that Engesser (1979) misinterpreted the description of the lower incisor of *Leptodontomys catalaunicus* in Huguency and Mein (1968:196) having two ridges although the authors described only one longitudinal edge (“...une bosse bien marquée du côté externe de la branche...”). Judging from the faunal list from de Bruijn et al. (1992) and descriptions of lower incisor ornamentation in Kalthoff (2000) Engesser's two-ridged lower incisor from La Grive originated from either *Cricetodon*, *Hispanomys*, *Eumyarion*, or *Anomalomys*.

Later and based on the figured two-ridged incisor fragment in Engesser (1979), Ruiz-Sanchez et al. (2009) attributed an isolated, two-ridged incisor from Morteral-20A to their new taxon *Eomyops noeliae*. That incisor almost certainly is an *Eumyarion* as judged from the faunal list of Morteral-20A (Ruiz-Sanchez et al., 2009).

To our knowledge and based on our material, no eomyid taxon features a two-ridged lower incisor ornamentation (Figure 5). Likewise based on our material, consisting of incisor material from toothed mandibles, we can state with certainty that both North American *Leptodontomys* and Eurasian *Leptodontomys/Eomyops* have one longitudinal edge (Figure 5i, s, t); although it is rather shallow in the former and well developed in the latter. In consequence, outer enamel ornamentation with two enamel ridges as distinctive character between the North American *Leptodontomys* and the Eurasian *Leptodontomys/Eomyops* does no longer hold.

4.5 | Incisor cross sections

Lower incisor cross sections show a high variability in our eomyid sample: many are variously oval-shaped (e.g., Figure 5a,

k, r, ai); others are subtriangular with a flat lingual side (e.g., Figure 5d, w, al), or – rarer – have roundish cross sections (Figure 5ah, av). In general, the enamel band is rounded; in some species such as *Ligerimys lophidens* (Figure 5u–w), *Paradjidaumo* sp. (Figure 5ad), *Megapeomys lavocati* (Figure 5ak), and *Centimanomys major* (Figure 5am), the enamel stretches far to the lateral side.

Engesser (1990) showed that lower incisor cross sections of species within *Eomys* have a rather low shape variability, coinciding with our results for this genus. We found that in other genera, incisor cross section may vary between species of the same genus but then seems to be intraspecifically uniform as seen in *Ligerimys lophidens* (Figure 5u–w) and *L. florancei* (Figure 5x, y). A final and unforeseen result is that cross sections can be highly variable at the intraspecific level as represented but 12 incisors of *Pseudotheridomys* aff. *parvulus* from Merkur-North, provided, that all belong to the same species. Shapes range from slender-oval to oval to subtriangular to round-shaped (Figure 5an–ay).

In sum, our study shows ambiguous results how incisor cross sections contribute to species identification.

4.6 | Phylogenetic relationships within Eomyidae and palaeobiogeographic implications

Flynn et al. (2008) subdivided the North American eomyids in two subfamilies, Yoderimyinae and Eomyinae, the latter one with the four tribes Namatomyini, Eomyini, Apeomyini and Ronquillomyini, and Eomyinae incertae sedis. The basal, mainly Eocene Yoderimyinae are represented in this study by *Zemiodontomys burkei*, which has a three-layered schmelzmuster that lacks the OMPI. In this respect *Zemiodontomys burkei* is similar to the Chadronian *Adjidaumo* (KOE 1994) and *Aulolithomys bounites*, and to the Orellan *Adjidaumo intermedius* and *Paradjidaumo trilophus*.

Eomyini is the clade with the longest stratigraphical record, ranging from middle Eocene to late Miocene. In our study, North American taxa include *Adjidaumo* spp., *Paradjidaumo* spp., *Leptodontomys douglassi*, *Neodjidaumo hemedapus*, an undetermined eomyid (KOE 3043), and *Pentabuneomys engesseri*, representing a time interval from late Eocene to late Oligocene (Chadronian to early Arikareean) (Flynn, 2008; Korth, 2008). Eurasian Eomyini include *Eomys* spp., *Eomyodon* spp., *Rhodanomys transiens*, *Ligerimys* spp., *Pentabuneomys*, *Keramidomys thaleri*, *Eomyops catalaunicus*, *Japaneomys yasunoi* and an unnamed Japanese eomyid species, representing a time interval from late Oligocene to late Miocene (Suevian to Vallesian, MP 21 to MN 10) (Engesser, 1999; Kimura et al., 2020).

An unexpected result of our study is the variability of schmelzmuster and enamel thickness in *Adjidaumo* and *Paradjidaumo*. Given that a genus should display only one schmelzmuster, the taxonomy of *Adjidaumo* and *Paradjidaumo* species should be reviewed. Our results support phylogenetic relationships of those species of *Adjidaumo* and *Paradjidaumo* species with OMPI, as well as with *Leptodontomys* and *Pentabuneomys*. Based on the distinctly different schmelzmuster and the weak/missing longitudinal edge, we consider *Neoadjidaumo* unrelated to these taxa.

The Oligocene Eurasian *Eomys* is generally considered to be an early Oligocene immigrant from North America and related to *Adjidaumo* (Engesser, 1999; Fahlbusch, 1970, 1973; Kimura et al., 2020; Maridet et al., 2010; Qiu, 1994; Wang & Emry, 1991). Schmelzmuster, enamel thickness and longitudinal edge support a relationship to those *Adjidaumo* species without OMPI, although we cannot exclude a possible relationship to *Paradjidaumo* species without OMPI.

According to Engesser (1999), the late Oligocene/early Miocene European *Rhodanomys* has to be considered as a descendant of *Eomys*. Schmelzmuster, enamel thickness, and longitudinal edge shape do not contradict this phylogenetic relationship.

The late Oligocene/early Miocene European *Eomyodon* is not closely related to contemporaneous *Eomys*, but could be a descendant of an early Oligocene *Eomys* somewhere in Eurasia (Engesser, 1999). Alternatively, Engesser (1999) suggested a phylogenetic relationship with a late Oligocene Chinese *Eomyodon* presently assigned to *Asianeomys* (Kimura et al., 2020; Wang & Emry, 1991). Schmelzmuster and enamel thickness are similar in *Eomys* and *Eomyodon*, so our results do not contradict a possible phylogenetic relationship of these two taxa.

The smallest of all eomyids, the Miocene *Keramidomys*, was originally considered as a descendant from *Pseudotheridomys* (Fahlbusch, 1975, 1979; Hartenberger, 1966), but Engesser (1999) pointed out that there are too many morphological differences between these two taxa. Consequently, *Keramidomys* is regarded as an Orleanian immigrant into Europe, with a possible Asian origin (Engesser, 1999; Kimura et al., 2020; Mein, 2009). Our results support this latter view: contrary to *Pseudotheridomys*, which has a four-layered schmelzmuster with OMPI, *Keramidomys* has a three-layered schmelzmuster without OMPI, making it unlikely that *Keramidomys* is a descendant from *Pseudotheridomys*. Recently, Kimura et al. (2019, 2020) suggested *Keramidomys* as a descendant of *Asianeomys* (which we could not sample), implying that the latter should have a three-layered schmelzmuster. In turn, both are sister taxa to *Japaneomys*, which has a four-layered schmelzmuster

with OMPI. If future studies show that *Asianeomys* also has a four-layered schmelzmuster, the phylogenetic relationship of *Keramidomys* and *Asianeomys* must be reconsidered.

The origin and phylogenetic relationships of Eurasian *Eomyops/Leptodontomys* with North American *Leptodontomys* is not yet resolved (de Bruijn et al., 2012; Engesser, 1999; Flynn, 2008; Kimura et al., 2020; Maridet et al., 2015; Qiu, 1994; Qiu & Li, 2016). Fahlbusch (1979) suggested a European origin with *Pentabuneomys* (at that time *Eomys*) as possible ancestor, and a subsequent spread to North America, while Engesser (1979) favoured an independent evolution of these eomyids. According to Engesser (1999), *Eomyops* is an early Miocene (MN 3) immigrant into Europe although not related to the North American *Leptodontomys*. Qiu (1994) proposed an Asian origin of *Leptodontomys* species that dispersed into Europe and North America, which is supported by recent findings of early Oligocene *Leptodontomys* in Inner Mongolia predating the European record (Kimura et al., 2020; Qiu & Li, 2016). Our results (schmelzmuster, enamel thickness and longitudinal edge) are consistent with relationship of European *Eomyops* either to *Pentabuneomys*, or to North American *Leptodontomys*.

Pentabuneomys is known from the late Oligocene of North America, and from the early Miocene of Eurasia, thus a North America origin of the genus can be assumed (Kimura et al., 2020; Korth, 2008; Qiu & Li, 2016). The similarity of schmelzmuster and enamel thickness support the close relationship of European and North American *Pentabuneomys*, although the late Oligocene (Arikarean) North American species has a very weak longitudinal ridge in contrast to the lower Miocene (MN 3) European species.

For a long time, *Ligerimys* was considered to be endemic to Europe, and to be derived there from *Pseudotheridomys* (Alvarez Sierra et al., 1987; Engesser, 1999; Escarguel & Aguilar, 1997; Fahlbusch, 1970, 1983). The recent discovery of *Ligerimys* in Inner Mongolia sheds new light on the origin of the genus (Kimura et al., 2020; Qiu & Li, 2016) because it may predate the European record. The schmelzmuster results are ambiguous and puzzling: *Ligerimys* could be the descendant of *Pseudotheridomys* (they share a four-layered schmelzmuster with OMPI), but incisor and enamel shape vary in *Ligerimys* and *Pseudotheridomys* and even within the two analysed species of *Ligerimys*. *Ligerimys lophidens* has no or at most a weak longitudinal edge in contrast to a well-developed one in *Pseudotheridomys* aff. *parvulus* and in *Ligerimys florancei*. Enamel thicknesses (thin to moderate) are similar in *Pseudotheridomys* and *Ligerimys*, but cross sections are variable in *Pseudotheridomys* aff. *parvulus* and in *L. florancei* while they are more triangular in *L. lophidens* and

the enamel extends well to the lateral side in the latter. The taxonomy of the genus *Ligerimys* also is in need of a revision.

Apeomyini are known from the late Oligocene to early/middle Miocene of Eurasia and North America (Engesser, 1999; Fahlbusch, 1968; Flynn, 2008; Kimura et al., 2020; Korth, 1992; Mörs & Flink, 2018; Smith et al., 2006). Fahlbusch (1968) and Engesser (1999) suggest a close relationship of *Apeomys* and *Pseudotheridomys*. Our results do not support this as *Apeomys* lacks the four-layered schmelzmuster with OMPI. The early Miocene, Holarctic distributed *Megapeomys* is generally regarded as closely related to *Apeomys* (Engesser, 1999; Fejfar et al., 1998; Flynn, 2008; Kimura et al., 2020). But the schmelzmuster in *Megapeomys* differs from all other Eomyidae, indicating that the phylogenetic position of this taxon needs to be reviewed.

In our sample, the late Eocene *Centimanomys major* is one of the stratigraphically oldest eomyids with an OMPI, though it is still thin (1–2 prisms), and the IPM makes an acute angle. It has a well-developed longitudinal edge and thick enamel. *Centimanomys* is somewhat similar to *Aulolithomys* but the latter has no OMPI layer but patchy areas where the IPM makes an acute angle to prisms. Beyond that, *Centimanomys* is not similar to any other North American eomyid of our sample.

The early/middle Miocene *Pseudotheridomys hesperus* is regarded by Flynn et al. (2008) as Eomyinae incertae sedis. Our study supports a relationship to the European *Pseudotheridomys* and to *Japaneomys*; possibly also to *Asianeomys*, which had been considered as Asian '*Pseudotheridomys*', but could not be sampled for our study.

According to Engesser (1999), the highly derived late Oligocene/early Miocene European *Pseudotheridomys* cannot be related to any other eomyid genus; with the exception of its possible descendant *Ligerimys* (but see above). Our results indicate a close phylogenetic relationship to the recently described *Japaneomys* (Kimura et al., 2019) and an unnamed eomyid from the early Miocene of Japan: these eomyids – although not representing the same taxon – have an identical schmelzmuster, enamel thickness is similar, and the cross sections are mostly similar.

To sum up the paleobiogeographic implications, we can state that the first eomyids that reached Europe (*Eomys*) in the early Oligocene had a three-layered schmelzmuster without OMPI, although in North America, a derived four-layered schmelzmuster with OMPI had evolved by the late Eocene (*Centimanomys*). The first dispersal of eomyids with derived four-layered schmelzmuster with OMPI from North America to Eurasia happened in the late Oligocene (*Pseudotheridomys*). A possible third and

fourth immigration event could have happened in the early Miocene (*Ligerimys*, *Japaneomys*) and in the middle Miocene (*Keramidomys*, *Eomyops*), but our study equally supports a Eurasian evolution of these taxa.

4.7 | Phylogenetic relationships of Eomyidae to other clades within Geomorpha

The suprafamilial position of Eomyidae is not yet solved. Wilson (1949:48) regarded them as “the most primitive known family of the Geomyoidea” on the basis of craniodental characters. More recently, they have been placed with Geomyoidea in the infraorder Geomorpha (Korth, 1994; McKenna & Bell, 1997; Wahlert, 1978, 1983), or alternatively have been regarded as close relatives to Geomorpha (Flynn, 2008; Flynn et al., 2008; Korth et al., 1991). Geomyoidea exclusively comprise the fossil and extant Geomyidae and Heteromyidae (Kalthoff & Mörs, 2021), or include also the extinct Heliscomyidae and/or Florentiamyidae (Flynn et al., 2008; Korth, 1994; Korth et al., 1991; McKenna & Bell, 1997; Nowak & Walker, 1999).

Korth and Emry (2013) introduced Pipestoneomyidae as sister taxon to Eomyidae within Eomyoidea. A key argument for this systematic allocation is the schmelzmuster of *Pipestoneomys bisulcatus* with uniserial, longitudinal HSB in a two-fold PI, which the authors consider “diagnostic of the Eomyidae” (Korth & Emry, 2013:295). The figured schmelzmuster of *Pipestoneomys bisulcatus* is de facto very similar to that of Eomyidae and dissimilar to the clades included in Geomorpha. The schmelzmuster architecture with uniserial, longitudinal HSB in a two-fold PI occurs in a number of other, non-related rodent clades such as hamsters, jumping mice, and dormice, the latter though not distributed in the New World (Kalthoff, 2000; Koenigswald, 1995a; Koenigswald & Kalthoff, 2007) and therefore cannot be regarded as diagnostic in a systematic sense. However, neither hamsters nor jumping mice had developed longitudinal HSB already in the late Eocene (middle to late Chadronian), implying that – in a stratigraphical sense – Korth and Emry’s (2013) argument still holds. If Pipestoneomyidae and Eomyidae indeed are sister taxa, longitudinal HSB were present in their common ancestor and would be a shared trait of Eomyoidea.

Incisor enamel microstructure does not support a phylogenetic relationship of Eomyidae with either Geomyidae, Heteromyidae, Heliscomyidae, or Florentiamyidae (Figure 6). Highly derived, longitudinal HSB as present in Eomyidae as early as late Eocene (Duchesnean/Chadronian) occur in none of these families (Kalthoff, 2000; Kalthoff & Mörs, 2021; Wahlert, 1968,

1983) nor do longitudinal HSB occur at that stratigraphic level in any other clades discussed by Wilson (1949). Instead, all analysed taxa of these families show a moderately derived schmelzmuster having transversally oriented HSB with a two- or one-fold PI and the PE consists of radial enamel (schmelzmuster types 2 and 3 sensu Kalthoff, 2000). In turn, Kalthoff and Mörs (2021) report a zone of highly derived modified radial enamel occurring exclusively in the PI of Geomyoidea (Geomyidae and Heteromyidae) but not in related Geomorpha, such as Heliscomyidae and Florentiamyidae, and it also is absent from Eomyidae. In sum, our incisor enamel microstructure results support the view that Eomyidae should be placed outside Geomorpha.

5 | CONCLUSIONS

The lower incisor enamel microstructure has been reviewed in 36 eomyid taxa from North America, Europe, and Japan, and subsequently compared to fossil and extant members of the Geomyidae, Heteromyidae, Florentiamyidae, and Heliscomyidae (Kalthoff & Mörs, 2021). The interpretation of our results led to the following conclusions:

1. Eomyidae show a broader range of lower incisor enamel microstructure variability than previously appreciated.
2. Eomyidae show a typical, highly apomorphic schmelzmuster with longitudinally oriented Hunter-Schreger bands (HSB) and a two- or three-fold portio interna (PI). The portio externa (PE) is comparably plesiomorphic with a single layer of radial enamel. As demonstrated here, longitudinal HSB are already present at a minimum age of late Eocene (Duchesnean/Chadronian).
3. The presence of a three-fold PI is a new and unique character in Rodentia and seems to be restricted to Eomyini and some genera currently considered incertae sedis within Eomyidae.
4. A two-fold PI consists of an inner portio interna (IPI), in which the interprismatic matrix (IPM) is perpendicular to the prism long axes, and an outer portio interna (OPI) with prism-parallel IPM. In a three-fold PI, an additional layer between OPI and PE is developed (introduced here as ‘outermost portio interna’: OMPI), in which the IPM again runs at an acute or right angle to the prisms (mirroring the IPI).
5. For North American Eomyidae, the stratigraphical oldest (i.e., minimum age) occurrence for a three-fold PI with a continuous ‘outermost portio interna’ (OMPI) is late Eocene (Chadronian). The minimum age

occurrence for a continuous OMPI in Europe is early Miocene (Orleanian, MN 3); however, the developmental onset of this third PI layer can be detected in the late Oligocene taxa. Our small Asian sample only allows a peep-hole into the early Miocene but clearly exhibits an exemplarily developed OMPI at that time interval.

6. Exceptions from the typical eomyid schmelzmuster are found in the European *Megapeomys lavocati*, and the North American taxa *Neoadjidaumo hemedapus* and Eomyidae indet. Diagonal to longitudinal HSB in an only one-fold PI (with perpendicular IPM) are present in all three taxa. Large body size is noted to be correlated with *M. lavocati*'s divergent schmelzmuster, while this remains unsolved for the two North American taxa.
7. The longitudinal edge is not a synapomorphy of Eomyidae. This character is present in most eomyid taxa (but not all) and also occurs in some other rodents of the mouse-related clade.
8. The North American *Leptodontomys* and the Eurasian *Eomyops* both have only one longitudinal edge. Earlier published evidence of two enamel ridges as a distinctive character for *Eomyops* is based on a misinterpretation.
9. Thin enamel bands ($\leq 70 \mu\text{m}$) are typical for Eomyidae and are especially characteristic in the European sample. Thick enamel bands ($> 90 \mu\text{m}$) mostly occur in the North American taxa.
10. No taxonomic, stratigraphic, or palaeogeographical pattern could be detected for the thickness of the particular enamel types and the occurrence and shape of the longitudinal edge.
11. Incisor cross sections show a high variability in our eomyid sample. In some genera, shapes can help in species identification; but other cases show variability even at the intraspecific level.
12. Lower incisor enamel microstructure does not offer arguments for a suggested phylogenetic relationship of Eomyidae to Geomyidae, Heteromyidae, Heliscomyidae, or Florentiamyidae. Thus, our results support the view that Eomyidae are placed outside Geomorpha.

AUTHOR CONTRIBUTIONS

DCK and OF designed the project. DCK, OF, and BEB collected, processed, and photographed the material; DCK and TM analysed the data; and DCK provided illustrations. All authors interpreted the data, drafted the manuscript, and approved the version to be published.

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CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

HUMAN AND ANIMAL RIGHTS

This article does not contain any studies with human participants or animals performed by any of the authors.

We declare that some minor adjustments to brightness or contrast have been made to the scanning electron micrographs. Adjustments apply equally across the entire images.

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