

## Early Rodent Incisor Enamel Evolution: Phylogenetic Implications

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Incisor enamel microstructure proved to be a very effective tool for assessment of phylogenetic relationships among the Rodentia. Pauciserial and multiserial Schmelzmuster are clearly distinct by structural characters such as orientation of interprismatic matrix, presence or absence of transition zones between Hunter-Schreger bands (HSB), inclination of HSB, enamel thickness, and others. Pauciserial HSB are structurally very close to the earliest known mammalian HSB found in Paleocene arctocyonids. Biomechanical arguments and outgroup comparison with mixodontians indicate that the pauciserial Schmelzmuster is a symplesiomorphy of the Rodentia. Transitional stages from pauciserial to multiserial Schmelzmuster were observed in middle Eocene ctenodactylids and from pauciserial to uniserial in middle to late Eocene anomalurids. The multiserial Schmelzmuster is considered a synapomorphy of the Hystricognathi, ctenodactylids, and pedetids. Schmelzmuster evolution reflects the early dichotomy of the Rodentia: In the Asian ctenodactyloid lineage a multiserial Schmelzmuster evolved once and in the North American/European ischyromyoid lineage a uniserial Schmelzmuster developed several times convergently. The pauci- to uniserial Schmelzmuster of the anomalurids excludes a close relationship to the phiomyids, because the ctenodactyloid-phiomyid lineage is characterized by the development of a multiserial Schmelzmuster.

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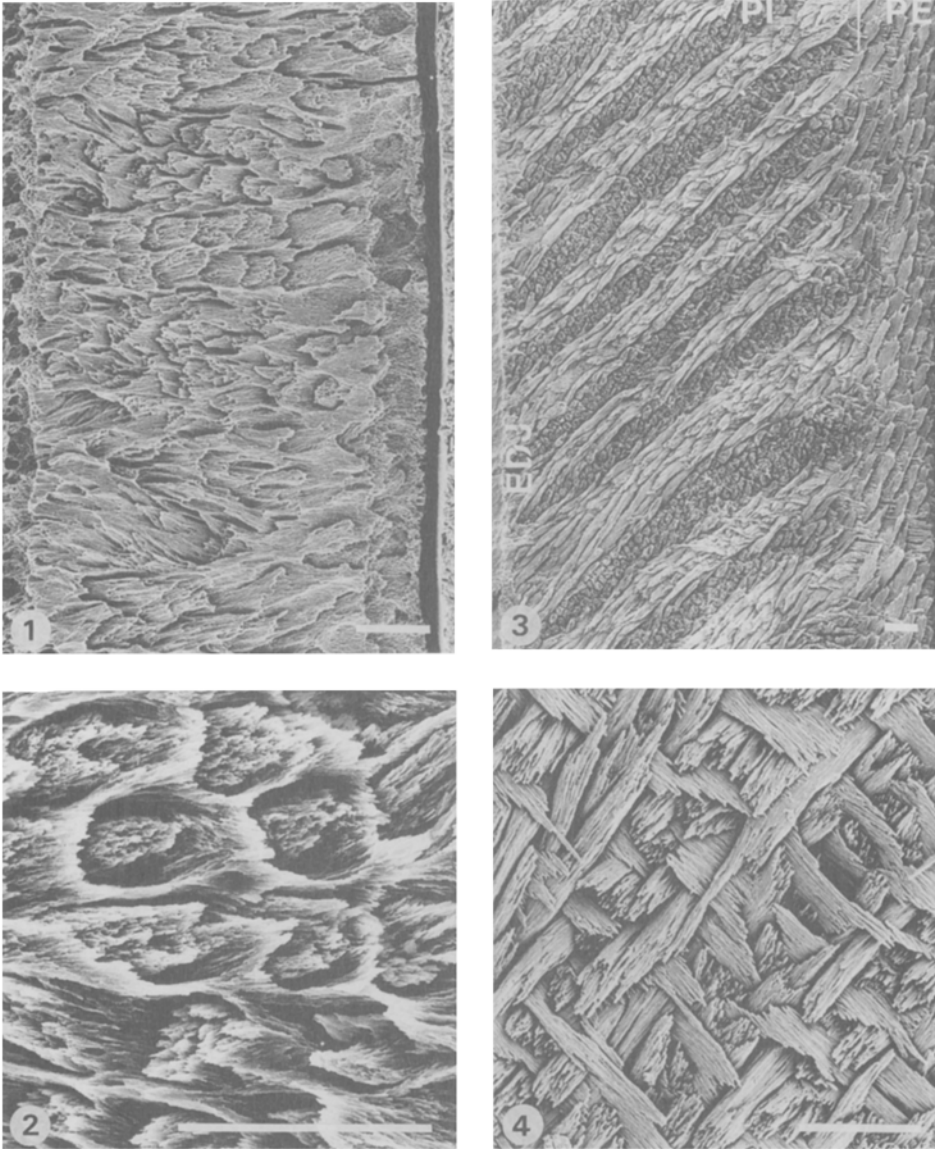
**KEY WORDS:** enamel microstructure; evolution; incisors; Mixodontia; Rodentia.

### INTRODUCTION

The highly derived, ever-growing rodent incisors are very effective tools for food processing, gnawing, and burrowing and may have consistently contributed to the great success of the Rodentia. In contrast to other teeth, the enamel of rodent incisors covers only the labial side and provides, in association with the softer underlying dentin, a self-sharpening cutting edge. Correlated with the high specialization of rodent incisors, their enamel microstructure shows the highest degree of complexity among Mammalia (Korvenkontio, 1934; Wahlert, 1968; Boyde, 1978; Koenigswald, 1980, 1985).

In most rodents the incisor enamel consists of two layers: an inner portion (portio

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**Figs. 1–4.** Pauciserial (Figs. 1 and 2) and multiserial Schmelzmuster (Figs. 3 and 4). SEM micrographs of longitudinal sections of lower incisor enamel. If not otherwise indicated, the EDJ is to the left and the tip of the incisor to the top in all following figures. Scale bar equals  $10\ \mu\text{m}$  in all figures. **Fig. 1:** In the pauciserial Schmelzmuster, HSB are not inclined and HSB thickness is highly variable, giving them an irregular appearance. Transition zones between HSB are missing and the IPM runs parallel to the prisms. *Paramys* sp. indet. (MA 16). **Fig. 2:** The prism-surrounding, parallel IPM is the key character for pauciserial HSB. *Tsagamys subitius* (MA 9; SEM print inverse). **Fig. 3:** In the multiserial Schmelzmuster, HSB are steeply inclined and prisms bend from one HSB to the next higher. A well-developed PE is present. In the PI, the IPM runs at an acute angle to the prisms. PE, portio externa; PI, portio interna; EDJ, enamel–dentin junction. *Phiomyidae* gen. et sp. indet. (MA 23). **Fig. 4:** Multiserial HSB with a rectangular IPM. This is the most derived multiserial enamel subtype; the IPM strengthens the enamel in the third dimension. *Africanomys minor* (MA 90).

interna; PI) with decussating prisms and an outer portion (portio externa; PE) with radial enamel, in which the prisms are oriented parallel to each other (Figs. 3 and 9–12). The decussating prisms appear as Hunter-Schreger bands (HSB) in longitudinal sections. The presence of two layers in the rodent incisor enamel has been regarded as a fundamental difference from lagomorphs, where only the PI with HSB is developed (Tomes, 1850). However, the PE may also be reduced in rodents, as in some Eocene ischyromyoids (Flynn *et al.*, 1987) and in the Pleistocene bathyergid *Heterocephalus jaegeri* (Martin, 1992b).

Biomechanically, HSB are interpreted as strengthening devices and crack-propagation inhibitors (Lehner and Plenck, 1936; Koenigswald, 1980; Pfretzschner, 1988, in press; Koenigswald and Pfretzschner, 1991), whereas the radial enamel of the PE is thought to help maintain a sharp cutting edge because of its slightly higher wear resistance (Rensberger and Koenigswald, 1980; Fortelius, 1984, 1985). Since the groundbreaking work of Korvenkontio (1934), the importance of rodent incisor enamel microstructure for phylogenetic questions has been obvious. Rodent incisor enamel evolves independently from the other dental traits (Koenigswald, 1988; Koenigswald and Clemens, 1992) and is particularly appropriate for comparative studies, because the incisors have roughly the same shape in all rodents and therefore are not strongly influenced by differing biomechanical constraints, in contrast to hypsodont and brachyodont molars.

Korvenkontio (1934) distinguished three basic enamel types in rodent incisors, based mainly on the width of the HSB. In the enamel type he called pauciserial, HSB generally are two to four prism layers wide (Figs. 1 and 2); it is restricted to Paleogene rodents. Multiserial HSB have been thought to be generally thicker, mostly comprising four to seven (and more) prism layers, and characterize the Hystricognathi, some Eocene and all (so far studied) post-Eocene Ctenodactyloidea, and *Pedetes* (Figs. 3, 4, and 24–27). Very distinct are uniserial HSB, where each band consists of only a single prism layer (Figs. 9–12). Uniserial HSB with parallel interprismatic matrix (IPM) are found in sciuriforms and with rectangular IPM in myomorphs (Boyde, 1978; Koenigswald, 1985).

The distinction of HSB only by their width proved not to be practical, because there exists a wide overlap between pauciserial and multiserial HSB. This caused disagreement and confusion about the question of which HSB should be considered pauciserial and which multiserial (Sahni, 1980; Hussain *et al.*, 1978; Flynn *et al.*, 1986; Coiffait *et al.*, 1984). Dauphin *et al.* (1988) even concluded that Korvenkontio's three basic HSB types form a continuum and therefore are unreliable for phylogenetic studies.

However, the observations of Korvenkontio (1934) and many subsequent authors (e.g., Wahlert, 1968; Boyde, 1978; Sahni, 1980, 1985; Koenigswald, 1985) on the distribution of HSB types among different rodent suborders were good evidence that there indeed exist three distinct evolutionary stages of HSB. The main difficulty was the disagreement on the definition of pauciserial and multiserial HSB and on which pattern represents the ancestral or primitive condition in Rodentia. A broad study of hystricognath and sciurognath rodent incisors (Martin, 1992b) has attempted to resolve these disagreements. The present study of incisor enamel of the earliest rodents from different continents sheds new light on their early enamel evolution and yields, for the first time, transitional stages from pauciserial to multiserial and from pauciserial to uniserial Schmelzmuster.

## MATERIALS AND METHODS

New specimens of Paleogene rodent and mixodontian incisors prepared for this investigation are listed in Table I. Additional data on the nature of the specimens and localities can be obtained by writing to the author. Except where noted, incisor samples were removed from skulls or mandibles with associated cheek teeth. Data on incisor enamels from other ischyromyoids, ctenodactyloids, and hystricognaths mentioned in the text, but not listed in Table I, are given by Martin (1992b).

Specimens were prepared by imbedding pieces of the incisors a few millimeters in length in artificial resin and then sectioning them longitudinally and radially. Subsequently the specimens were ground, polished, and etched for 2–4 sec with 2 *N* HCl to make morphological details visible. During grinding and polishing care was taken to orient the planes of section precisely, to avoid distortion for measurements. After rinsing and drying, the specimens were coated with gold and examined with a scanning electron microscope (JSM-6300). The samples are housed under the reference numbers (MA) given in the author's enamel collection at the Freie Universität Berlin.

Table I. Rodent and Mixodontian Incisors Examined

Taxon	Specimen <sup>a</sup>	Locality	Age
Ischyromyoidea			
<i>Ailuravus</i> sp. indet.	L	Premontré, France	Early Eocene
<i>Paramys</i> sp. indet.	L	Mancy, France	Early Eocene
Anomaluroidea			
Cf. Zegdoumyidae <sup>b</sup>	?U	Glib Zegdou, Algeria	Late early to early middle Eocene
Cf. Zegdoumyidae <sup>b</sup>		Chambi, Tunisia	Late early to early middle Eocene
Cf. Anomaluridae <sup>b</sup>		Bir el Ater, Algeria	Late Eocene
<i>Anomalurus</i> sp. indet.	U/L	La Maboré, Republic of Central Africa	Recent
Ctenodactyloidea			
<i>Tsagamyx subitus</i>	L	Tsagan Kushu, Mongolia	Early Eocene
<i>Euboromys</i> sp. indet.	L	Khaychin Ula II, Mongolia	Middle Eocene
Cf. <i>Tamquammys</i>	L	Khaychin Ula II, Mongolia	Middle Eocene
<i>Africanomys minor</i>	L	Pataniak 6, Morocco	Late Miocene
Phiomorpha			
Cf. Phiomorpha <sup>b</sup>		Bir el Ater, Algeria	Late Eocene
Caviomorpha			
<i>Branisamys luribayensis</i>	L	Salla Luribay, Bolivia	?Late Oligocene
<i>Cephalomys bolivianus</i>	L	Salla Luribay, Bolivia	?Late Oligocene
<i>Incamys bolivianus</i>	L	Salla Luribay, Bolivia	?Late Oligocene
<i>Sallamys pascuali</i>	L	Salla Luribay, Bolivia	?Late Oligocene
Cricetidae			
Cricetidae indet.	L	Mergen, Mongolia	Middle Eocene
<i>Eucricetodon atavus</i>	U	Itardies, France	Early middle Oligocene
?Mixodontia			
<i>Orogomys</i> sp. indet.	L	Tsagan Kushu, Mongolia	Early Eocene
<i>Alagomys inopinatus</i>	L	Tsagan Kushu, Mongolia	Early Eocene
<i>Rhombomylus</i> sp. indet.		Hubei-Province, China	Early middle Eocene

<sup>a</sup>U, upper incisor; L, lower incisor.<sup>b</sup>Specimens represented by isolated incisors.

Materials for this study were provided by the Laboratoire de Paléontologie, Université Montpellier II, by the Museum National d'Histoire Naturelle, Paris (MNHN), and by the Division of Paleontology and Stratigraphy, Geological Institute of the Academy of Sciences, Ulan Bator, Mongolian People's Republic (PSS). Other specimens were obtained from the individuals listed in the Acknowledgments.

### Glossary of Terms Used

*Enamel type*: Units of enamel where prisms have similar orientations (e.g., Hunter-Schreger bands).

*Hunter-Schreger bands (HSB)*: Layers of prisms, one to several prisms wide. In the bands, prisms run parallel; in adjacent bands, they decussate at a high angle.

*Interprismatic matrix (IPM)*: Oriented hydroxyapatite crystallites that are not bundled into prisms.

*PLEX, prismless external layer (Martin, 1992b)*: Outermost layer of the enamel, without prisms, consisting of confluent crystallites of IPM.

*Prisms*: Rodlike elements consisting of bundled hydroxyapatite crystallites; the most important constructing element of enamel.

*Prism sheath*: Space separating prism and IPM, which was filled with proteoglycans in the living tooth.

*Radial enamel*: Enamel type in which prisms run parallel.

*Schmelzmuster (Koenigswald, 1980)*: Three-dimensional arrangement of enamel types.

## RESULTS

### Redefinition of Pauciserial and Multiserial Schmelzmuster or Enamel Pattern

The insufficiency of the band width for distinction between pauciserial and multiserial HSB made a redefinition by structural differences necessary. Table II is based on a broad study of more than 110 hystricognath (multiserial) and sciurognath (mostly pauciserial) rodents (Martin, 1992b). The most important characters to distinguish pauciserial and multiserial Schmelzmuster are the orientation of the IPM in the PI and the transition zones between adjacent HSB.

In pauciserial HSB (Figs. 1, 2, 5, 7, 8, and 13), the IPM always surrounds the prisms and IPM crystallites run parallel to prisms. Prisms have the same inclination as HSB and transition zones are lacking. The structural features given in Table II are the key characters for pauciserial HSB. The band width is not of great value, because pauciserial HSB can reach up to six prisms per band in rodent incisors and even more in rodent molars and incisors of mixodontians.

In multiserial HSB, the IPM never surrounds the prisms. Three subtypes of multiserial HSB can be distinguished, depending on the orientation of the IPM. These are the subtypes with parallel IPM (most primitive), acute angular anastomosing IPM (Figs. 24-27), and rectangular IPM forming interrow sheets (most derived; Fig. 4). Prisms are

**Table II.** Major Differences Between Pauciserial and Multiserial Schmelzmuster in Rodent Incisor Enamel

Pauciserial enamel	Multiserial enamel
1. Crystallites of IPM run parallel to prisms in PI.	1. Crystallites of IPM usually run at an acute or right angle to prisms in PI.
2. IPM is thick and surrounds prisms in PI.	2. IPM is thin and does not completely surround prisms in PI.
3. A distinct prism sheath is present.	3. The prism sheath is poorly developed.
4. Transition zones of prisms between adjacent HSB are lacking.	4. Transition zones are evident between adjacent HSB.
5. HSB exhibit little or no inclination.	5. HSB are apically inclined (usually between 25 and 50°).
6. Prisms in PI are irregularly rounded in cross section.	6. Prisms in PI are oval or laterally flattened in cross section.
7. Number of prisms per HSB varies between 1 and 6 (average, 3).	7. Number of prisms per HSB usually varies between 3 and 7.
8. Number of prisms per HSB is highly variable in same incisor.	8. Number of prisms per HSB is relatively constant in same incisor.
9. Prisms in PE have a relatively low inclination (25–55°).	9. Prisms in PE are steeply inclined (up to 80°).
10. IPM is relatively thick in PE.	10. IPM is relatively thinner in PE.
11. Prisms of PE are only slightly flattened or oval in cross section.	11. Prisms of PE are flattened laterally (lancet shaped) in cross section.
12. Total enamel layer is relatively thin (usually 50–100 μm).	12. Total enamel layer is relatively thick (usually more than 100 μm).

more steeply inclined than HSB and therefore are forced to bend from one to the next higher HSB, forming transition zones. The primitive status of the subtype with parallel IPM becomes evident from its early stratigraphical appearance and the biomechanical role of the IPM. A rectangular IPM is more effective, strengthening the enamel in the third dimension, and helps better to prevent crack propagation.

### Incisor Enamel in Early Rodents Studied (Table III)

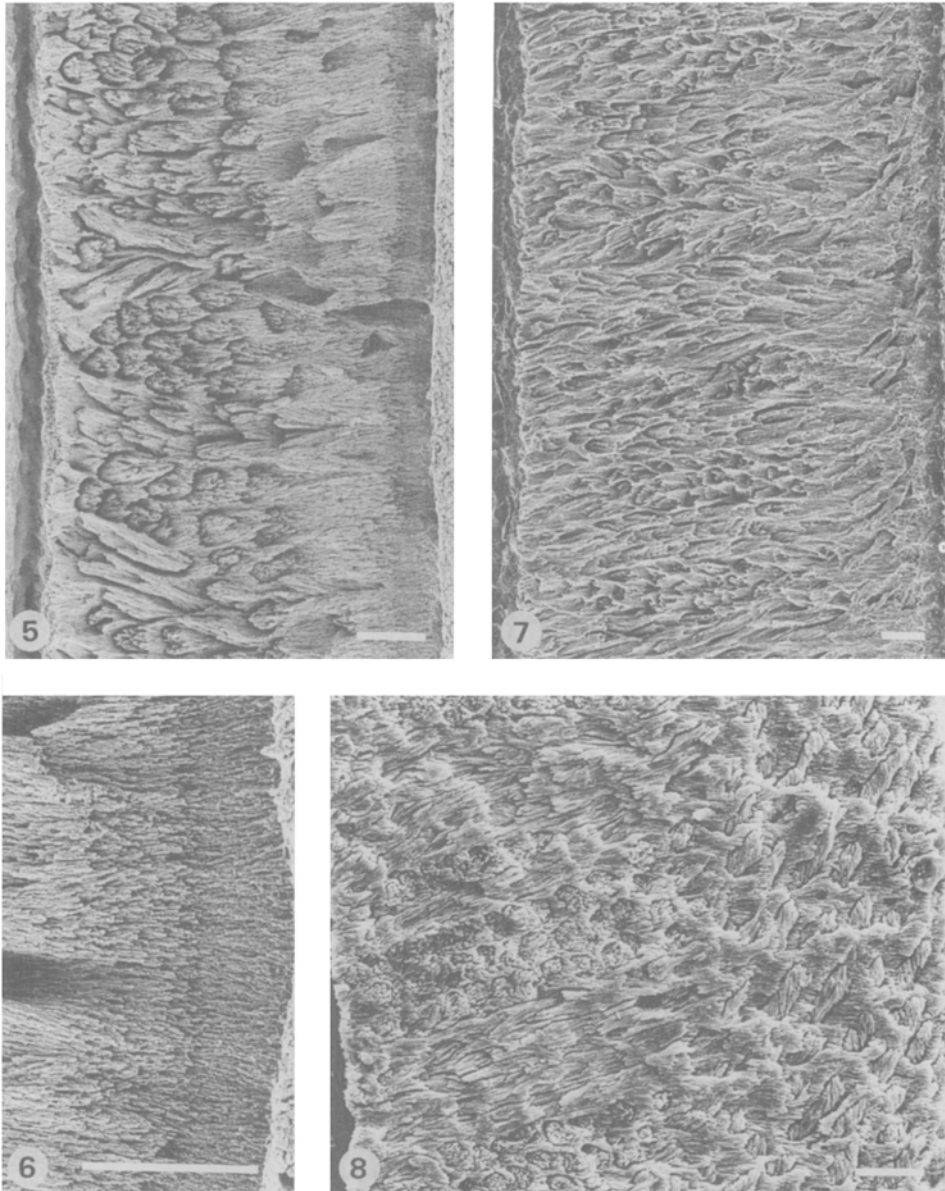
#### *Ischyromyoidea (Figs. 1, 5, and 6)*

The *Ischyromyoidea* studied here, *Ailuravus* and *Paramys*, have typical pauciserial Schmelzmuster, with parallel surrounding IPM in the PI and only a slightly inclined HSB. No differences from the Schmelzmuster of the North American ischyromyoids are obvious (Martin, 1992b).

#### *Anomaluroidea (Figs. 9–12)*

The Eocene anomaluroid incisors referred to *Zegdomyidae* and *Anomaluridae* have Schmelzmuster transitional from the pauciserial to the uniserial condition with parallel IPM in the PI. Most HSB are one to two prisms wide; rarely, bands with three prisms occur. In the Glib Zegdou incisor more two- and three-layered HSB occur than in the others. Between Chambi and Bir el Ater incisors, no differences in band width are obvious.

The Schmelzmuster in upper and lower incisors of the extant *Anomalurus* is fully uniserial and has retained parallel IPM in the PI.

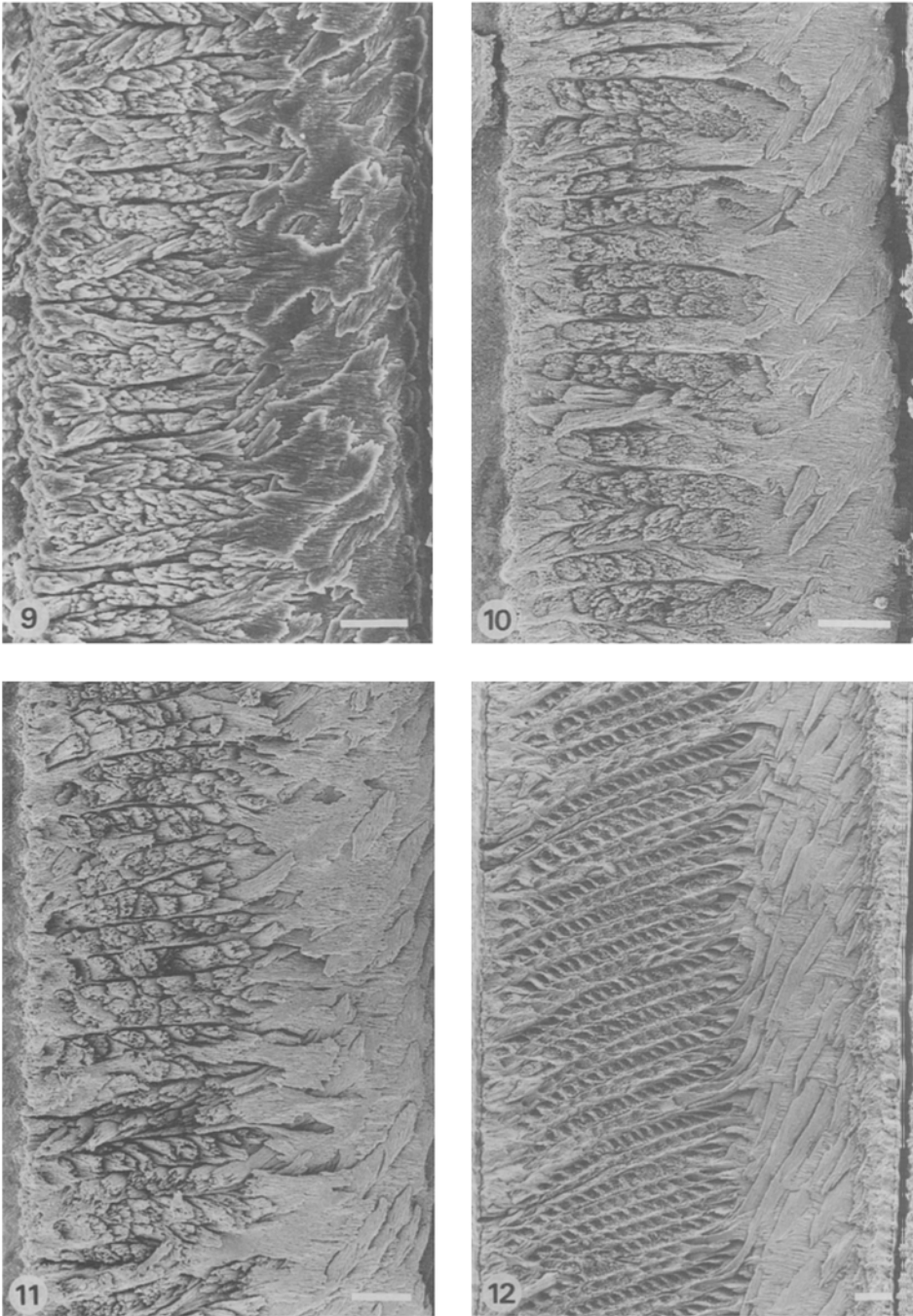


**Figs. 5–8.** SEM micrographs of longitudinal sections of lower (Figs. 5 and 6) and upper (Figs. 7 and 8) incisor pauciserial enamel. **Figs. 5 and 6:** *Ailuravus* sp. indet. (MA 15). **Fig. 5:** *Ailuravus* shows a typical pauciserial Schmelzmuster with distinct PE. **Fig. 6:** In the PE, prisms do not bend apically but run parallel to the IPM, forming a thick PLEX. **Fig. 7:** *Protadelomys* sp. indet. (Theridomyoidea), Eocene, Bouxwiller (MA 17). In *Protadelomys*, the enamel band is much thicker than in *Ailuravus*, and in the PE, prisms bend apically. **Fig. 8:** *Cocomys lingchaensis*, early Eocene, China; SEM print inverse. In *Cocomys*, the PE with steeply inclined prisms comprises nearly half of the enamel thickness.

Table III. Incisor Enamel Features in Some Early Tertiary Rodents

Taxon	Schmelzmuster	Prisms per HSB	Inclination of HSB (deg)	Enamel thickness ( $\mu\text{m}$ )	Percentage of PE thickness	PE prism inclination (deg)	IPM in PI
Ischyromyioidea							
<i>Atiluravus</i>	Pauciserial	2-4	0-5	60	25	0	Parallel
<i>Paramys</i>	Pauciserial	2-3	0	50	25	45	Parallel
Anomaluroidea							
Cf. Zegdomyidae	Transitional, pauci- to uniserial	1-3	0	50-65	30-50	45	Parallel
Cf. Anomaluridae	Transitional, pauci- to uniserial	1-3	0	60-65	25-40	50-60	Parallel
<i>Anomalurus</i>	Uniserial	1	15-25	90-120	35-40	65-70	Parallel
Ctenodactyloidea							
<i>Tsagamys</i>	Pauciserial	1-3	0	50	35	45	Parallel
<i>Euboromys</i>	Transitional, pauci- to multiserial	2-4	0-5	50-55	60	40-50	Slightly angular
Cf. <i>Tamquammys</i>	Multiserial	3-5	35-40	60-70	Lacks PE	---	Slightly angular
Phiomorpha							
Cf. Phiomorpha	Multiserial	3-5	45-50	100-165	20-25	60-70	Acute angular (20-45°)
Caviomorpha							
<i>Branisamys</i>	Multiserial	4-7	30-35	320-350	20	70	Acute angular (45°)
<i>Cephalomys</i>	Multiserial	3-5	50-55	125	20	75-80	Acute angular
<i>Incamys</i>	Multiserial	3-4	45	200	15	65-70	Acute angular (50°)
<i>Sallamys</i>	Multiserial	3-4	40	130	20	60-65	Acute angular
Cricetidae							
Sp. nov.	Uniserial	1	15-20	25-30	35-45	45-60	Parallel
?Mixodontia							
<i>Alagomys</i>	Pauciserial	1-3	45	20	Lacks PE	---	Parallel
<i>Orogomys</i>	Pauciserial	3-5	45	25	35	65	Parallel
<i>Rhombomylus</i>	Pauciserial	4-7	35	100-110	Lacks PE	---	Parallel





**Figs. 9–12.** SEM micrographs of longitudinal sections of anomaluroid incisor enamel. **Fig. 9:** Cf. Zegdoumyidae, Algeria (MA 77). The Schmelzmuster is pauciserial, with a tendency toward thinning of HSB. A well-developed PE with apically inclined prisms is present. **Fig. 10:** Cf. Zegdoumyidae, Tunisia (MA 21). This Schmelzmuster is transitional from pauci- to uniserial. **Fig. 11:** Cf. Anomaluridae, Algeria (MA 22). In this Schmelzmuster, transitional from pauciserial to uniserial, about 50% of the HSB are uniserial. **Fig. 12:** *Anomalurus* sp. indet.; SEM print inverse (MA 85). The extant *Anomalurus* has a fully developed uniserial Schmelzmuster retaining parallel IPM.

*Ctenodactyloidea (Figs. 13–16)*

The early to middle Eocene ctenodactyloid incisors from Mongolia reveal a transition from pauciserial to multiserial Schmelzmuster. The early Eocene *Tsagamys subitatus* has a typical pauciserial Schmelzmuster with a parallel-surrounding IPM in the PI. In the middle Eocene *Euboromys* a slightly angular IPM in the PI and single prism transitions from one HSB to the next higher indicate a change to the multiserial condition. The inclination of HSB is still weak, and prisms in the PE are moderately inclined. The Schmelzmuster of cf. *Tamquammys* is fully multiserial, with an acute angular IPM in the PI and transition zones between adjacent HSB.

*Phiomorpha (Figs. 3, 24, and 25)*

Among the isolated phiomorph incisors from Algeria, three size classes have been distinguished. They all have fully developed multiserial Schmelzmuster with an acute angular, anastomosing IPM in the PI. In the lower incisor of the smallest class the angle between prisms and the IPM is more than 45°, indicating a transitional stage to rectangular interrow sheets. In all incisors a clearly distinct PE is present.

*Caviomorpha (Figs. 26 and 27)*

All Deseadan caviomorphs studied have a fully developed multiserial Schmelzmuster with an acute angular IPM and a clearly distinct PE. The large incisors of *Branisamys luribayensis* have the thickest enamel and the widest HSB. Unlike the Neogene and Recent echimyids, *Sallamys pascuali* has not yet acquired a rectangular IPM in the PI.

*Cricetidae (Figs. 20 and 21)*

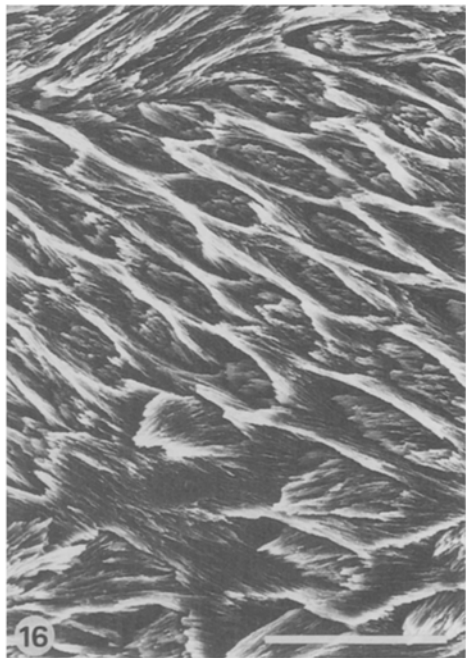
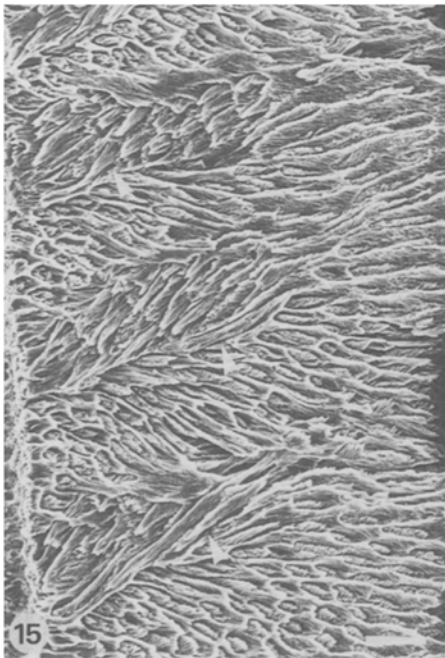
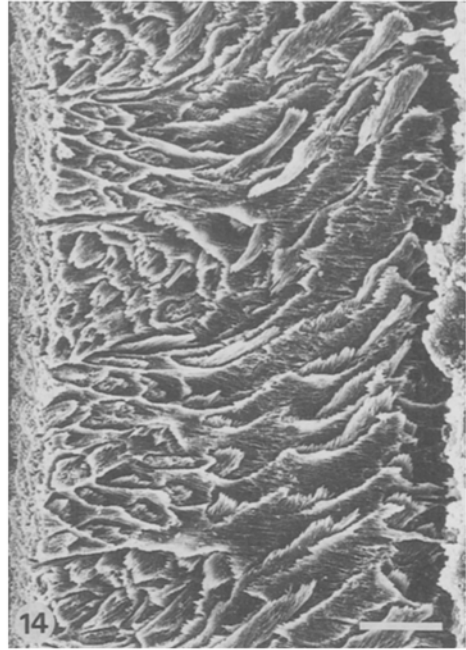
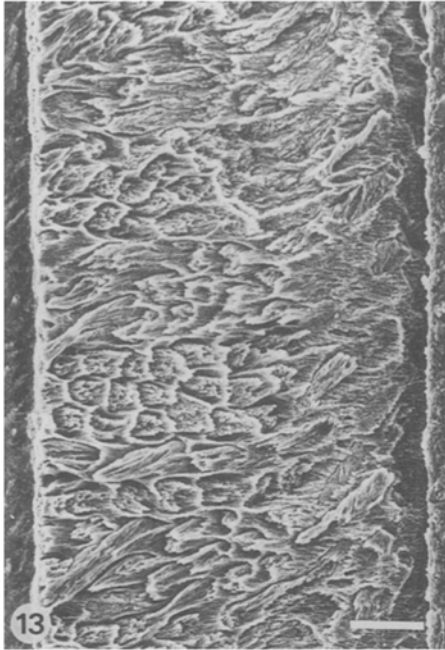
All three cricetid incisors from the middle Eocene of Mongolia have fully uniserial Schmelzmuster with a well-developed PLEX. The enamel is extremely thin and has a clearly distinct PE with strongly flattened prisms.

*?Mixodontia (Figs. 17–19)*

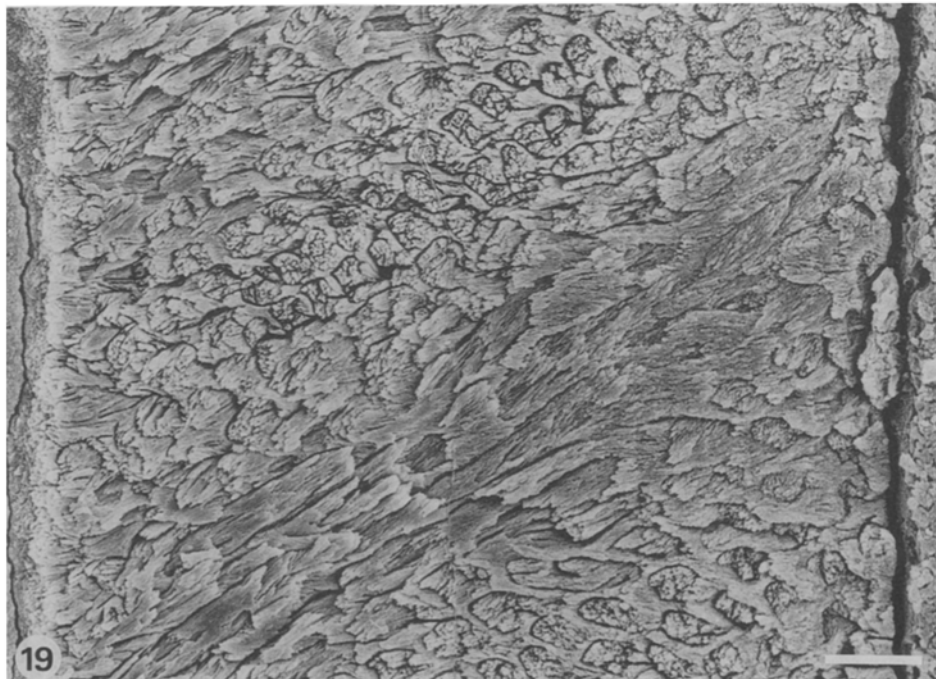
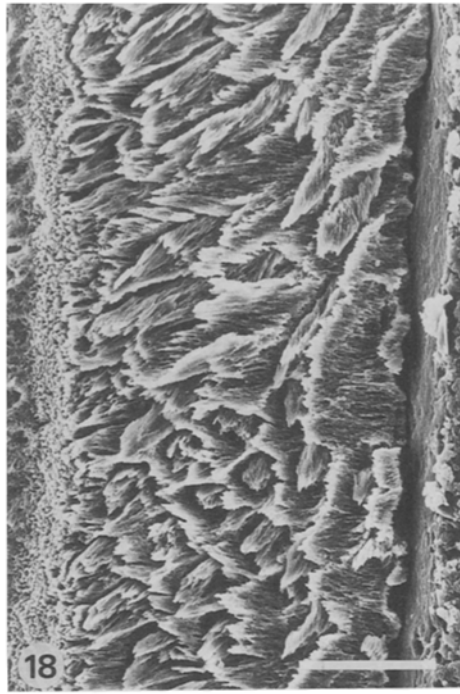
The Schmelzmuster of *Alagomys inopinatus* resembles very closely the pauciserial condition, but the enamel lacks a PE. The prisms are irregularly rounded and their diameter (3 µm) is scarcely reduced in comparison to that found in the enamel of other small mammals (3.5–5 µm); therefore, the proportions between prism diameter and enamel thickness appear to be somewhat displaced in this extremely thin enamel. The HSB are clearly pauciserial but comparatively steeply inclined.

The Schmelzmuster of *Orogomys* closely resembles the pauciserial condition. It is two-layered and slightly thicker than that of *Alagomys*. The HSB are very similar to those of *Alagomys* but are somewhat thicker. In the PI, prism cross sections are irregularly rounded and only scarcely flattened in the PE.

The Schmelzmuster of *Rhombomylus* is structurally clearly pauciserial but the HSB are somewhat thicker and steeper inclined than in the typical rodent pauciserial Schmelzmuster; a PE is lacking.



**Figs. 13–16.** SEM micrographs of longitudinal sections of ctenodactyloid incisor enamel. **Fig. 13:** *Tsagamys subitius*; SEM print inverse (MA 9). *Tsagamys* has a typical pauciserial Schmelzmuster like other early ctenodactyloids. **Fig. 14:** *Euboromys* sp. indet. (MA 6). In *Euboromys* the IPM begins to run angular to the prisms, a first step toward multiserial HSB. **Figs. 15 and 16:** Cf. *Tamquammys* (MA 5). **Fig. 15:** Cf. *Tamquammys* is the first rodent known with a fully acute angular, anastomosing IPM. Note the prism transitions between HSB (arrows). A PE is lacking. **Fig. 16:** The IPM anastomoses regularly, and the angle between prisms and the IPM is clearly visible. Prism cross sections are oval to lancet shaped.



**Figs. 17–19.** SEM micrographs of longitudinal sections of supposed mixodontian incisor enamel. **Fig. 17:** *Alagomys inopinatus*; SEM print inverse (MA 11). The incisor enamel of the tiny *Alagomys* is extremely thin. The pauciserial HSB are relatively steeply inclined and a PE is lacking, both characters which also characterize the mixodontian *Rhombomylus*. **Fig. 18:** *Orogomys* sp. indet. (MA 10). The enamel of *Orogomys* is only slightly thicker than that of *Alagomys*. As in *Alagomys* and *Rhombomylus*, the pauciserial HSB are unusually steeply inclined. **Fig. 19:** *Rhombomylus* sp. indet. *Rhombomylus* has pauciserial HSB which are somewhat thicker and more steeply inclined than those of the Rodentia.

## DISCUSSION

The pauciserial HSB in the incisor enamel of early Paleogene rodents structurally resemble the earliest known eutherian HSB, which occur in widely separated lineages, such as Paleocene arctocyonids (Koenigswald *et al.*, 1987) and late Paleocene/early Eocene mixodontians (Li and Ting, 1985; Koenigswald, 1988; Martin 1992b, in press). Pauciserial HSB in rodent incisors are thinner and less inclined than those found in mixodontians and early therians and can be derived from these by slight thinning. The more primitive, thicker pauciserial HSB apparently have been retained in early rodent molars.

Pauciserial HSB characterize the incisors of the oldest rodents known, belonging to different superfamilies, and occur on all continents where rodents were present during the early Paleogene (Europe, North America, Asia, and North Africa). This and the parallel IPM, which is less efficient in strengthening the enamel than the angular IPM of multiserial HSB, are good evidence that pauciserial HSB are primitive and a symplesiomorphic character for the Rodentia. From the pauciserial stage two lineages evolved, one leading to uniserial and the other to multiserial HSB (Martin, 1992a,b). Investigation of early rodent representatives from different continents makes it possible to reconstruct the early evolution of the rodent incisor Schmelzmuster.

### North America

Although North America is probably not the continent of rodent origin, up to now it has yielded the oldest known rodents. An incisor from the late Paleocene (Tiffanian) of Montana, referred to *Acritoparamys atavus*, shows typical pauciserial HSB (Martin, 1992b). The PE is not very distinct and appears somewhat unusual, because the prisms are oriented perpendicularly to the enamel–dentin junction (EDJ), with parallel IPM (see also Flynn *et al.*, 1987). Therefore, it is difficult to differentiate the prisms from the IPM.

Slightly younger Paleogene ischyromyids such as *Leptotomus*, *Thisbemys*, and *Knighthomys* also possess typical pauciserial HSB. Even *Protoptychus* (Protoptychidae) and members of Wood's (1985) supposedly incipiently hystricognathous "Frani-morpha," such as *Prolapsus* (?Sciuravidae), *Frani-mys*, and *Reithroparamys*, have clearly pauciserial HSB, with no tendency to the multiserial type (Martin, 1992b). The youngest rodent with pauciserial HSB hitherto known is the ischyromyid *Manitsha* sp. from the early Oligocene (Wahlert, 1968). All other Oligocene and younger North American rodents investigated so far show uniserial HSB (except Pleistocene caviomorph immigrants).

### Europe

Like their North American relatives, the European paramyids have pauciserial HSB. Flynn *et al.* (1987) investigated isolated incisors from the early Eocene locality Silveirinha (Portugal), where the oldest European rodents come from; they show typical pauciserial HSB with a well-developed PE. I found typical pauciserial HSB in early Eocene *Paramys* sp. indet. from Mancy in the Paris basin (Fig. 1) and *Ailuravus* sp. indet. from Premontré (Fig. 5 and 6). A pauciserial Schmelzmuster has also been detected in the middle Eocene *Masillamys* from Messel and early members of the Theridomyoidea (Martin, in preparation).

## Asia

The immense augmentation of early Paleogene rodents from Asia in the last two decades indicates that this continent is most probably the center of origin of the Rodentia (Dashzeveg *et al.*, 1987), even if no rodents older than early Eocene age have been found. The oldest Asian rodents are ctenodactyloids from Mongolia, such as *Cocomys*, *Euboromys*, and *Tsagamys* (Dashzeveg, 1990a). All exhibit pauciserial Schmelzmuster (*Cocomys*, *Tsagamys*) or a transitional stage from pauciserial to multiserial condition (*Euboromys*).

### Mixodontia

Most authors consider Mixodontia the sister group of Rodentia (e.g., Li, 1977; Hartenberger, 1977, 1980; Li and Ting, 1985) and therefore their incisor enamel microstructure is of particular interest. The HSB in the incisors of the upper Paleocene and Eocene mixodontians *Heomys*, *Eurymylus*, *Gomphos elkema*, *Zagmys insolitus*, and *Rhombomylus* structurally resemble those of the earliest Asian rodents, even if they are somewhat thicker. Flynn *et al.* (1987) observed, in a lower incisor of *Zagmys insolitus*, a HBS width of five to eight, frequently seven, prisms. Therefore the HSB of mixodontians are good predecessors for pauciserial HSB in rodent incisors.

In *Heomys* and *Eurymylus* a well-developed PE is present, while it is lacking in *Gomphos*, *Zagmys* (Flynn *et al.*, 1987), and *Rhombomylus* (Fig. 19).

### Alagomyidae and Orogomyidae

Dashzeveg (1990b) described two species of rodentlike small mammals from the early Eocene of the Naran-Bulak formation, *Alagomys inopinatus* and *Orogomys obscurus*, and put them in two new families, Alagomyidae and Orogomyidae. He positioned *Alagomys* and *Orogomys* "at the origin of the orders Rodentia and Mixodontia" but stated that their phylogenetic relationships remain unclear. The Schmelzmuster observed in the incisors of *Alagomys inopinatus* (Fig. 17) and *Orogomys* sp. indet. (Fig. 18) are somewhat unusual. Both resemble very closely the pauciserial condition, but the enamel of *Alagomys inopinatus* is extremely thin and lacks a PE. Because a two-layered Schmelzmuster has been detected in all Ctenodactyloidea investigated so far (except for cf. *Tamquammys*), it seems more likely that *Alagomys* is not a rodent, but a member of the Mixodontia.<sup>2</sup> The enamel of *Orogomys* is slightly thicker and has a distinct PE, being closer to *Cocomys* (Fig. 8) and early Ctenodactyloidea in this regard. However, the HSB are more steeply inclined and somewhat thicker than in the pauciserial Schmelzmuster of the Ctenodactyloidea. Therefore, *Orogomys* may also be a mixodontian rather than a rodent.

### Ctenodactyloidea

*Cocomys lingchaensis*, the most primitive ctenodactyloid rodent known, has a typical pauciserial Schmelzmuster (Fig. 8), rather than the "multiserial/pauciserial" type

<sup>2</sup>M. Dawson (personal communication, 1993) considers *Alagomys* to be a rodent, while P. Butler (personal communication, 1993) doubts this view due to the position of the zygomatic arch.

claimed by Li *et al.* (1989). This is indicated by the parallel surrounding IPM in the PI, lacking transition zones between adjacent HSB, the low inclination of HSB, and other features typical of pauciserial Schmelzmuster (Martin, 1992b).

Eocene Chapattimyidae are likewise characterized by pauciserial Schmelzmuster (Sahni, 1980; Martin, 1992b). A typical pauciserial Schmelzmuster with well-developed PE has been found in the early Eocene *Tsagamys subitus* (Fig. 13), referred to the Cocomyinae by Dashzeveg (1990a).

A transitional stage from pauciserial to multiserial has been detected in the incisors of *Euboromys* sp. indet. from the middle Eocene, referred to the Advenimurinae by Dashzeveg (1990a) [for nomenclatorial clarification, see Dashzeveg and McKenna (1991)], and the oldest fully developed multiserial Schmelzmuster has been found in an incisor (Figs. 15 and 16) from the middle Eocene of Khaychin Ula, Mongolia (Martin, in press), referred to the ctenodactyloid *Tamquammys* (Hartenberger, personal communication).

From the Oligocene onward the ctenodactylids have multiserial HSB, beginning with an acute angular IPM as in *Leptotataromys*. At least by the middle Miocene they had acquired a rectangular IPM (*Sayimys sivalensis*), which also characterizes the extant species (Martin, 1992b).

#### *Early Cricetids*

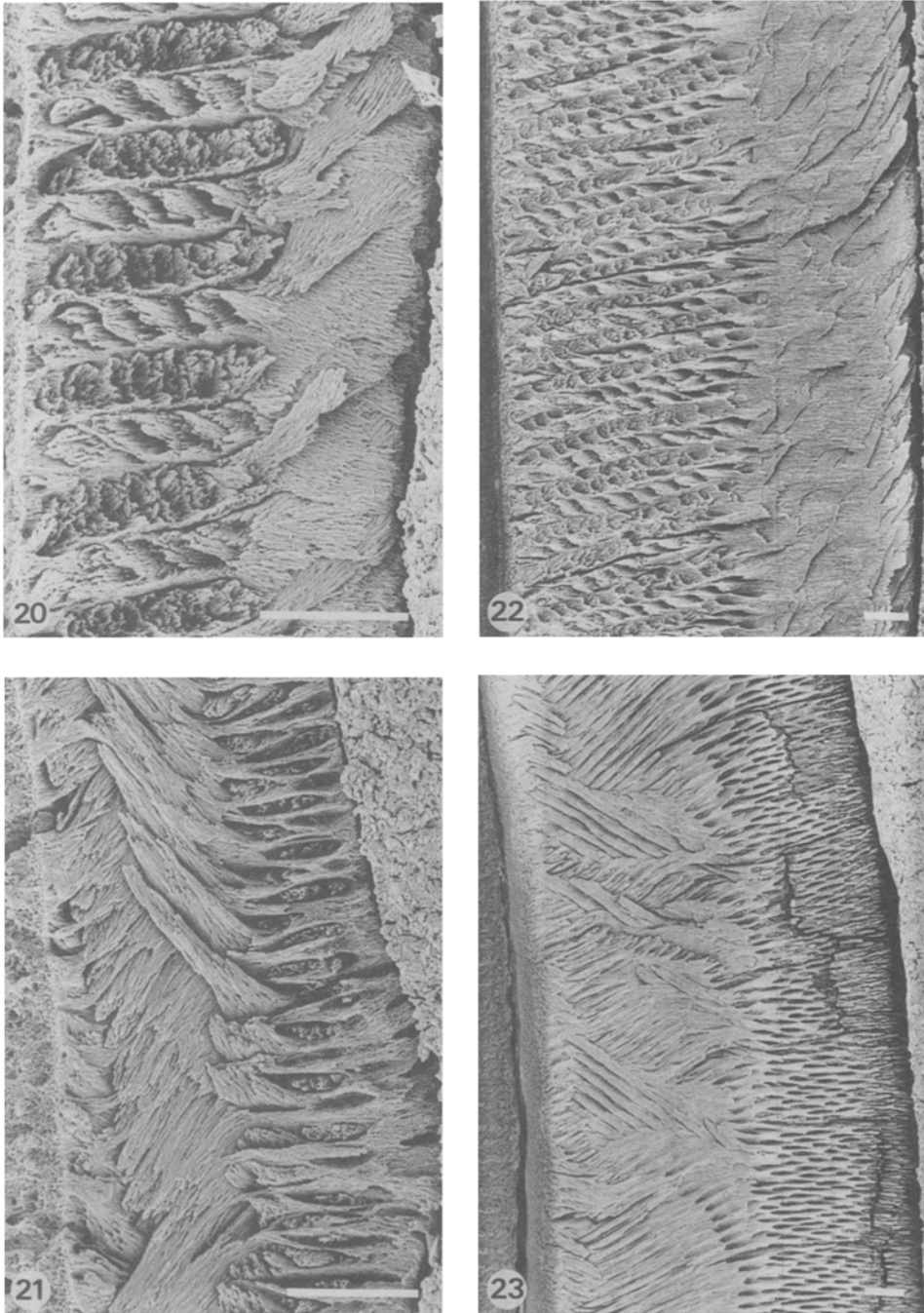
Apparently the evolution of uniserial HSB also took place much earlier than hitherto believed. In the incisors of three specimens of yet undescribed cricetids (PSS 41-50, 41-83, 41-85), belonging to at least two species (Hartenberger, personal communication) from the middle Eocene of Mongolia, fully developed uniserial HSB have been detected (Figs. 20 and 21). These are primitive, only slightly inclined uniserial HSB with a comparatively thin, parallel IPM. They can easily be derived from pauciserial HSB by thinning. This Eocene cricetid enamel structurally resembles that of later cricetids, e.g., *Eucricetodon atavus* from the early middle Oligocene (Figs. 22 and 23).

### North Africa

#### *Early Anomaluroids*

Except for the Fayum, the African Paleogene rodent record is sparse. However, at least two lineages can be distinguished in the Eocene. One, the anomaluroids, was present in Africa at least since the early Eocene (Vianey-Liaud *et al.*, 1993); the other, the phiomyids, was present since the late Eocene (Jaeger *et al.*, 1985). The oldest rodent remains of Africa are known from early to middle Eocene deposits of Glib Zegdou, Algeria (Gevin *et al.*, 1975), and the apparently slightly younger Chambi locality, Tunisia (Hartenberger *et al.*, 1985; Hartenberger, 1986; Vianey-Liaud *et al.*, in press).

The only rodent incisor (isolated) from Glib Zegdou, referable to the anomaluroid family Zegdoumyidae (Vianey-Liaud *et al.*, in press) because of associated molars, has pauciserial HSB with a strong tendency toward thinning of the bands (Fig. 9). An even more derived Schmelzmuster, transitional from pauci- to uniserial, has been detected in two isolated incisors from Chambi (Fig. 10), likewise referable to the Zegdoumyidae (Vianey-Liaud *et al.*, in press) because of molars found in the same locality.



**Figs. 20–23.** SEM prints of cricetid incisor enamel: Figs. 20 and 22, longitudinal sections (SEM prints inverse); Figs. 21 and 23, cross sections. **Figs. 20 and 21:** Cricetidae indet., middle Eocene (MA 13), lower incisor. This earliest known cricetid already has a fully developed uniserial Schmelzmuster with parallel IPM. **Figs. 22 and 23:** *Eucricetodon atavus* (MA 37), lower incisor. The Schmelzmuster of *Eucricetodon* closely resembles that of the middle Eocene cricetid from Mongolia, but the enamel layer is more than three times thicker.



From the late Eocene locality Bir el Ater in Algeria, two groups of rodents (anomalurids and phiomorphs) have been described from isolated molars (Jaeger *et al.*, 1985). Two groups of isolated rodent incisors from this locality can also be distinguished by their gross morphology. According to molar size, the largest incisor fragments can be attributed to the anomalurids. In these incisors a Schmelzmuster with pauciserial to primitive uniserial HSB is detected (Fig. 11). Due to the occurrence of many uniserial HSB, in addition to two- and three-layered HSB, this enamel type is transitional between pauciserial and uniserial. In a second, probably lower, incisor the HSB are one to two prisms thick, with the uniserial condition predominant, indicating that this enamel is more derived.

### *Phiomorpha*

The oldest known African phiomorphs are from the late Eocene of Bir el Ater represented by isolated molars and incisors (Coiffait *et al.*, 1984). Jaeger *et al.* (1985) described *Protophiomys algeriensis* from these isolated molars and indicated the presence of several other new phiomorph species. Among the isolated incisors (clearly distinct from the anomalurid incisors), at least three size classes (uppers and lowers) can be distinguished. All have fully developed multiserial Schmelzmuster with acute angular, anastomosing IPM (Fig. 3, 24, and 25).

The next younger multiserial HSB have been detected in the incisors of late Eocene/early Oligocene phiomorphs from the Fayum, most of them closely resembling those from Bir el Ater. In *Metaphiomys* a fully developed rectangular IPM forming interrow sheets is present (Martin, 1990a,b, 1992a,b). Multiserial HSB with rectangular IPM also characterize the two extant phiomorph species (*Thryonomys swinderianus* and *Petromys typicus*).

Pleistocene and Recent Hystricidae have multiserial Schmelzmuster with parallel to acute angular IPM in the PI and steeply inclined prisms in the PE. Bathyergidae are characterized by multiserial Schmelzmuster with a rectangular IPM in the PI. In the PE, prisms run horizontally (inclination, 0°), apparently a synapomorphy in the Hystriconathi.

### South America

Until the latest Pliocene, when the first cricetids arrived via the emerging Panama land bridge in South America (Reig, 1978), caviomorphs were the only rodents in that continent. They first appear in deposits of Deseadan age (late Oligocene) in Patagonia and Bolivia (Wood, 1949; Hoffstetter and Lavocat, 1970; Lavocat, 1976; Patterson and Wood, 1982). Flynn *et al.* (1991) recently reported a single rodent specimen from a newly discovered rich mammal fauna in the Chilean Andes (Wyss *et al.*, 1990) without specifying it. This fauna is considered to be of early Oligocene age and the rodent remains direct evidence that the caviomorphs were present before the Deseadan in South America. There are two contrasting hypotheses for the origin of caviomorphs. Wood (e.g., 1981, 1985) considers Middle American ischyromyoids ("Framimorpha") as ancestral to Caviomorpha. On the other hand, Lavocat (e.g., 1969, 1971, 1981) and Hoffstetter (1971, 1972; also Hoffstetter and Lavocat, 1970) consider Paleogene African Thryonomyoidea as ancestors of Caviomorpha, a view which is supported by many shared

derived characters. The derived multiserial Schmelzmuster found in the incisors of early Oligocene Thryonomyoidea and Deseadan Caviomorpha strongly supports the latter hypothesis (Martin, 1990a,b, 1992b).

All Deseadan caviomorph species investigated have fully developed multiserial Schmelzmuster with acute angular and even rectangular IPM (*Platypittamys brachyodon*), showing the same derived characters as the North African phiomorphs (Martin, 1990a,b, 1992b). This was confirmed by study of the enamel of *Branisamys luribayensis* (Fig. 26) and additional specimens of *Sallamys pascuali*, *Incamys bolivianus* (Fig. 27), and *Cephalomys pascuali* from Bolivia.

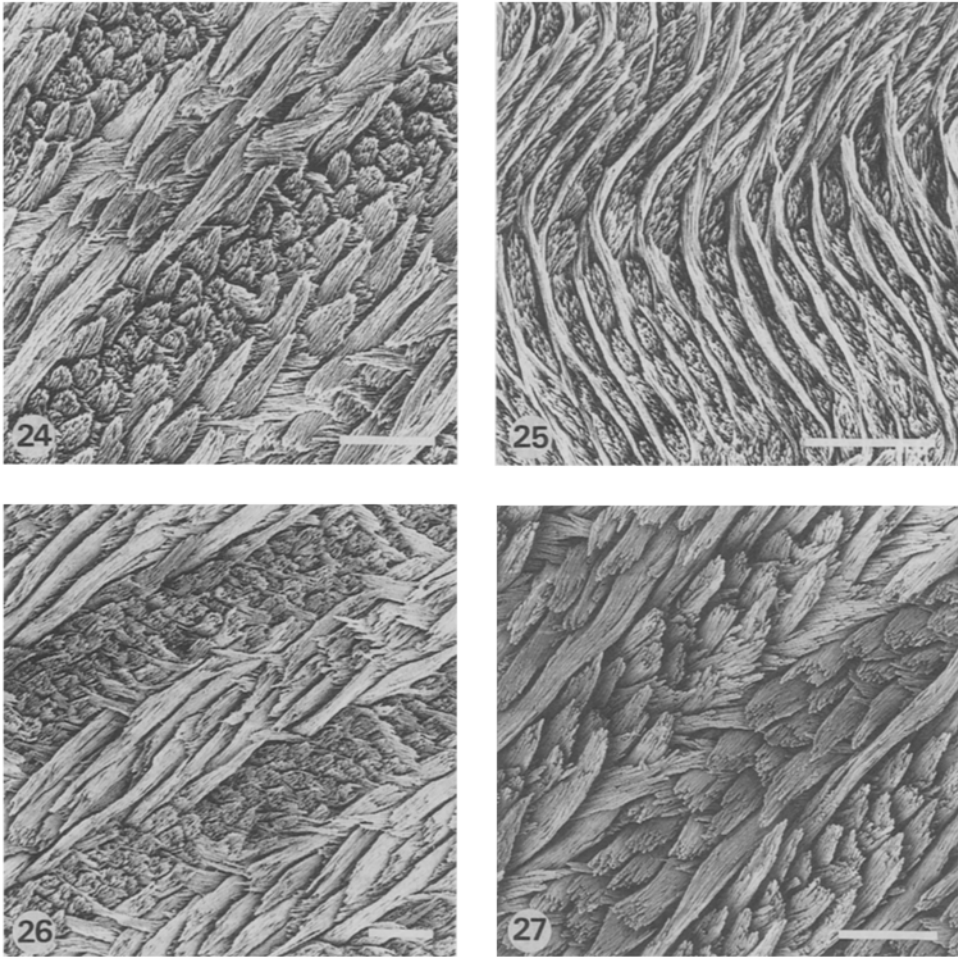
A pauciserial Schmelzmuster has never been detected in a Paleogene South American rodent. The derived multiserial Schmelzmuster of Deseadan caviomorphs indicates that these cannot belong to the initial rodent radiation and that their immediate ancestors must have been relatively derived when they arrived in South America. Until the late Pliocene, when the first cricetids with uniserial HSB appeared, only rodents with multiserial Schmelzmuster in their incisors were present in South America.

### Transition from Pauciserial to Multiserial Schmelzmuster

It has been suggested by several authors that the pauciserial Schmelzmuster is the predecessor of the multiserial type (Wahlert, 1968; Sahni, 1980, 1985, 1989; Flynn *et al.*, 1987), but transitional stages to support this hypothesis have not been found (Flynn *et al.*, 1987). A Schmelzmuster transitional from pauciserial to multiserial has been demonstrated here for the first time in the incisor enamel of the middle Eocene ctenodactyloid *Euboromys* sp. indet. (Fig. 14). This is direct evidence for the derived status of multiserial HSB, because the early Eocene ctenodactyloids (e.g., *Cocomys* and *Tsagamys*) have pauciserial Schmelzmuster. The occurrence of multiserial HSB in the middle Eocene (cf. *Tamquammys*; Figs. 15 and 16) is much earlier than known previously (early Oligocene phiomorphs) and indicates that enamel structure diversification took place very early during rodent evolution. The next younger multiserial Schmelzmuster are those of late Eocene phiomorphs (cf. *Protophiomys algeriensis*) from Algeria, and all post-Eocene Ctenodactylidae and Hystricognathi are characterized by multiserial Schmelzmuster.

Pauciserial HSB can be derived easily from primitive mammalian HSB by thinning, which might have been a first step to improve inhibition of crack propagation. This suggests that pauciserial HSB are primitive and a common heritage of the earliest Rodentia.

The derived status of multiserial HSB is evident not only from their later stratigraphic occurrence, but also from biomechanical considerations. The most important derived characters of multiserial HSB are the angular IPM (Martin, 1992b) and the transition zones (Wahlert, 1984), where prisms bend from one HSB to the next higher. Both characters can be interpreted as adaptations to strengthen the enamel and to prevent crack propagation. An IPM running at an angle differing from the prisms, 90° in the extreme, strengthens the enamel in the third dimension. The bending of prisms from one band to the next higher likewise improves the strength of the enamel. Koenigswald (1980, 1985), without discussing IPM orientation, considered multiserial HSB primitive because they are often slightly thicker than pauciserial HSB and therefore should be less efficient for the prevention of crack propagation. However, he now agrees with the character polarity



Figs. 24–27. SEM prints of multiserial HSB of phiomorph and caviomorph lower incisors; Figs. 24, 26, and 27, longitudinal sections; Fig. 25, cross section. **Figs. 24 and 25:** Phiomysidae gen. et sp. indet., Algeria (MA 24). The multiserial HSB of the earliest known phiomysids closely resemble those of the caviomorphs from the Deseadan. **Fig. 26:** *Branisamys luribayensis*, Deseadan (MA 78). This largest known early caviomorph has relatively thin multiserial HSB with an acute angular IPM. **Fig. 27:** *Incamys bolivianus*, Deseadan; SEM print inverse (MA 80). The HSB of *Incamys* are almost identical to those of the Algerian phiomorph in Fig. 24.

indicated by the stratigraphical occurrence, after the important functional role of IPM orientation and transition zones for the strengthening of the enamel became clear (Koenigswald and Clemens, 1992).

#### Transition from Pauciserial to Uniserial Schmelzmuster

Uniserial HSB can be derived easily from pauciserial HSB by thinning and apparently evolved several times convergently in North American/European rodents. The primitive transverse uniserial HSB with parallel IPM later were modified in most groups,

by a rectangular IPM in myomorphs or a vertical orientation of HSB in eomyids (Wahlert and Koenigswald, 1985) and certain gliroids (Koenigswald, 1993), for example.

Hitherto the oldest uniserial HSB were known from late Eocene to middle Oligocene Theridomyidae (*Nesokerodon minor* and *Sciurormys typicus*) and early Oligocene Ischyromyidae (*Titanotheriomys veterior*) and Cylindrodontidae (*Cylindrodont fontis*) (Korvenkontio, 1934). Now the range of uniserial HSB can be extended to the middle Eocene and, with transitional stages, possibly to the early Eocene. The supposed anomaluroid incisors from the North African localities Glib Zegdou and Chambi have Schmelzmuster with HSB transitional from pauciserial to uniserial. From the HSB thickness the Glib Zegdou incisor is closer to the pauciserial status, while those of Chambi resemble more the uniserial type. If the dating from composition of the mammal fauna of these localities is correct (Sudre, 1979; Hartenberger *et al.*, 1985; Hartenberger, 1986), the transition from pauciserial to uniserial HSB took place in anomalurids during the first half of the Eocene.

On the other hand, the middle Eocene cricetids from Mongolia with fully developed uniserial HSB indicate that uniserial HSB evolved at least two times independently in the early/middle Eocene. This early cricetid enamel can be distinguished from that of the anomalurids by its extreme thinness and the strongly flattened prisms in the PE. Other rodent taxa in which a change from pauciserial to uniserial has been reported are Ischyromyidae (Korvenkontio, 1934) and Theridomyoidea (Martin, in preparation).

#### Ancestry of a One- or Two-Layered Schmelzmuster

Flynn *et al.* (1987) discussed the question of whether a one- or two-layered Schmelzmuster was primitive for the Rodentia. They reported a one-layered Schmelzmuster for the mixodontians *Zagmys insolitus*, *Rhombomylus*, and *Gomphos elkema*, whereas *Mimolagus rodens*, *Heomys orientalis*, and *Eurymylus* have a two-layered Schmelzmuster. Except for cf. *Tamquammys* (Fig. 15) all studied early Asian ctenodactyloids have two-layered Schmelzmuster, whereas there exists some variation among the oldest North American ischyromyoids. Flynn *et al.* (1987) found, in two specimens referred to *Acritoparamys atavus*, a one-layered Schmelzmuster, while another of the same species had a two-layered Schmelzmuster. One specimen referred to *Acritoparamys atwateri* had a two-layered Schmelzmuster with slightly inclined prisms and nearly parallel IPM in the PE. A specimen referred to *Acritoparamys atavus* from the Tiffanian of Montana has a two-layered Schmelzmuster with horizontal prisms in the PE (Martin, 1992b).

Radial enamel is the primitive condition for mammalian Schmelzmuster (Koenigswald *et al.*, 1987). Koenigswald (1985) presented a model for the development of HSB in the inner part of radial enamel in primitive mammals. Therefore, he argued that a two-layered Schmelzmuster is primitive for Rodentia. This view was doubted by Flynn *et al.* (1987), but they did not make a decision. The crucial question is whether the radial enamel of the PE in Rodentia is homologous to the primitive radial enamel of early mammals or whether it has been added after HSB were established. The presence of an outer layer of radial enamel in the earliest eurymylids *Eurymylus* and *Heomys* suggests that the PE with radial enamel of the early Ctenodactyloidea is indeed a primitive feature in the Rodentia. Under this assumption a reduction of the PE in cf. *Tamquammys*, the only known ctenodactyloid without PE, and some ischyromyoids must be postulated.

### Interrelationships of Rodents with Multiserial Schmelzmuster

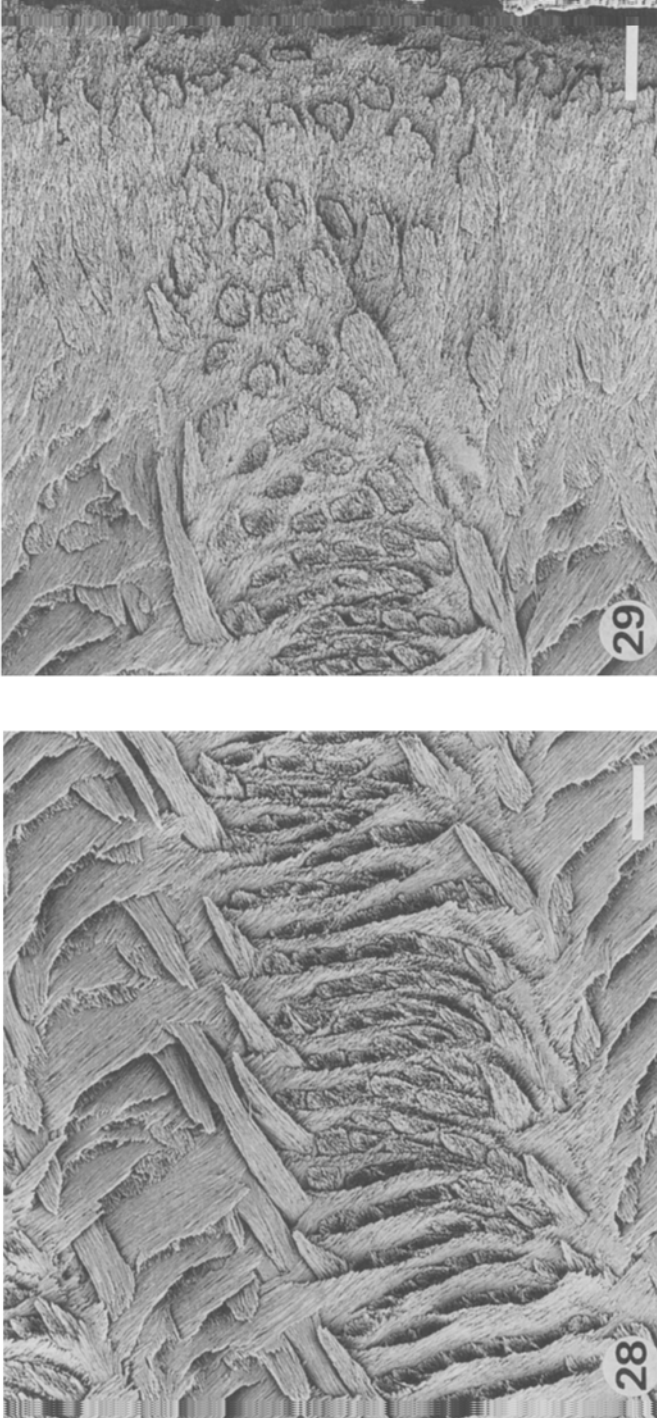
The pauciserial Schmelzmuster is a symplesiomorphy of Rodentia characterizing the basal ctenodactylids (e.g., *Cocomys*, Eocene chapattimyids) and ischyromyoids (e.g., *Acritoparamys* and other paramyids). The multiserial Schmelzmuster is derived and can be used for assessing phylogenetic questions, if a careful character analysis is provided. This is true despite the occurrence of convergence and parallelism, which are common in enamel evolution (Koenigswald and Pascual, 1990).

A multiserial Schmelzmuster is restricted to the Hystricognathi [Thryonomyoidea (incl. Bathyergoidea), Hystricidae, and Caviomorpha], Ctenodactylidae (beginning with *Euboromys* and cf. *Tamquammys*), and *Pedetes* (Schmelzmuster is unknown in fossil pedetids) and separates these from the extant Sciuomorpha and Myomorpha, which have uniserial Schmelzmuster. This confirms the hypothesis of a basal divergence of the Rodentia (Hartenberger, 1980; Luckett and Hartenberger, 1985) represented by *Acritoparamys* and *Cocomys*. In the lineage evolving from *Cocomys*, giving origin to the Hystricognathi, a multiserial Schmelzmuster was evolved at least since the middle Eocene. In the other lineage, evolving from *Acritoparamys*, a uniserial Schmelzmuster apparently was developed several times independently (Fig. 30).

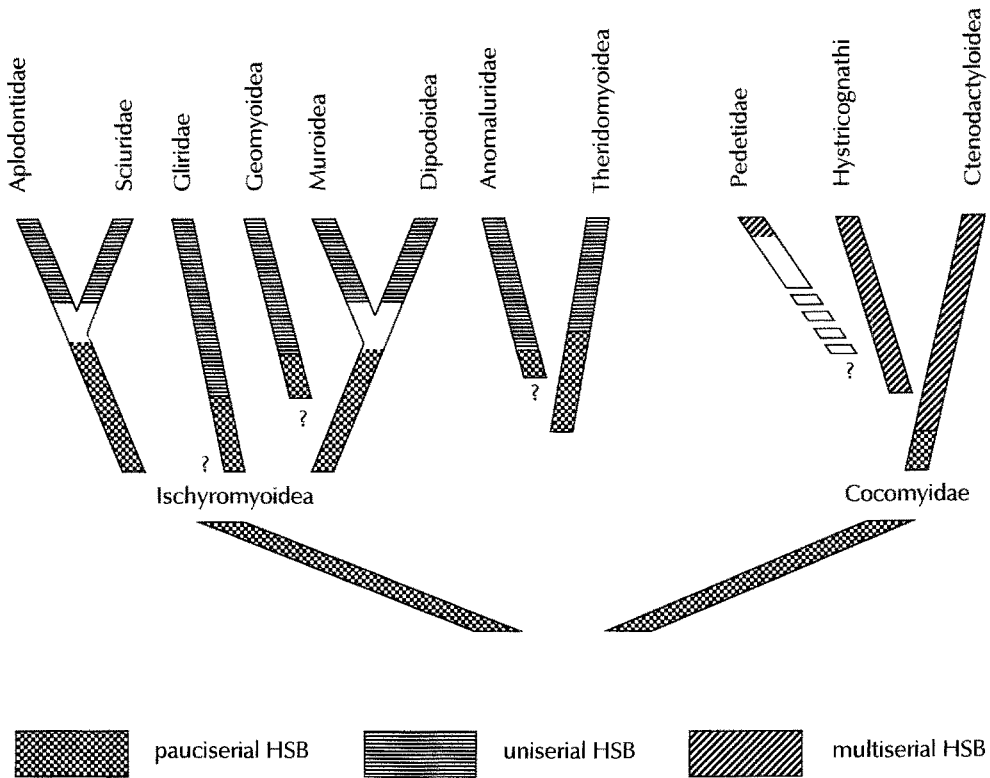
The multiserial Schmelzmuster is a synapomorphy of the Hystricognathi, Ctenodactylidae (sensu Dawson *et al.*, 1984), Baluchimyinae, and *Pedetes*; despite the increasing number of rodent species studied, it has never been detected outside this group. With rare exceptions where the PE is reduced (cf. *Tamquammys*, *Heterocephalus jaegeri*), the multiserial Schmelzmuster of rodents consists of a PI with HSB and a PE with radial enamel. This typical arrangement of enamel types distinguishes the multiserial rodent Schmelzmuster from convergent structures in other therians. In the rodent-like incisors of the Malagasy primate *Daubentonia madagascariensis* for example, multiserial HSB with interrow sheets occur (Figs. 28 and 29). These multiserial HSB are thicker [seven to nine prisms per band (Koenigswald, 1988; own observations)] than in rodent incisors with interrow sheets in the HSB. The most striking difference to the rodent Schmelzmuster is the outer layer in the *Daubentonia* Schmelzmuster, which has been interpreted as radial enamel (Koenigswald, 1988). However, in the lower incisor studied here, this outer layer is formed by HSB with parallel IPM (Fig. 29). In HSB of multiserial rodent Schmelzmuster, such a turn of the IPM from rectangular to parallel has never been observed.

The multiserial Schmelzmuster in the incisors of vombatid marsupials and the artiodactyl *Myotragus* (Koenigswald, 1985) can be distinguished from the rodent Schmelzmuster by the thicker HSB (six to nine prisms per band in *Myotragus*) and the inner layer of radial enamel at the EDJ [25% in vombatid marsupials and 10–15% in *Myotragus* (Koenigswald, 1985)].

The multiserial Schmelzmuster of ctenodactylids and hystricognaths corresponds in width and inclination of HSB, orientation of IPM, total enamel thickness (teeth of the same size), and ratio of PI and PE, which makes a synapomorphic condition very probable. This provides strong support for the hypothesis of a common ancestry of ctenodactylids and hystricognaths (Fig. 30), as proposed in a working hypothesis by Luckett and Hartenberger (1985); this is also consistent with George's (1985) analysis of reproductive features in rodents and the findings of Beintema *et al.* (1991) from their tandemly combined  $\alpha$ - and  $\beta$ -hemoglobin sequences. Apparently, the multiserial Schmelzmuster



**Figs. 28 and 29.** Inverse SEM prints of lower incisor enamel, longitudinal section, of the primate *Daubentonia madagascariensis*. Recent, coll. Institut des Sciences de l'Évolution, Montpellier (MA 82). **Fig. 28:** In the PL, the HSB of *Daubentonia* resemble those of rodents with rectangular IPM. **Fig. 29:** The PE reveals the convergence; in *Daubentonia*, the PE is formed by HSB with parallel, surrounding IPM, which has never been observed in Rodentia in this combination.

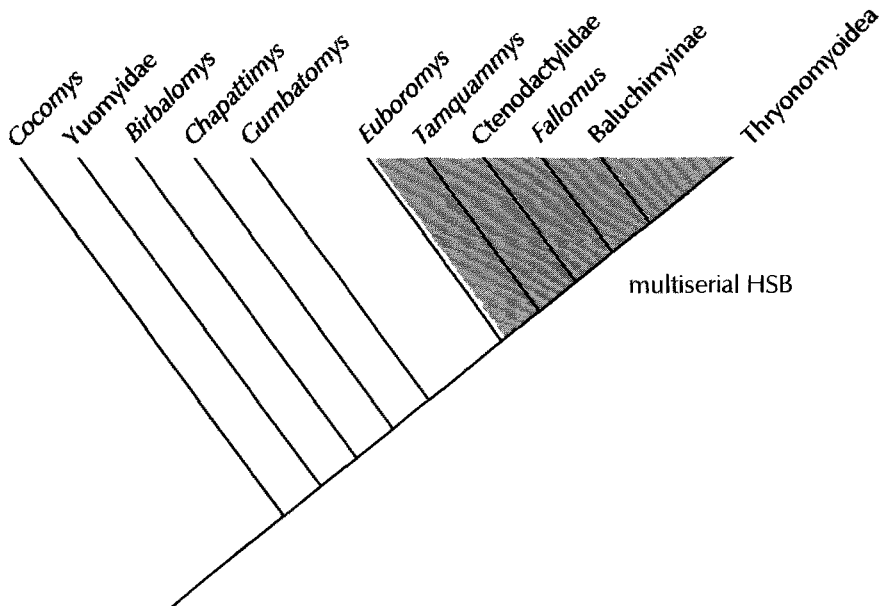


**Fig. 30.** Incisor Schmelzmuster distribution projected on the phylogenetic diagram presented by Lockett and Hartenberger (1985). The distribution of uniserial and multiserial HSB confirms the hypothesis of a basal dichotomy of the Rodentia. From the ischyromyoid group, rodents with pauci- to uniserial HSB evolved. Starting from the cocomyids, in the ctenodactyloid lineage (cf. *Tamquammys*) multiserial HSB were developed. Anomaluridae and Theridomyoidea are not closely related to Hystricognathi and Ctenodactyloidea, because they have pauci- to uniserial Schmelzmuster.

was evolved before the ctenodactylid–hystricognath dichotomy, because it is detected in the middle Eocene ctenodactyloids *Euboromys* and cf. *Tamquammys*. Before the enamel structure of these early ctenodactyloids was known, an independent origin of multiserial Schmelzmuster in the Ctenodactylidae was assumed (Martin, 1992b). Rectangular IPM forming interrow sheets apparently was developed independently in the ctenodactyloids (Baluchimyinae, Ctenodactylidae) and Hystricognathi (Phiomorpha, Cavimorpha), because it is present in the phiomorphs since the early Oligocene but not known before the Miocene in the relatively well studied ctenodactyloids.

On the other hand, hystricomorphy and multiserial incisor enamel are not correlated, as can be seen in the hystricomorphous anomalurids, which have uniserial Schmelzmuster. Hystricomorphy occurs in several rodent lineages that are not closely related and therefore has less phylogenetic value.

Flynn *et al.* (1986) presented a cladogram of relationships of ctenodactyloids, discussing three possible phylogenetic positions of the Thryonomyoidea. The validity or



**Fig. 31.** Modified version of the diagram of ctenodactyloid relationships given by Flynn *et al.* (1986), with revised position of the Ctenodactylidae and Thryonomyoidea. Using incisor enamel microstructure as a strong character, Ctenodactylidae and Thryonomyoidea must be placed in the monophyletic group with multiserial Schmelzmuster (shaded triangle), and cannot be put in the sister-group position of Ctenodactyloidea resp. Chapattimyidae as proposed by Flynn *et al.* (1986). Positions of other families and genera from the diagram of Flynn *et al.* (1986) were not reconsidered critically. *Euboromys* is just at the transition from pauciserial to multiserial HSB, while in *Tamquammys* fully multiserial HSB are present.

weight of their derived dental characters is difficult to evaluate. Using the multiserial Schmelzmuster as a strong argument, the Thryonomyoidea (and other Hystricognathi) should be placed (at present knowledge) after the branching of *Euboromys*, when a multiserial Schmelzmuster has been developed. A sister group position of the Thryonomyoidea to the Baluchimyinae makes the Ctenodactyloidea and Chapattimyidae paraphyletic groups (Fig. 31). The paraphyletic nature of the Chapattimyidae is also supported by the distribution of the multiserial Schmelzmuster among the Ctenodactyloidea, where it occurs in the Ctenodactylidae and Chapattimyidae (Baluchimyinae). In the cladogram of ctenodactyloid relationships presented by Flynn *et al.* (1986), multiserial enamel is used as synapomorphy of the Baluchimyinae, but not indicated for the Ctenodactylidae, which are placed as a sister group of the taxon formed by Yuomyidae and Chapattimyidae (including Baluchimyinae). Using the multiserial Schmelzmuster as synapomorphy, the Baluchimyinae should be placed close to the Ctenodactylidae. The chapattimyids with pauciserial Schmelzmuster may be regarded as stem-group representatives of the Ctenodactylidae as proposed by Hartenberger (1982).

### Anomaluroid Relationships

Vianey-Liaud *et al.* (in press) discuss the ancestry of the anomaluroids and the early history of rodent evolution in Africa. Based on molar morphology, the Zegdomyidae



is considered to be the ancestral stock of the Anomaluridae, first represented by isolated molars in the late Eocene of Bir el Ater (Jaeger *et al.*, 1985). Zegdomyidae is believed to be derived from Ischyromyidae and is considered as the sister group of North American Sciuravidae and European Gliridae. A close relationship to the Chapattimyidae has been excluded due to loss of the hypoconulid and other dental characters. Hartenberger (1990), after an analysis of 17 dentocranial characters, considered the Anomaluridae and Theridomyidae as possible sister groups with closer relationships to the Phiomyidae. However, Vianey-Liaud *et al.* (in press) noted that 5 characters among the 17 used for that analysis are unknown for Anomaluridae and Phiomyidae.

The pauci- to uniserial Schmelzmuster of the incisors referred to the Zegdomyidae and Anomaluridae excludes a close relationship of anomalurids and phiomyids, because phiomyids are characterized by a derived multiserial Schmelzmuster. The transitional Schmelzmuster from pauciserial to uniserial of the Zegdomyidae indicates another evolutionary lineage leading to the uniserial HSB with parallel IPM in the extant *Anomalurus*. Likewise, the Chapattimyidae can be excluded from a direct anomalurid ancestry, because their pauciserial HSB are transformed to multiserial in middle Eocene ctenodactylids (Fig. 30).

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