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Specialized Enamel in Incisors of Eomyid Rodents

JOHN H. WAHLERT[1] AND WIGHART VON KOENIGSWALD[2]

ABSTRACT

The three-layered Schmelzmuster in lower incisors of eomyid rodents is described. It shows that even the specialized uniserial enamel in rodents can be further modified. The *portio interna* in eomyids is divided into two parts, and the Hunter-Schreger bands are longitudinal rather than transverse as is common in rodents. The inner part of the *portio interna* shows a type of uniserial enamel found in myomorphs in which all three axes are strengthened by fibers. The outer part resembles uniserial bands in sciurids, because crystallites of interprismatic matrix are parallel to the prisms. This complex Schmelzmuster and a longitudinal thickening of the enamel near the lateral side of the incisor are unique, derived characters of the Eomyidae.

ZUSAMMENFASSUNG

Für die unteren Schneidezähne der Eomyiden wird ein dreischichtiges Schmelzmuster beschrieben, das zeigt, dass sogar der spezialisierte uniseriale Schmelz der Nager eine weitere Modifizierung erfahren kann. Die *Portio interna* ist bei den Eomyiden zweigeteilt und die Hunter-Schreger-Bänder stehen longitudinal statt transvers wie es bei den Nagern allgemein üblich ist. Der innere Teil der *Portio interna* zeigt den myomorphen Typ des uniserialen Schmelzes, in den alle drei Raumrichtungen durch Fasern versteift sind. Der äussere Teil ähnelt hingegen dem uniserialen Schmelz, wie er von den Sciuriden bekannt ist. Hier liegen die Kristallite der interprismatischen Matrix parallel zu den Prismen. Das komplexe Schmelzmuster sowie der laterale Längswulst im Schmelz sind autapomorphe Merkmale, die die Eomyiden charakterisieren.

[1] Research Associate, Department of Vertebrate Paleontology, American Museum of Natural History; Assistant Professor of Biology, Department of Natural Sciences, Baruch College, CUNY.

[2] Curator of Paleontology, Abteilung für Geologie, Paläontologie und Mineralogie, Hessisches Landesmuseum, Darmstadt, Federal Republic of Germany.

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INTRODUCTION

Eomyids are small, extinct rodents that are distributed stratigraphically from middle Eocene through Pliocene in both North America and Eurasia. Fahlbusch (1979) described a close relationship between the two groups that involves multiple intercontinental exchanges. In the course of studies on enamel one of us (J.H.W.) discovered unusual structures within the enamel of lower incisors, which we describe here from North American and European specimens.

Knowledge of enamel structure is related to the development of technical equipment. As early as 1850 Tomes published descriptions and illustrations of rodent and lagomorph incisor enamels. He showed that rodents have two layers of enamel in contrast to lagomorphs, which have but a single layer. Korvenkontio (1934) called the two layers the *portio interna* and *portio externa.* The *portio interna* of rodent incisors appears banded, and the bands are formed by zones of enamel prisms with different orientations. Tomes observed two basic kinds of enamel bands in living rodents and within these kinds certain variants that form subclasses. Subsequent to this discovery, incisor enamel microstructure has been included in phylogenetic studies of the Rodentia. Korvenkontio (1934) extended the investigation to other living taxa and included many fossil forms. He named the two kinds of enamel bands in living rodents multiserial and uniserial enamels, and he described a third arrangement, pauciserial, which he found in certain extinct rodents. Wahlert (1968) summarized the data on incisor enamel histology based on light microscopy. Multiserial enamel, for example, occurs in all hystricognathous rodents; uniserial in sciurids, castorids, and myomorphs; and pauciserial in extinct protrogomorphous rodents, notably the paramyids, sciuravids, and pseudosciurids. The high resolution of the scanning electron microscope makes individual structural elements of the enamel visible and allows three-dimensional reconstruction of their orientations. It is not the aim of this paper to describe a curiosity in eomyids but to show that a highly specialized structure, such as the uniserial Hunter-Schreger bands of certain rodents, may undergo further evolution.

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TECHNICAL TERMS

We use the customary vocabulary to describe the several levels of organization of enamel structure (Koenigswald, 1980, 1982). The levels include individual elements of structure, the arrangement of these elements into enamel types, and the Schmelzmuster, which is the combination of enamel types.

Individual elements. Hydroxyapatite crystallites are arranged in two ways. Enamel prisms (=enamel rods) are bundles of crystallites that extend from the enamel-dentine junction to the outer surface of the tooth. Interprismatic matrix consists of crystallites that are oriented in parallel; when these crystallites are at an angle to the prisms, the matrix is easily distinguished.

Enamel types. Prisms, arranged in parallel or with their orientations varying in a periodic fashion, form homogeneous structural units that constitute the enamel types. Two types, radial and banded enamel, occur in rodent incisors. Radial enamel, the most primitive type in mammals, is characterized by parallel prisms that rise apically from the enamel-dentine junction toward the surface of the tooth. Banded enamel, the second type, is found in most mammalian orders. The Hunter-Schreger bands are usually transverse layers of prisms that have similar orientation; since the prisms in adjacent bands decussate, the bands appear light and dark in alternation under the light microscope. Prisms are labeled in the figures in each of two adjacent Hunter-Schreger bands. The intersection of Hunter-Schreger bands with the plane of section produces band profiles. In rodent incisors the thickness of bands is usually greatest in multiserial enamel (4 or more prisms wide), intermediate in pauciserial (2 to 4), and least in uniserial (1 to 2). Only the uniserial type of Hunter-Schreger bands is relevant in this study.

Schmelzmuster. Enamel is usually a composite of enamel types, termed Schmelzmuster. Since each enamel type has specific biomechanical properties, the combinations may reflect stress patterns (Koenigswald, 1980, 1982). The *portio externa* in rodent incisors is formed by radial enamel; the *portio interna* of multiserial, pauciserial, or uniserial enamel. In myomorph rodents the enamel of the *portio interna* is uniserial.

Planes of section. There are three chief planes of section (fig. 1). A longitudinal (=sagittal) section is perpendicular to the enamel-dentine junction and parallel to the long axis of the tooth; it usually cuts an incisor segment through its greatest depth and exposes the enamel from apical to basal ends. The tangential (=frontal) section is tangent to the enamel-dentine junction, usually at the anteriormost part of its curvature; it exposes all depths in the enamel. The cross (=transverse) section cuts through the incisor from labial to lingual sides; it exposes the arch of enamel from mesial to lateral sides of the incisor.

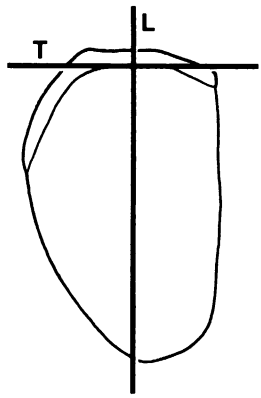


FIG. 1. Planes of section of a rodent incisor. The cross section in the plane of the page is intersected at right angles by the planes of longitudinal (L) and tangential (T) sections.

SPECIMENS EXAMINED

We examined incisors that represent only a part of the diversity of eomyids in the Old and New Worlds. Specimens were abraded, polished, and then etched briefly with very dilute hydrochloric acid in preparation for viewing. The catalogue numbers of specimens contain acronyms of several institutions:

ACM, Amherst College, Pratt Museum, Albert E. Wood collection field number
AMNH, American Museum of Natural History
BSPGM, Bayerische Staatssammlung für Paläontologie und historische Geologie, Munich
F:AM, Frick Collection, American Museum of Natural History
KU, University of Kansas, Museum of Natural History
SÚÚG, Central Geological Institution, Prague.

In the following list the number of incisors examined is one and the tooth is a lower incisor, unless other data are specified.

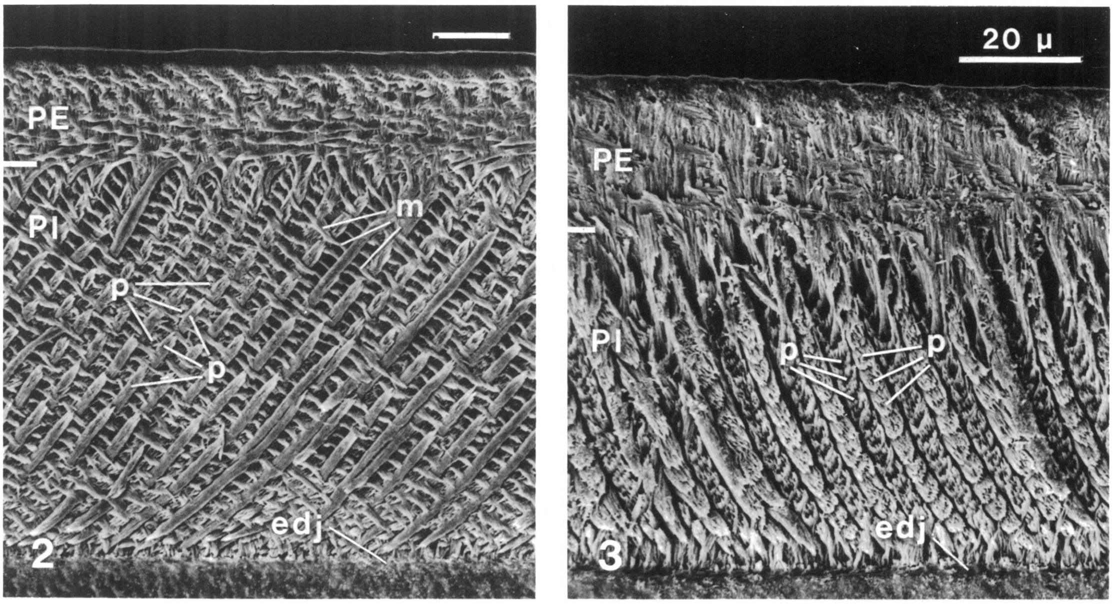
Adjidaumo, ACM, AEW 35-68-2-5-1, 1 mi. S of Scenic, Pennington Co., S.Dak., USA; Orellan, Oligocene.

Centimanomys major, F:AM 97804 (mandible), SW end of Seaman Hills, Niobrara Co., Wyo., USA; Chadronian, Oligocene.

Eomys zitteli, BSPGM, Gaimersheim, Bavaria, Federal Republic of Germany; AMNH 11024 (mandible), Peublanc, St. Gérand le Puy, Allier, France; Arvernian, Oligocene.

Leptodontomys catalaunicus, SÚÚG (4 specimens), Suchomasti, Bohemia, ČSSR; Turolian, Miocene.

Ligerimys florancei, BSPGM (2 specimens), Erkertshofen 1, Bavaria, Federal Republic of Germany; Orleanian, Miocene.



FIGS. 2 and 3. **2.** Longitudinal section of uniserial enamel in lower incisor of *Ondatra zibethicus*; apex is to the right. **3.** Longitudinal section of uniserial enamel in upper incisor of *Ondatra zibethicus*; apex is to the left.

Abbreviations: **edj,** enamel-dentine junction; **m,** interprismatic matrix; **p,** enamel prism; **PE,** *portio externa,* and **PI,** *portio interna* with division indicated at left. Scale bars = 20 μ.

Paradjidaumo minor, F:AM 94877 (mandible), SE corner of Chalky Buttes, Slope Co., N. Dak., USA; Orellan, Oligocene.

Paradjidaumo trilophus, ACM, AEW 31-8-20-4 (mandible), S.Dak., USA; AMNH 96856 (mandible), Chalky Buttes, Slope Co., N. Dak., USA; F:AM 94970 (mandible), Little Badlands, Stark Co., N. Dak., USA; Orellan, Oligocene.

Paradjidaumo sp., F:AM 102150 (upper incisor from skull), 5–6 mi. SE of Douglas, Converse Co., Wyo., USA; F:AM 108023 (mandible), 8 mi. N of Rocky Ford, Shannon Co., S. Dak., USA; Orellan, Oligocene.

Pseudotheridomys hesperus, KU 10197 (mandible), Quarry A, Martin Canyon, Logan Co., Colo., USA; Hemingfordian, Miocene.

Rhodanomys transiens, BSPGM, Coderet, Allier, France; Arvernian, Oligocene.

Yoderimys burkei, F:AM 97802 (mandible), NW end of Seaman Hills, Niobrara Co., Wyo., USA; Chadronian, Oligocene.

UNISERIAL ENAMELS

The incisors of the Myomorpha and Sciuromorpha are characterized by uniserial Hunter-Schreger bands in the *portio interna.* The bands are one prism wide and are usually transverse to the longitudinal axis of the incisor. The prisms of adjacent layers decussate at about 90°, a feature most easily seen in cross sections.

Boyde (1978) drew attention to differences between the uniserial enamels of sciurids and myomorphs. He pointed out that in sciurids the bands are generally not inclined, and interprismatic matrix is lacking or very sparse in the *portio interna*; in myomorphs, on the other hand, the Hunter-Schreger bands are inclined apically, and the interprismatic matrix descends and crosses them at nearly a right angle. We have examined lower incisors of several sciurid genera and propose that interprismatic matrix is indeed present in them, but it is hidden because the crystallites of the matrix are parallel to those of the prisms. We have observed that the interprismatic matrix is obvious close to the enamel-dentine junction where it is at an angle to the prisms. A short distance from the junction, crystallites are seen turning into the direction of the prisms, and the matrix seems to vanish.

The matrix becomes visible again where the prisms turn apically as they enter the radial enamel of the *portio externa*. In some photographs the interprismatic matrix could be identified as a collar around the prisms. A similar enamel has been observed in myomorphs. Examination of *Ondatra* revealed that the enamel of the lower incisor has the myomorph structure described by Boyde (fig. 2). The upper incisor, however, possesses a sciurid-like condition in which interprismatic matrix runs parallel to the prisms (fig. 3); the bands in this enamel are inclined, and thus differ from those of sciurids. We use the phrase "myomorph type of uniserial enamel" in reference to the condition in lower incisors that is known only in this group of rodents. Incisor enamels of myomorphs appear to be fertile ground for comparative investigation.

Neither the sciurid nor the myomorph type of enamel appears to be ancestral to the other. We assume that in primitive uniserial enamel the crystallites of interprismatic matrix would have run at a slight angle between the prisms as in the more primitive pauciserial enamel. This assumption is in accord with Korvenkontio's (1934) hypothesis that uniserial structure is derived from the pauciserial type. Wilson (1972) speculated that uniserial enamel resists breakage more effectively than pauciserial and that it arose together with changes in the jaw musculature that increased biting force. The special myomorph version of uniserial enamel forms an almost homogeneous structure that may resist stresses equally in all directions, since all three axes in space are strengthened by fibers. The biomechanical advantage of the uniserial enamel in sciurids is difficult to comprehend. We have observed transition in orientation of crystallites of interprismatic matrix from the direction of one prism into that of a prism in the adjacent band; this suggests that the matrix may bond the bands into a continuous structure. Both the myomorph and sciurid types of uniserial enamel are found side by side in the lower incisors of eomyids.

EOMYID INCISOR ENAMEL

The fact that rodents use the lower incisors more actively than the uppers is reflected in the higher growth rates of the lowers (Shadle et al., 1936, 1938, 1944). Enamels of the Gliridae and Dipodidae (Korvenkontio, 1934) show that specializations are most likely to occur in the lower incisors. The special nature of the enamel in eomyids is most clearly developed in the lower incisors, and we restrict our study primarily to these teeth.

Enamel covers only the labial face of the incisor. The covering is asymmetrical, because the enamel extends farther onto the lateral side than onto the mesial side, which is almost free of the substance. The lower incisors of eomyids are characterized by a thickening of the enamel that forms a longitudinal ridge between the anterior and lateral faces of the enamel cover (fig. 4).

The Schmelzmuster of enamel in lower incisors of eomyids is complex. The *portio externa* is formed of radial enamel as is usual in rodents. The *portio interna* shows uniserial Hunter-Schreger bands, but, in contrast to the common transverse orientation seen in most uniserial enamels, these bands are almost parallel to the longitudinal axis of the incisor. A slight inclination may be present, but a perfect longitudinal section that would allow the exact attitude of the bands to be determined is difficult to prepare, since the incisor is a segment of a conical helix.

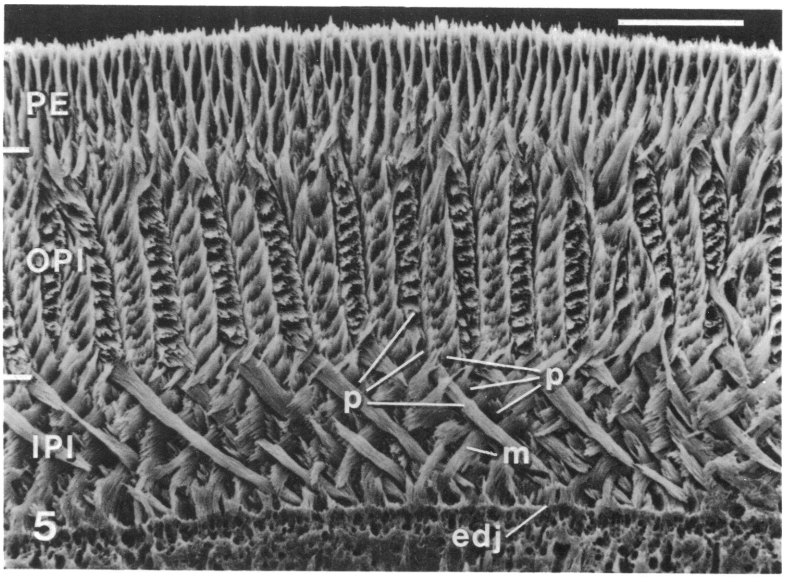
The cross section (fig. 5) reveals further differentiation; the *portio interna* is divided into inner and outer parts that are distinguished by markedly different orientations of the band profiles. In the inner part of the *portio interna* the bands and the prisms within them have a strong lateral inclination of about 45° to the enamel-dentine junction. In the most lateral region of the enamel the angle appears to be even more acute. The prisms of the inner part are widely separated by a prominent interprismatic matrix. Crystallites of the matrix are oriented at an angle of 45° toward the mesial side of the tooth, the opposite direction from the prisms, and they cross the prisms at an angle of 90° in this view. In a longitudinal section (fig. 6) that is nearly parallel to the long axis of the tooth, the profiles of the Hunter-Schreger bands in the inner part appear as rows of prisms running almost parallel to the enamel-dentine junction. The slight difference in inclination between the plane of section and the attitude of the bands gives the rows the appearance

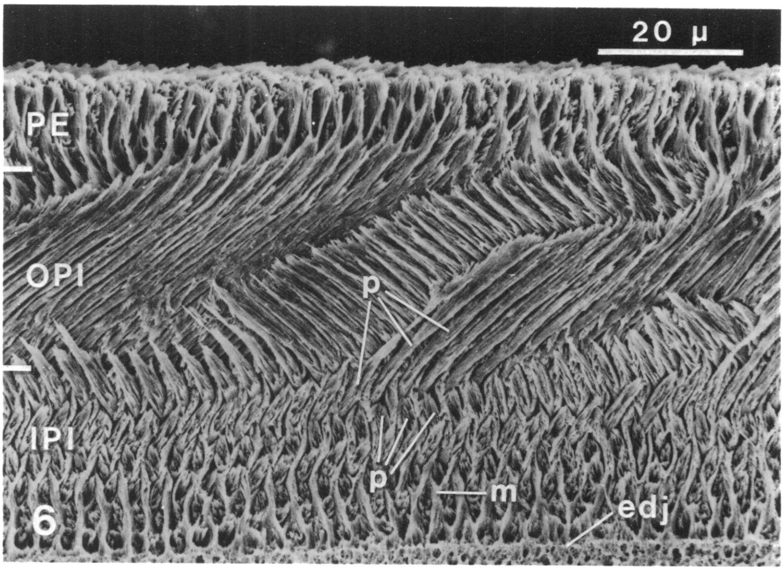
FIG. 4. Cross section of lower left incisor, *Paradjidaumo trilophus,* AMNH 96856. Apex is toward viewer; mesial side to the right.

Abbreviations: **edj,** enamel-dentine junction; **IPI,** inner part of *portio interna*; **OPI,** outer part of *portio interna*; **PE,** *portio externa.* Scale bar = 50 μ.

of being inclined outward at a low angle from the enamel-dentine junction. The tangential section (fig. 7) shows that in the inner part all prisms, whether they point apically or basally, tend toward the lateral side of the incisor, and that prisms are widely separated by interprismatic matrix.

In the outer part of the *portio interna* the cross section (fig. 5) shows that the Hunter-Schreger bands are nearly longitudinal as well. However, the lateral inclination of band profiles is not as great as in the inner part. At the anterior side of the tooth the band profiles stand almost perpendicular to the enamel-dentine junction. The rounded surface of the dentine necessitates tilting of the Hunter-Schreger bands on both mesial and lateral extremities of the enamel. The band profiles on the mesial side are inclined mesially and on the lateral side, laterally. Lateral to the ridge the inclination of band profiles becomes slightly greater; the Hunter-Schreger bands are not longitudinal in this region but show a transition to almost horizontal orientation. This suggests that in three dimensions the bands have a gradual change in inclination and that they become more and more vertical towards the anterior side of the incisor. In longitudinal section (fig. 6) the Hunter-Schreger bands of the outer part are widely exposed, because the plane of the bands lies close to the plane of section. Prisms of different bands decussate at a high angle. In tangential section (fig. 8) the bands appear as tightly packed rows of prisms with a nearly vertical attitude. The section also shows that



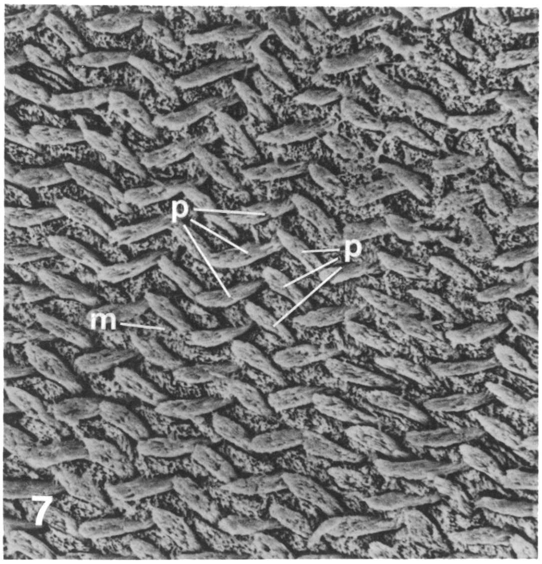


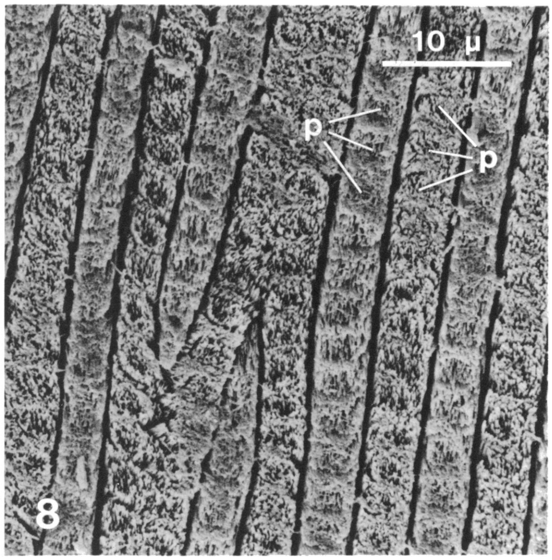
FIGS. 5 and 6. **5.** Cross section of lower left incisor, *Paradjidaumo trilophus,* AMNH 96856; detail of figure 4. Apex is toward viewer; mesial side to the right. **6.** Longitudinal section of lower left incisor, *Paradjidaumo minor,* F:AM 94877. Apex is to the right; mesial side is behind plane of page.

Abbreviations: **edj,** enamel-dentine junction; **m,** interprismatic matrix; **IPI,** inner part of *portio interna*; **OPI,** outer part of *portio interna*; **p,** enamel prism; **PE,** *portio externa.* Scale bars = 20 μ.

the Hunter-Schreger bands bifurcate as they do in most enamels. This creates problems in defining the precise angle between longitudinal Hunter-Schreger bands and the longitudinal axis of the tooth.

The interprismatic matrix in the outer part of the *portio interna* is not readily apparent, and the prisms appear to touch one another in all planes of section. In tangential views, especially, the cross sections of prisms appear to be wider than in the inner part. We attribute this widening to the interprismatic





FIGS. 7 and 8. **7.** Tangential section through inner part of *portio interna*. **8.** Tangential section through outer part of *portio interna*.
Lower right incisor of *Paradjidaumo*, F:AM 108023. Apex is up; mesial side to the right.
Abbreviations: **m,** interprismatic matrix; **p,** prism. Scale bar = 10 μ.

matrix; crystallites of the matrix appear to parallel those of the prisms, and thus a prism is almost indistinguishable from its surrounding matrix. In some sections we could identify crystallites of matrix leaving the direction of one prism and changing to that of a prism in the next band.

The transition between the inner and outer parts of the *portio interna* is not abrupt; both the Hunter-Schreger bands and interprismatic matrix are continuous between the parts. In tangential section, where the transition is observed over a long distance, the gradual change is clear. The amount of interprismatic matrix separating the prisms decreases, while the prisms appear to grow in width and to be closer together.

The *portio externa* is typical radial enamel in which the prisms are inclined apically and are parallel to one another (figs. 5, 6). The radially directed crystallites of the interprismatic matrix interweave with the prisms and separate them widely. The transitional zone between the *portio interna* and the *portio externa* is of great interest because of the longitudinal orientation of the Hunter-Schreger bands. All the prisms of the different bands must turn into parallel alignment. In the set of bands in which the prisms ascend toward the outside of the enamel, the required bending is slight. Prisms in the alternating bands descend, and these must bend sharply to become parallel to those of the other set. Both degrees of bending were observed together in several sections. The transitional zone also shows a gradual increase in the amount of interprismatic matrix as the Hunter-Schreger bands vanish. The chief features of enamel structure in lower incisors of eomyids are assembled in a hypothetical block diagram (fig. 9).

The two layers of the *portio interna* and that of the *portio externa* continue through almost the entire arch of the enamel in cross section (fig. 4). On the anterior face the three layers are nearly equal in width. The thickening of the enamel in the ridge is due mostly to expansion of the outer part of the *portio interna* as well as of the radial enamel of the *portio externa*. In the most lateral part of the enamel cover the *portio externa* and the inner part of the *portio interna* become thinner, while the outer part of the *portio interna* retains its width for a greater distance.

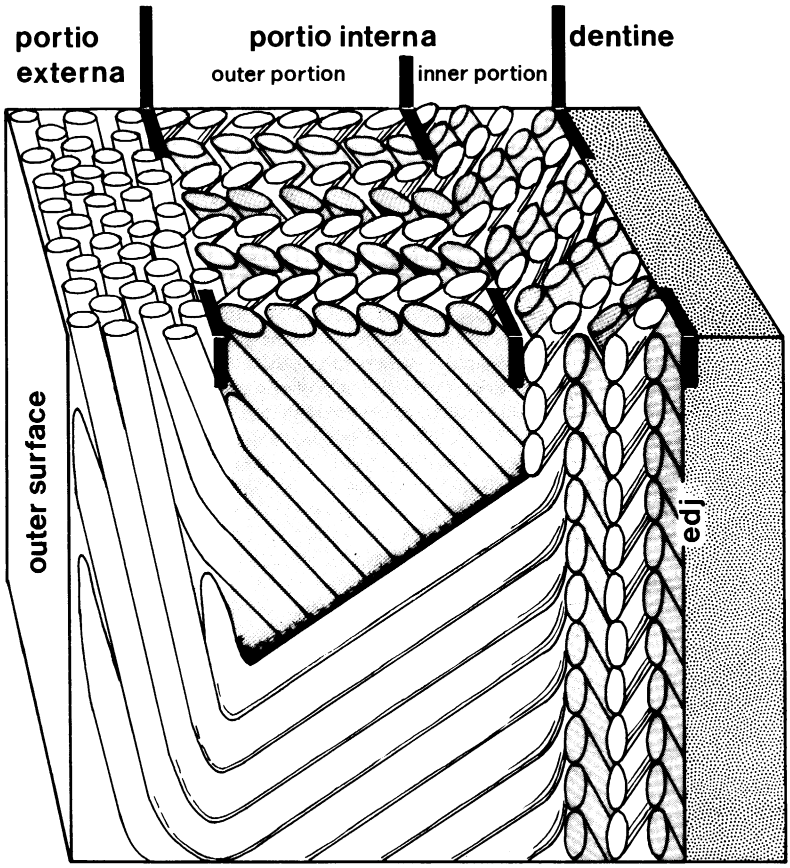
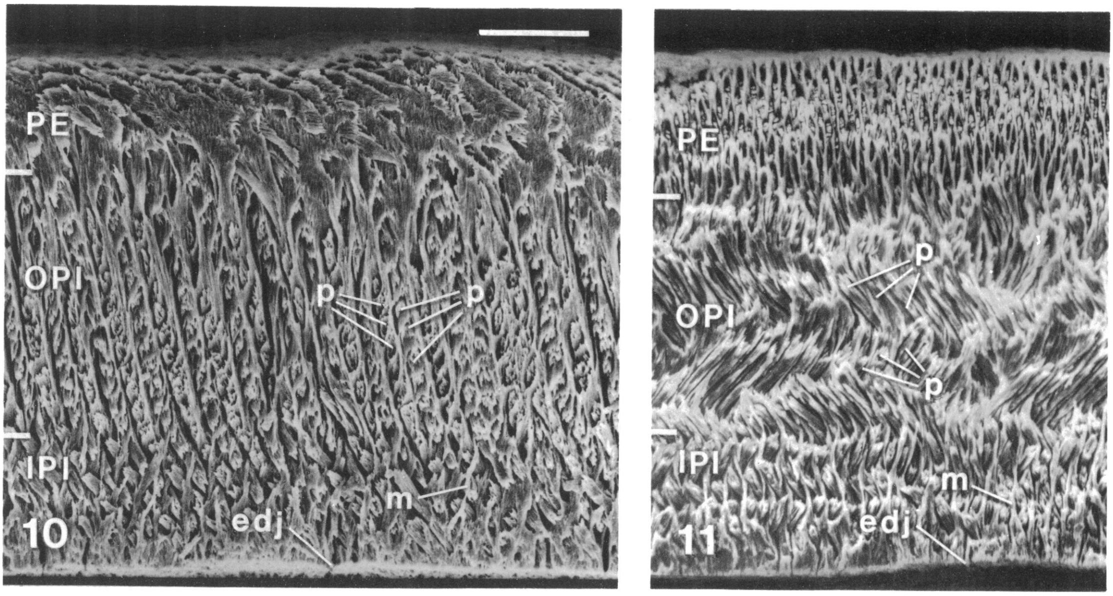


FIG. 9. Block diagram, lateral view, of enamel prism orientations in lower left incisor of an eomyid. Apex is up. Intersection of prisms with longitudinal and cross section planes shown; **edj**, enamel-dentine junction.

We have sectioned only one upper incisor, because eomyid skulls are rare. Upper incisors have no distinguishing ridge and are not easily identified in isolation. The enamel of the upper incisor is structurally intermediate between the enamel of lower incisors of eomyids and the type seen in the upper incisor of *Ondatra* (fig. 3). The Hunter-Schreger bands are oriented transversely and are inclined apically. The *portio interna* is clearly divided into two layers (figs. 10, 11) chiefly by different relationships of matrix to prisms. In the inner part crystallites of interprismatic matrix radiate from the enamel-dentine junction, whereas prisms and their crystallites ascend apically and those of adjacent bands decussate. In the outer part crystallites of both matrix and prisms are parallel; the matrix is visible ensheathing the prisms in longitudinal view, and it can be seen bending from one prism to another in adjacent bands in the cross section. The apical inclination of the Hunter-Schreger bands is greater in the inner than the outer part of the *portio interna.* The decussation of prisms in adjacent bands is greater in the outer part. The *portio externa* has the structure typical of rodent incisors.

Structural differences indicate that changes in enamel of upper and lower incisors are not precisely correlated; here the upper teeth appear to be more primitive. Throughout the *portio interna,* prisms of adjacent Hunter-Schreger bands are oriented laterally and mesially in upper incisors. There is no common lateral orientation of prisms in the inner part. The apical inclination of bands is steeper in



FIGS. 10 and 11. **10.** Longitudinal section of upper incisor. **11.** Cross section of upper incisor; apex is toward viewer.
Paradjidaumo, F:AM 102150. Abbreviations as in figure 5. Scale bar = 20 μ.

the inner than in the outer part of the *portio interna,* but the primitive attitude of the bands, horizontal to the long axis of the tooth, is retained in upper incisors.

From the genera examined we assume that the general pattern of the uniserial enamel described in lower incisors is characteristic of the entire family. Differences may be expected to occur in two features. The lateral inclination of the Hunter-Schreger bands between inner and outer parts of the *portio interna* may be less pronounced, and the bands may be more or less oblique to the longitudinal axis of the incisor. The difficulty of preparing an exactly defined section, the helical shape of incisors, and the limited number of specimens available for sectioning make it impossible for us to demonstrate any obvious differences among taxa in the family. Only the incisor of *Eomys zitteli* shows no clear difference in orientation of the longitudinal Hunter-Schreger bands between the inner and outer parts of the *portio interna* in cross section. The smaller difference between the two parts may be a more primitive condition than that which we have described.

DISCUSSION

Two specializations can be observed in the enamel of lower incisors in eomyids. First, the Hunter-Schreger bands are oriented almost parallel to the long axis of the tooth. Second, the *portio interna* consists of two different forms of uniserial enamel. The inner part of the *portio interna* is basically like the uniserial enamel found in lower incisors of myomorphs, but, since the bands in eomyids are longitudinal instead of transverse, a cross section of this region looks like the longitudinal section of the *portio interna* in a myomorph incisor. In eomyids the cross section reveals that the decussating prisms of the inner part point laterally away from the enamel-dentine junction, and the crystallites of the interprismatic matrix are inclined mesially and cross the prisms at right angles. In contrast, the outer part of the *portio interna* in eomyids is similar to the uniserial enamel in sciurids and in the upper incisors of at least some myomorphs because the crystallites of the matrix are parallel to the prisms in both. Again, the transverse section of this region in the lower incisor of an eomyid looks like the longitudinal section of the *portio interna* of a sciurid.

We assume that the observed specializations characterize the Eomyidae because they occur in common in a diverse group of taxa from both the Old and New Worlds. As more specimens of Eocene and early Oligocene taxa are found, it will be possible to test this hypothesis.

The combination of two kinds of uniserial enamel in lower incisors characterizes eomyids, but it does not indicate close relationship to either sciurids or myomorphs. Wilson (1949) concluded that the eomyids are more closely related to myomorphs than to sciurids; therefore, we propose that the special eomyid Schmelzmuster is derived from the myomorph type of uniserial enamel. The myomorph type, in which all three axes are strengthened by fibers, has not been observed in any other rodent group. The enamel of upper incisors in eomyids demonstrates a possible mode for development of more specialized structure in lower incisors from the myomorph condition. The division of the *portio interna* into two parts may have occurred prior to reorientation of its structural components.

Heteromyids and geomyids may be regarded as sister groups to the eomyids, as can be deduced from Thaler (1966, fig. 1). Wood's hypothesis (1980) that the heteromyids are derived from eomyids is not supported by our observations, since heteromyids have the simpler uniserial Schmelzmuster common in most myomorphs. However, taxa ancient enough to approach the time of common ancestry have not been sampled. Enamel structure of *Meliakrouniomys,* which Harris and Wood (1969) said "seems to be an eomyid on the way to becoming a heteromyid," will be of great interest. Specimens of this early Chadronian genus are still too rare to be sacrificed in sectioning.

Our data shed no further light on the relationship of eomyids to sciuravids that was proposed by Fahlbusch (1979) and others. The enamel of the *portio interna* of *Sciuravus* is pauciserial (Wahlert, 1968), and this type may be the structural precursor of any uniserial enamel in rodents (Korvenkontio, 1934).

Eomyids have a more complex Schmelzmuster than do most other rodents. The statement of Tomes (1850) that rodent incisor enamel is two layered in contrast to the single layer in lagomorphs has to be altered. Further modification of the two-layered condition might lead to a more complex structure in various groups. However, it is wrong to assume that a higher number of layers always indicates a more derived condition, since a three-layered enamel can be primitive as well, as was shown in arvicolid molars (Koenigswald, 1980, 1985).

Rensberger and Koenigswald (1980) have shown that the attitude of the prisms relative to the direction of occlusal stresses affects the resistance of the enamel to wear. A large angle seems to result in greater wear than does a smaller angle. The direction of stress during gnawing varies and depends on the direction of bite. It is likely that in rodent incisors the vertical component is always an important vector. In the radial enamel of the *portio externa,* the enamel type regarded as primitive for mammals, the steeply inclined prisms make only a small angle with the direction of vertical stress and thus are in almost optimal position. Radial enamel, however, has low resistance to cracks. Uniserial Hunter-Schreger bands, in contrast, are highly resistant to fracturing. Arrangement of the bands transversely and nearly perpendicular to the enamel-dentine junction appears to be primitive and is common in the pauciserial enamel of paramyids and *Sciuravus* and in the uniserial enamel of sciurids. Since such prisms are oriented at almost right angles to the direction of occlusal stress, resistance to wear is low. Two different evolutionary pathways that reduce the angle between prisms and occlusal stress can be observed. In one, the transverse bands are inclined apically; this can be regarded as the common derived condition. Eomyids, however, show a second condition, which also occurs in parallel in dipodoids and glirids: the Hunter-Schreger bands are no longer in the usual transverse orientation but are more or less longitudinal to the axis of the tooth. The reasons why eomyids possess two different types of uniserial enamel in the lower incisors or why the angle of lateral inclination of bands differs in the inner and outer parts of the *portio interna* cannot be explained on the basis of current knowledge of microstructure and function.

LITERATURE CITED

Boyde, A.
1978. Development of the structure of the enamel of the incisor teeth in the three classical subordinal groups of the Rodentia. *In* P. M. Butler and K. A. Joysey (eds.), Development, function and evolution of teeth. Pp. 43–58. New York, Academic Press.

Fahlbusch, V.
1979. Eomyidae—Geschichte einer Säugetierfamilie. Paläont. Z., vol. 53, pp. 88–97.

Harris, J. M., and A. E. Wood
1969. A new genus of eomyid rodent from the Oligocene Ash Spring local fauna of Trans-Pecos Texas. Pearce-Sellards Ser., no. 14, pp. 1–7.

Koenigswald, W. v.
1980. Schmelzstruktur und Morphologie in den Molaren der Arvicolidae (Rodentia). Abh. senckenb. naturforsch. Ges., vol. 539, pp. 1–129.
1982. Enamel structure in the molars of Arvicolidae (Rodentia, Mammalia), a key to functional morphology and phylogeny. *In* B. Kurten (ed.), Teeth: Form, function, and evolution. Pp. 109–122. New York, Columbia Univ. Press.
1985. Evolutionary trends in the enamel of rodent incisors. *In* W. P. Luckett and J.-L. Hartenberger (eds.), Evolutionary relationships among rodents: a multidisciplinary analysis. New York, Plenum Press. In press.

Korvenkontio, V. A.
1934. Mikroskopische Untersuchungen an Nagerincisiven, unter Hinweis auf die Schmelzstruktur der Backenzähne. Ann. Zool. Soc. Zool.-Bot. Fennicae Vanamo, vol. 2, pp. i–xiv, 1–274.

Rensberger, J. M., and W. v. Koenigswald
1980. Functional and phylogenetic interpretation of enamel microstructure in rhinoceroses. Paleobiol., vol. 6, pp. 477–495.

Shadle, A. R., W. R. Ploss, and E. M. Marks
1944. The extrusive growth and attrition of the incisor teeth of *Erethizon dorsatum.* Anat. Rec., vol. 90, pp. 337–341.

Shadle, A. R., N. I. Valvo, and K. M. Eckhert
1938. The extrusive growth and attrition of the incisor teeth of *Cavia cobaya.* Anat. Rec., vol. 71, pp. 497–502.

Shadle, A. R., L. G. Wagner, and T. Jacobs
1936. The extrusive growth and attrition of the incisors in albino and hybrid *Rattus norvegicus* (Erxleben). Anat. Rec., vol. 64, pp. 321–325.

Thaler, L.
1966. Les rongeurs fossiles du Bas-Languedoc dans leurs rapports avec l'histoire des faunes et la stratigraphie du Tertiare d'Europe. Mém. Mus. Nat. d'Hist. Natur., sér. C, Sci. Terre, vol. 17, pp. 1–295, pls. 1–27.

Tomes, J.
1850. On the structure of the dental tissues of the Order Rodentia. Phil. Trans. Roy. Soc. London, 1850, pp. 529–567, pls. 43–46.

Wahlert, J.
1968. Variability of rodent incisor enamel as viewed in thin section, and the microstructure of the enamel in fossil and Recent rodent groups. Breviora, no. 309, pp. 1–18.

Wilson, R. W.
1949. On some White River fossil rodents. Carnegie Inst. Washington Publ. 584, pp. 27–50, pls. 1–2.
1972. Evolution and extinction in early Tertiary rodents. 24th Int. Geol. Congr., 1972, sec. 7, pp. 217–224.

Wood, A. E.
1980. The Oligocene rodents of North America. Trans. Amer. Phil. Soc., vol. 70(pt. 5), pp. 1–68.