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Evolution of Mammalian Dental Enamel

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INTRODUCTION

Comparative odontology is a major aspect of vertebrate paleontology. The extensive literature on mammalian evolution contains many detailed and accurate descriptions of the phylogenetic changes in the form (size and shape) of enamel-covered tooth crowns, but this interest in gross tooth morphology has not extended to the microscopic structure of enamel (Simpson, 1929, 1936; Butler, 1939; Mills, 1964).

The evolution of dental tissues has recently been reviewed (Peyer, 1963; Moss, 1964), and there is general agreement that all vertebrate teeth are homologous. They are covered by a hard refractile tissue that is identified as enamel in all Recent and fossil mammals, reptiles, and most Amphibia (Moss, 1964). Enamel arises from an inner enamel epithelium by a sequence of homologous odontogenetic inductions. The extension of this homology to the outer layer of teeth and toothlike structures in fish is controversial. Some authors claim that this outer tissue is true ectodermal enamel (Moss, Jones, and Piez, 1964), whereas others (Kvam, 1946; Schmidt and Keil, 1958) claim a mesodermal (mesectodermal) origin for it. This point, to be reviewed elsewhere, is beyond the scope of the present paper.

There is general agreement that the enamel of all Recent mammals

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is prismatic, although the internal organization of such prisms is not identical in all species (Boyd, 1966; Shobusawa, 1952; Schmidt and Keil, 1958). It is also agreed that the enamel of reptilian teeth, both Recent and fossil, is non-prismatic (Poole, 1956; Schmidt and Keil, 1958; Lehner and Plenk, 1936). In the face of an almost complete lack of data (Carter, 1922), there is a tacit assumption that the prismatic structure arose simultaneously with the appearance of mammalian teeth.

Poole (1956) reported that the dental enamel of certain fossil mammal-like reptiles is non-prismatic. The structural bases for these observations are discussed in detail below. A recent study of the teeth of two late Triassic mammals demonstrates that these very early mammalian enamels are also non-prismatic, although they differ structurally from those of presumed reptilian precursors (Moss and Kermack, 1967). Since these findings established the fact that gross evolution and microscopic structural evolution of enamel were not simultaneous events, the present more comprehensive study was undertaken.

Within the limitations imposed by available material, these data support two hypotheses: (1) that a prismatic (discontinuous) enamel structure was acquired gradually only by therians, and (2) that prismatic (discontinuous) enamel had appeared no later than the early Cretaceous.

Acknowledgments

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Some of the Recent material was supplied by Dr. McKenna, Dr. Richard G. Van Gelder, and Mr. Hobart M. Van Dusen of the American Museum. Other Recent material we provided ourselves.

Abbreviations

A.M.N.H., the American Museum of Natural History
C.U., Columbia University
F.M.N.H., Field Museum of Natural History, Chicago
K.U., the University of Kansas, Lawrence
M.C.Z., Museum of Comparative Zoology, Harvard University
P.U., Princeton University
S.M.P.-S.M.U., Shuler Museum of Paleontology, Southern Methodist University
U.C.M.N., Museum of Paleontology, University of California
Y.P.M., Peabody Museum of Natural History, Yale University

Materials

Teeth of the forms listed below were studied in thin section:

Reptilia: Pelycosauria, Sphenacodontidae, *Sphenacodon ferox* (Y.P.M., uncat.), early Permian, Aroyo de Agua, New Mexico.

Therapsida: Bauriidae, *Sesamodon brownii* (A.M.N.H., uncat.), early Triassic, South Africa.

Traversodontidae: Cynodont, undescribed and unnamed (Y.P.M., uncat.), middle Triassic, Luangwa Valley, Tanzania.

Tritylodontidae: *Bienotherium yunnanense* (Y.P.M., uncat.), late Triassic, Lufeng, Yunnan, China.

Mammalia (non-therian): Monotremata, *Ornithorhynchus* (A.M.N.H. No. 1302), Recent.

Docodonta: *Morganucodon* (U.C., uncat.), late Triassic. *Docodon* sp. indet. (Y.P.M. No. 20992), late Jurassic, Como Bluff, Wyoming.

Triconodonta: Triconodontid, gen. et sp. indet. (Y.P.M. No. 13631), late Jurassic, Como Bluff, Wyoming. *Astroconodon denisoni* (F.M.N.H. No. PM1188), Trinity Sands, early Cretaceous, Tricon Gully, ridge 1, area 1, Montague County, Texas.

Multituberculata: Plagiaulacid (Y.P.M., uncat.), gen. et sp. indet., Morrison Formation, late Jurassic, Como Bluff, Wyoming. Plagiaulacid (F.M.N.H. No. PM956), gen. et sp. indet., Trinity Sands Formation, early Cretaceous, Tricon Gully, ridge 1, area 2, Montague County, Texas. *Meniscoessus* sp. (Y.P.M., uncat.), late Cretaceous, Lance Formation, Lance Creek, Wyoming. *Cimolodon* (K.U., uncat.), late Cretaceous (K.U. Alberta locality 2), Upper Edmonton Formation, Alberta, Canada. Multituberculate (A.M.N.H. No. 80007), gen. et sp. indet., late Cretaceous, Campanian, Mesa Verde Formation, Wyoming. *Taeniolabis taoensis* (Y.P.M. No. 14452), early Paleocene, San Juan Basin, New Mexico. Multituberculate incisor and premolar (P.U., uncat.), gen. et sp. indet., mid-Paleocene. *Ectypodus* (A.M.N.H. No. 80919), Eocene, Lower Wasatch, 4-Mile beds, locality II, East Alheit, Colorado, 1961 expedition.

Mammalia (therian): Pantotheria, unnamed pantothere (U.C., uncat.), late Triassic, Wales. Dryolestid (Y.P.M. No. 13783g), gen. et sp. indet., late Jurassic, Como Bluff, Wyoming. Pappotheriid (S.M.P.-S.M.U., uncat.), "Trinity lower molar, Type 5," early Cretaceous, Alabama, Wise County, Texas; methatherian-

eutherian grade.

Marsupialia: *Alphadon* (U.C.M.P. locality V5711), late Cretaceous, Lance Formation, Wyoming. *Pediomys* (U.C.M.P. locality V5711), late Cretaceous, Lance Formation, Wyoming. Didelphid (Y.P.M., uncat.), gen. et sp. indet., Lance Formation, late Cretaceous, Lance Creek, Wyoming. Marsupial, gen. et sp. indet. (A.M.N.H. No. 59696), late Cretaceous, Campanian, Mesa Verde Formation, Wyoming. *Macropus* sp. (A.M.N.H., uncat.), Recent, Australia. *Dactylonax* (A.M.N.H. No. 191044), Recent, New Guinea. *Didelphis virginiana* (C.U., uncat.), Recent.

Placentals, fossil: *Gypsonictops* (U.C.M.P. locality V5711), late Cretaceous, Lance Formation, Wyoming. Primate (P.U., uncat.), Paleocene. Carnivore (P.U., uncat.), Paleocene. Primate (P.U., uncat.), Eocene. Carnivore (P.U., uncat.), Eocene. Rodent (P.U., uncat.), Eocene. *Hyracotherium* (P.U., uncat.), Eocene. *Coryphodon* (Y.P.M., uncat.), Eocene.

Placentals, Recent: *Blarina* (A.M.N.H. No. 1250). *Microgale cowani* (A.M.N.H., uncat.). *Rattus norvegicus* (C.U., uncat.). *Mus domesticus* (C.U., uncat.). *Tupaia glis* (C.U., uncat.). *Microcebus* sp. (C.U., uncat.). *Galago crassicaudatus* (C.U., uncat.). *Tarsius spectrum* (C.U., uncat.). *Saimiri sciurias* (C.U., uncat.). *Lagothrix* sp. (C.U., uncat.). *Macaca mulatta* (C.U., uncat.). *Homo sapiens* (C.U., uncat.).

METHODS

All the teeth were embedded in a clear, cold-cure dental acrylic (Acri-Lux), fixed to a slide with Lakeside 70 and ground to an average thickness of 10 μ; a series of silicon carbide papers, ranging from 180 to 500 grit was used. Most sections were washed in absolute alcohol, xylol, and then embedded in H.S.R. mounting medium (n = 1.54). Some sections were dried overnight at 110° C. and mounted directly without being washed. All sections were studied in transmitted light, as well as with phase and polarization optics. Dark field studies were made on some specimens.

All the photographs (except figs. 3, 25, and 28) were taken between crossed nicols, with the major polarization axes parallel to the sides of the illustration.

Polarization Microscopy of Enamel

Despite the current research interest in enamel structure, and the consequent greater frequency of publications dealing with polarization microscopy, it is by no means true that all workers interested in the comparative aspects of the dental tissues are familiar with these methods. Because much of the significance of the present paper is based on the results of these methods, a brief statement of the pertinent points is necessary. The theory of polarization microscopy and its application to the study of enamel structure were discussed extensively in a number

of recent publications (Schmidt and Keil, 1958; Gustafson, 1959; Bennett, 1961; Crabb and Darling, 1962; Carlström, 1964).

Enamel hydroxyapatite crystallites are essentially rod-shaped. The long axis of a crystallite is identical with the optic or *c* axis. These *c* axes, on the average, are normal to the outer enamel surface, i.e., parallel to prism length. It has recently been shown that, whereas the *c* axes of adjacent apatite crystallites tend to lie in the same mean direction, in a given limited volume of enamel, the *a* axes probably have a random arrangement (Glimcher *et al.,* 1965). The interpretation of the optical activity of a given ground section must take into account the fact that a volume of enamel is represented. Because the average enamel prism has a diameter of about 5 μ, sections thicker than this will demonstrate the resultant activity of several prisms, in which individual spatial orientation and intrinsic crystallite orientation need not be, and probably are not, in precise register (Glimcher *et al.,* 1965).

The examination of enamel with a polarizing microscope, then, is best carried out with the ground section sufficiently thin to obviate the problems of too great a superimposition of non-registered prisms or crystallites, or both, and prepared so that the crystallite *c* axes are essentially horizontal to the plane of the section. Under these conditions the enamel will demonstrate the following properties: the section will be dark when the *c* axes are parallel to either of the mutually perpendicular planes of the polarizer or of the analyzer; maximal brightness is attained when the *c* axes are at an angle of 45 degrees to both of the planes. In this manner the mean orientation of crystallites (i.e., the position of maximum birefringence) in a given section of enamel may be determined.

The sign of birefringence is ascertained when a first-order red plate is inserted into the optic train between the crossed polarizer and analyzer. Since hydroxyapatite gives a negative sign of birefringence, we know that the fast ray direction of the polarized light is identical with the path of the extraordinary ray, which in turn is identical with optic axis of the crystallite. When the *c* axis of a negatively birefringent material is placed diagonally in a "northeast-southeast" direction (in the positive quadrants) a yellow color will appear, while a blue color is perceived in the "northwest-southeast" diagonal position (the negative quadrants).

Several factors produce birefringence when enamel is examined with polarization microscopy. The first is the intrinsic negative birefringence of the apatite coupled with the intrinsic positive birefringence of the fibrous component of the organic matrix. The observed intrinsic birefringence is the algebraic sum of the two opposing signs. Immature

enamel has a relatively large amount of fibrous organic matrix and usually shows positive birefringence. In the present qualitative study of mature enamel, we may safely disregard the now negligible organic component. The second factor relates to form birefringence. Simply expressed, form birefringence, with regard to enamel, will be observed when the essentially parallel rod-shaped crystallites are surrounded by a medium of which the index of refraction differs significantly from that of the enamel. Such form birefringence is positive in sign, and will become increasingly significant (in an algebraic sense) in two cases: when the volume of the surrounding medium is relatively large compared with the volume of the crystallites (it reaches a theoretical maximum at 50%); or when the index of refraction of even a relatively small amount of the surrounding medium is significantly different from that of enamel (n = 1.62). In practice this positive form birefringence may be observed in certain enamels (see below) when the section is observed in air (n = 1.0) after thorough drying. A hydrated enamel viewed under water (n = 1.33) will be negative, and little more "negativity" is qualitatively observed by substituting the usual mounting media (n = 1.54). Again, in practice, form birefringence may be safely disregarded in almost all cases (see below for a discussion of Recent marsupial enamels), particularly in the study of fossil teeth.

RESULTS

The dental enamel of the earliest mammals is non-prismatic or continuous in structure, and thus it resembles, but is not identical with, the enamel structure of advanced mammal-like reptiles. The chief difference between the two lies in the apparent orientation of the mean preferential *c*-axis orientation of the crystallites. None of the Jurassic mammalian enamels differs in any significant way from the two late Triassic enamels examined. In the non-therian line of mammalian evolution I found no evidence of prismatic enamel in any fossil tooth. The Recent monotreme *Ornithorhynchus* also has a continuous enamel structure.

In therian evolution, prismatic structure first appears, and then only partially, in the early Cretaceous in the Pappotheriidae. In all subsequent therians, placentals as well as marsupials, both fossil and Recent enamels demonstrate a discontinuous, prismatic structure in a major portion of the tissue. The optical differentiation between prismatic and non-prismatic enamel is important in the present context. The general optical properties of non-prismatic enamel are given in the following paragraphs, with a distinction made between the type of continuous enamel found

in mammal-like reptiles and that found in early mammals. A fuller statement of the relationship between optical behavior and the crystallographic structure of enamel is given in the discussion below. Throughout I use the term "continuous enamel" as synonymous with "non-prismatic enamel," and "discontinuous enamel" as synonymous with "prismatic enamel."

Synapsid Reptile Enamel

The four synapsid reptilian enamels examined demonstrate a common pattern of optical behavior. In ordinary transmitted and plane polarized light, as well as in phase optics, these enamels are non-prismatic. They all have a diffuse sprinkling of small black dots in section. In many cases, these dots are arranged in vertical rows, running normal to the dento-enamel junction, which itself is essentially smooth. Although these synapsid reptilian enamels are non-prismatic, they are not totally structureless. All four demonstrate what are interpreted as "tubules," which in many cases are filled, for a portion of their length at least, with black dots. The "tubules" lie normal to both the dento-enamel junction and to the outer enamel surface, and are from 6 μ to 8 μ apart (fig. 1).

With crossed nicols the structure of the enamel is clearly revealed. Parallel to either of the two major polarization axes a series of alternating dark and light bands appear (fig. 2). These run vertically through the thickness of the enamel, although this appearance obviously is altered by the plane of the section in some cases, so that both incomplete and decussating bands are observed. The mean width of these bands is: *Bienotherium,* 8 μ; Transversodontidae, cynodont, 6.5 μ; *Sphenacodon ferox,* 8 μ; *Sesamodon brownii,* 6.5 μ. The bands are not observed when the section is rotated 45 degrees to the position of maximum birefringence. During the initial rotation, from either of the major axes, it is observed that, in general, alternate dark bands migrate either with, or contrary to, the direction of rotation. Continued rotation to the diagonal position (45°) results in a uniform, bandless appearance (fig. 1).

With a first order red plate in the optical train, the enamel is negatively birefringent with respect to band length (or positive with respect to the enamel surface). When the section is examined in the extinction position, a regular, repetitive sequence of colored bands is seen, of which the order is blue-red-yellow-red-blue.

These data indicate that synapsid reptilian enamel is structurally non-prismatic, or continuous. A graphic presentation of the mean preferential *c* axis crystallite orientation of a given volume of enamel is shown in figure 3. This pattern is essentially sinusoidal in nature. My data

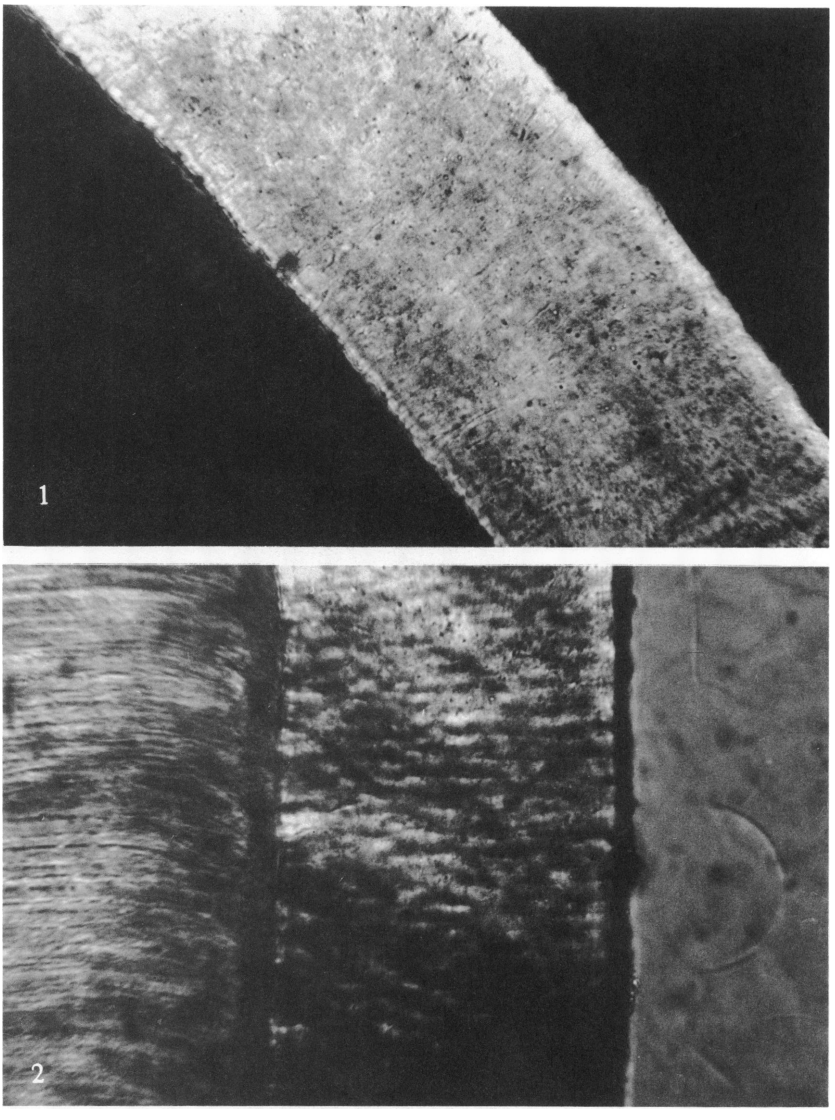


FIG. 1. The enamel of *Sesamodon brownii* (uncatalogued). The outer enamel surface faces the upper right. The tubules within the enamel are visible. In this diagonal position none of the typical bands appear.

FIG. 2. The enamel of *Sesamodon brownii* (uncatalogued), showing the maximum appearance of the alternate dark and light bands.

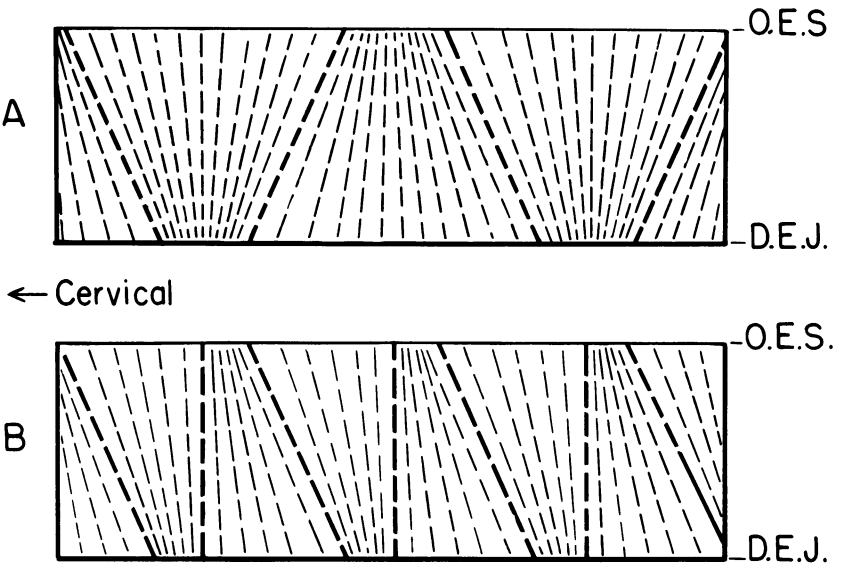


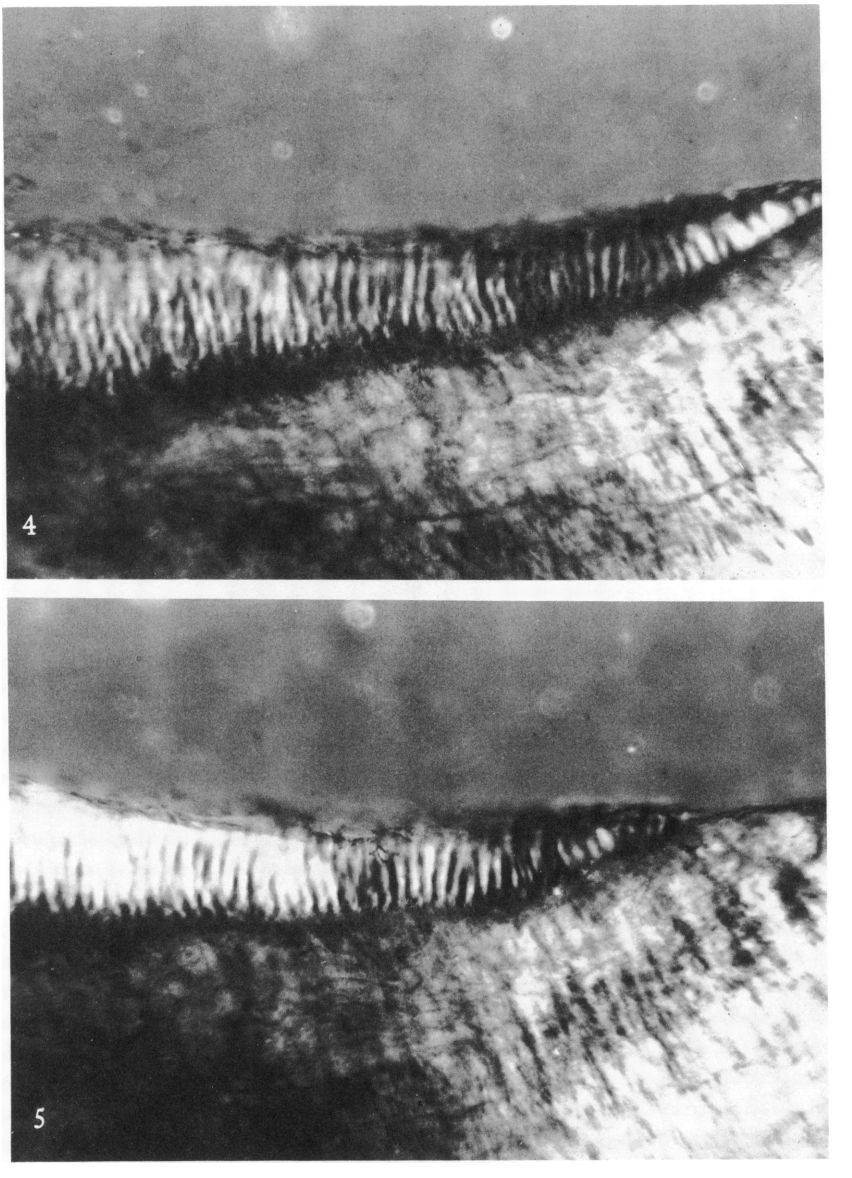
FIG. 3. A schematic illustration of the structural organization of two types of non-prismatic, continuous enamel. A. The idealized pattern of the mammal-like reptiles. B. The different pattern found in all continuous mammalian enamels. The lines represent the mean direction of the *c* axes of the hydroxyapatite crystallites. The occasional heavier lines are for emphasis only.

Abbreviations: D.E.J., dento-enamel junction, with cuspal to the right and gingival to the left; O.E.S., outer enamel surface.

support and confirm those of Poole (1956).

LATE TRIASSIC MAMMALS

Two species were available for study, *Morganucodon* and an "unnamed Welsh pantothere." A preliminary report of findings on these earliest known mammalian enamels has been published (Moss and Kermack, 1967). Sufficient material permitted both longitudinal and horizontal sections to be prepared for *Morganucodon.* Both these late Triassic enamels are essentially similar. In transmitted light, as in reflected light, they are structureless and homogeneous. Both enamels are uniformly dark and dark field illumination. With phase optics a series of faint horizontal striae are observed. With plane polarized light a very faint impression of vertical striae or bands is obtained. These vertical bands, alternating dark and light, become readily apparent with crossed nicols when the enamel layer is placed parallel to either major polarization axis (figs. 4, 5). Rotation to the diagonals, the positions of maximum brightness,



FIGS. 4, 5. The enamel of *Morganucodon* (uncatalogued). 4. The maximum appearance of the banded structure. 5. A slight shift of the section to the left, together with a minimal degree of clockwise rotation.

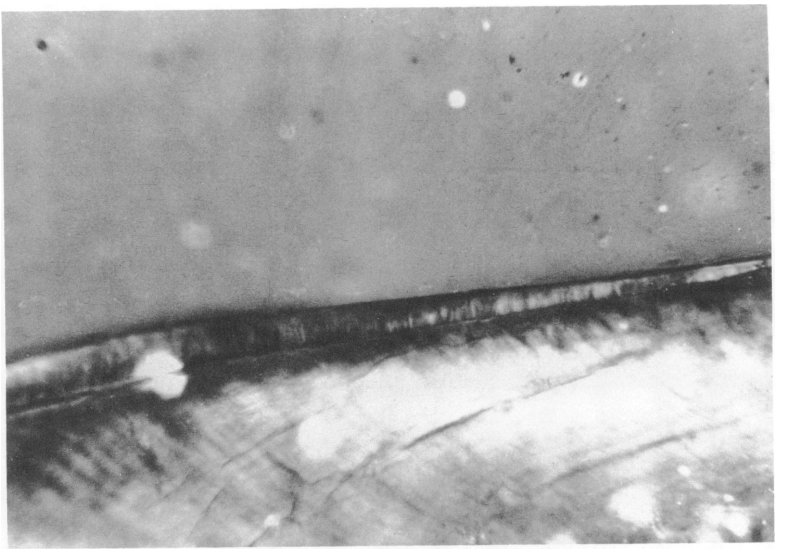


FIG. 6. The enamel of an unnamed Welsh pantothere (uncatalogued). Maximal appearance of the bands are shown.

abolishes the enamel band structure completely. In *Morganucodon,* the thickness of the enamel at the cusp tip is about 80 μ, and the band

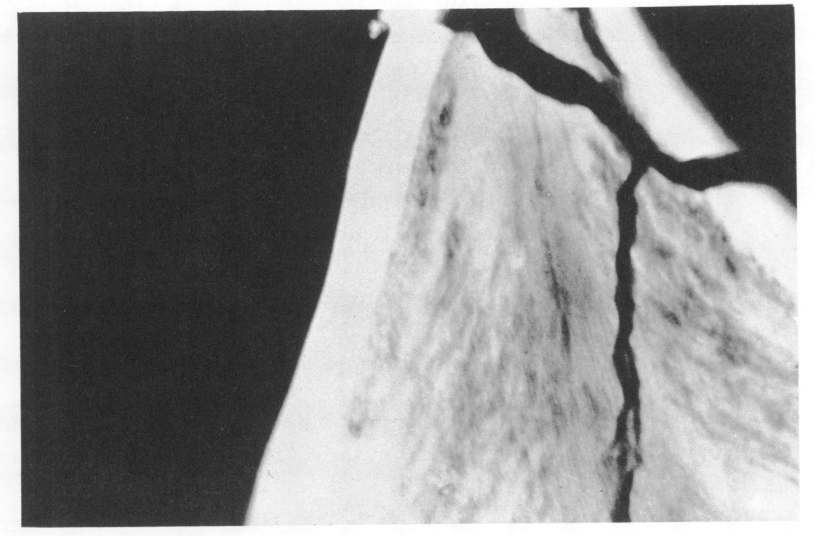


FIG. 7. A microradiograph of a *Morganucodon* tooth (uncatalogued). The cracks are artifacts of preparation.

width is approximately 4.0 μ. The only significant difference noted in the pantotherian enamel is in band width, with an observed mean value of 1.4 μ (fig. 6).

An interesting observation is made when *Morganucodon* enamel is rotated slightly toward the diagonal from the major polarization axes under crossed nicols. Each dark band is observed to split into two "demi-bands" which then migrate in opposite directions, one-half cuspally, one-half cervically in longitudinal sections. They then fuse to form a new dark band which is appreciably thinner than either of the original dark bands. Continued rotation causes these secondary dark bands to disappear also. With a first order red plate in place, the enamel is negative with respect to band length. When the enamel surface is parallel to either major polarization axis, a series of sequentially repeated colored bands is observed. The color array, however, is significantly different from what it is in the enamels of the synapsid reptiles. In the two late Triassic mammals the sequence is blue-red-blue when the enamel surface is horizontal and yellow-red-yellow when the enamel surface is vertical.

A microradiograph of a section, 50 μ in thickness, of a *Morganucodon* tooth was made (25 volts; 10 milliamperes; 15 minutes). Figure 7 shows an apparently uniform mineralization throughout the enamel. All these data suggest that these two enamels are non-prismatic or continuous. The mean preferential *c*-axis crystallographic orientation of the enamel apatite is essentially normal to the surface, with minor, but regular, alterations of direction. These data further suggest that this orientation differs significantly from that observed in the enamel of the synapsids. The sinusoidal pattern observed in the latter forms is replaced in the early mammals with what may best be termed a saw-toothed pattern (fig. 3). The structural bases for these patterns are discussed below.

In the following paragraphs, a number of other continuous enamels are described. For the sake of brevity, only those features that are significantly different from those described above are mentioned. Similarly, for prismatic, discontinuous enamel structure, one general description suffices for all.

Non-therian Enamels

Docodonta (*Docodon*, Late Jurassic): This is a structureless, continuous (non-prismatic) enamel; the width of the alternating dark and light bands is about 1.5 μ, with the enamel surface parallel to a major polarization axis under crossed nicols.

Triconodonta (Triconodont, Late Jurassic): The enamel is continuous (non-prismatic) in structure. Band width averages 2.7 μ.

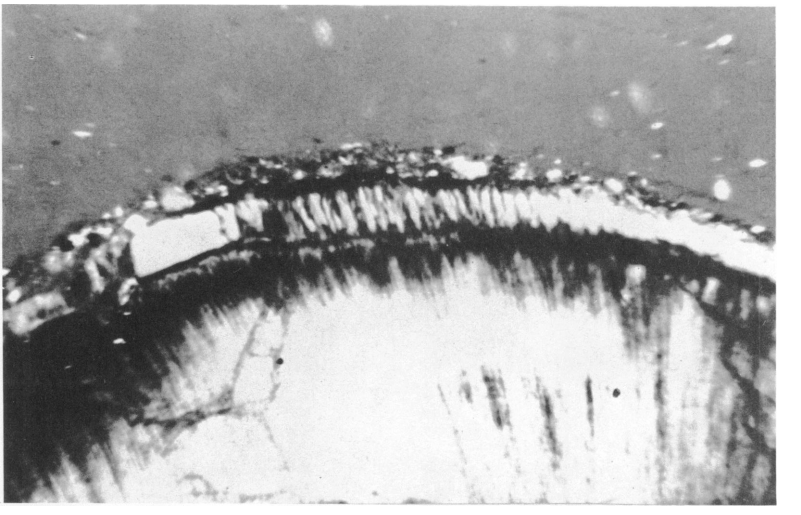
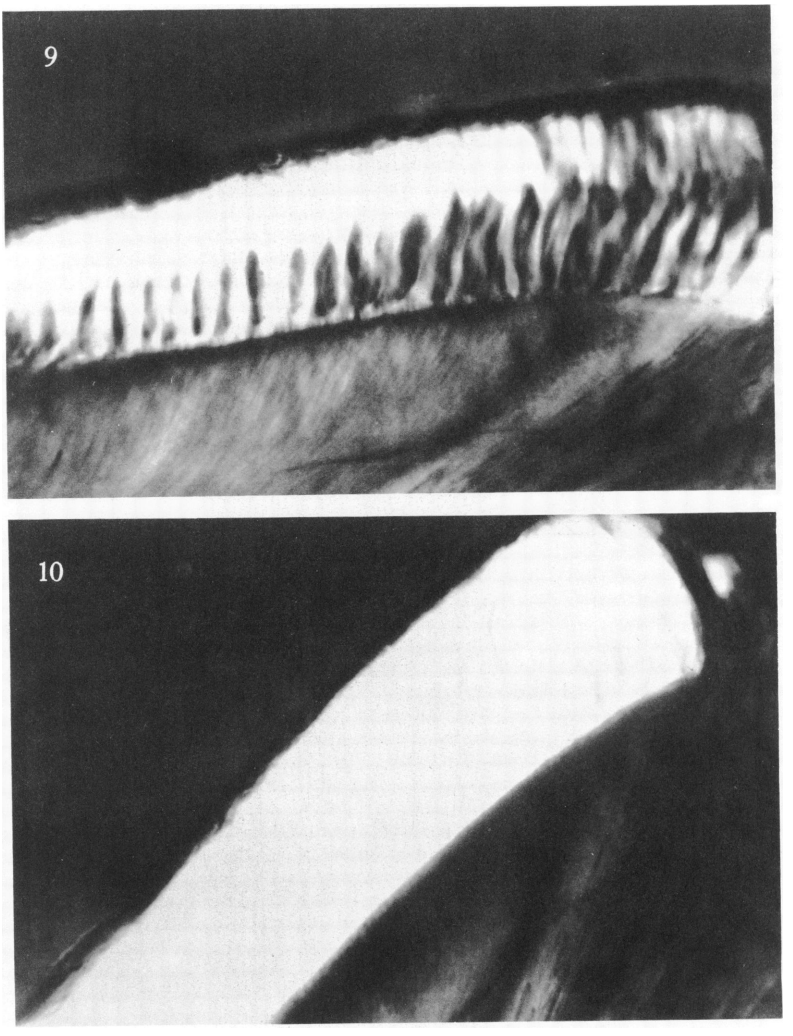


FIG. 8. The enamel of a plagiaulacid multituberculate (uncatalogued) of the late Jurassic shows a typical banded appearance when parallel with a major axis of polarization.

Astroconodon denisoni (EARLY CRETACEOUS, ALBIAN): This enamel appears identical with that of the geologically earlier triconodont (band width, 4 μ).

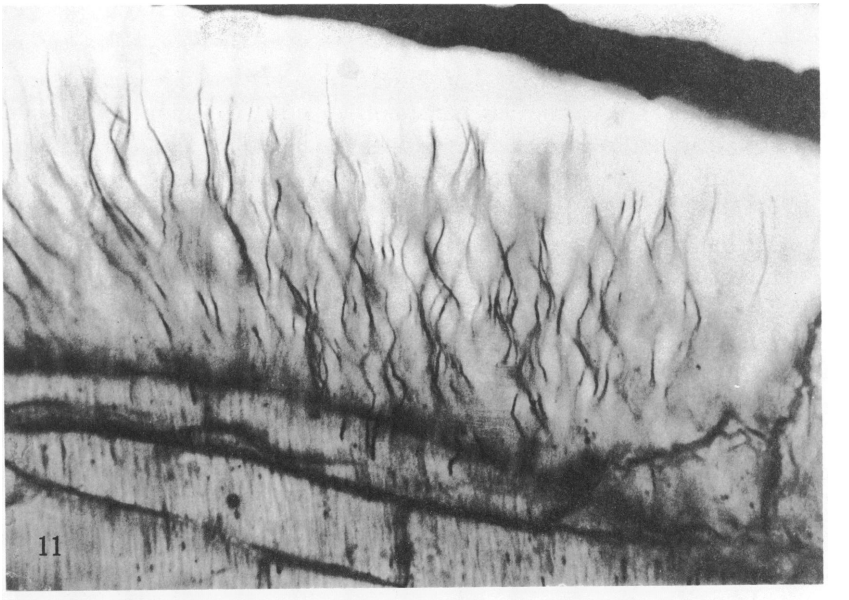
MULTITUBERCULATA: I was fortunate in having a good range of specimens. With one possible exception (*Taeniolabis taoensis,* early Paleocene) all these enamels are "tubular," that is, vertically running spaces are observed within the enamel. The nature of these tubules is discussed below, where it is suggested that they represent a non-calcified portion of the enamel "prism." The earliest multituberculate in our series is a late Jurassic plagiaulacid. This has a non-prismatic, continuous enamel (fig. 8). Aside from its tubular inclusions, it does not differ in its optical behavior from the other mammalian teeth so far described. The width of its alternating bands averages 7.0 μ. In the particular tooth studied there is a dark, black-brown stained layer between a thin unstained outer layer and a thicker unstained inner layer in the cuspal enamel. No such stained layer is observed in the lateral enamel surfaces. The tubules, although not filled with any particulate matter, are easily visualized in phase microscopy. The early Cretaceous multituberculate enamel is identical in all respects.

The next specimen is an unidentified multituberculate from the upper Cretaceous (Campanian) of Wyoming. This also has a tubular, con-



FIGS. 9, 10. 9. The banded structure of the enamel of a late Cretaceous (Campanian) multituberculate (A.M.N.H. No. 80007). 10. The disappearance of these bands on rotation of the section to a diagonal position.

tinuous enamel. The banded structure (each band is about 5 μ in width) is well seen (figs. 9, 10). The enamel differs from that of the earlier multituberculates in one interesting respect. There seems to be a two-layered structure in the enamel, which has an average over-all thickness of 80 μ. More precisely, the bands make a noticeable bend near the



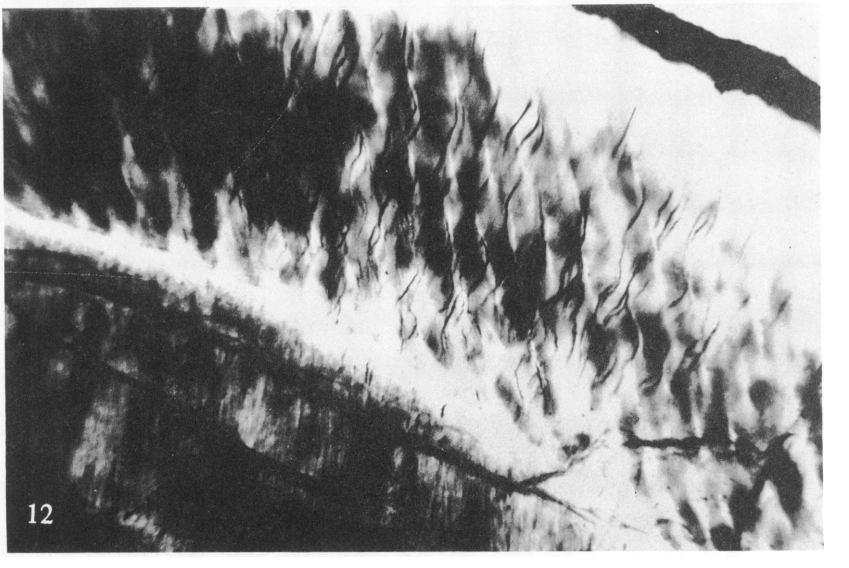


FIG. 11. The spiral form of the enamel "tubules" in the continuous enamel of *Meniscoessus* (uncatalogued), a late Cretaceous multituberculate. This is the thick, inner layer of enamel, with the dentin seen below and the two outer layers of enamel indicated at the upper right.

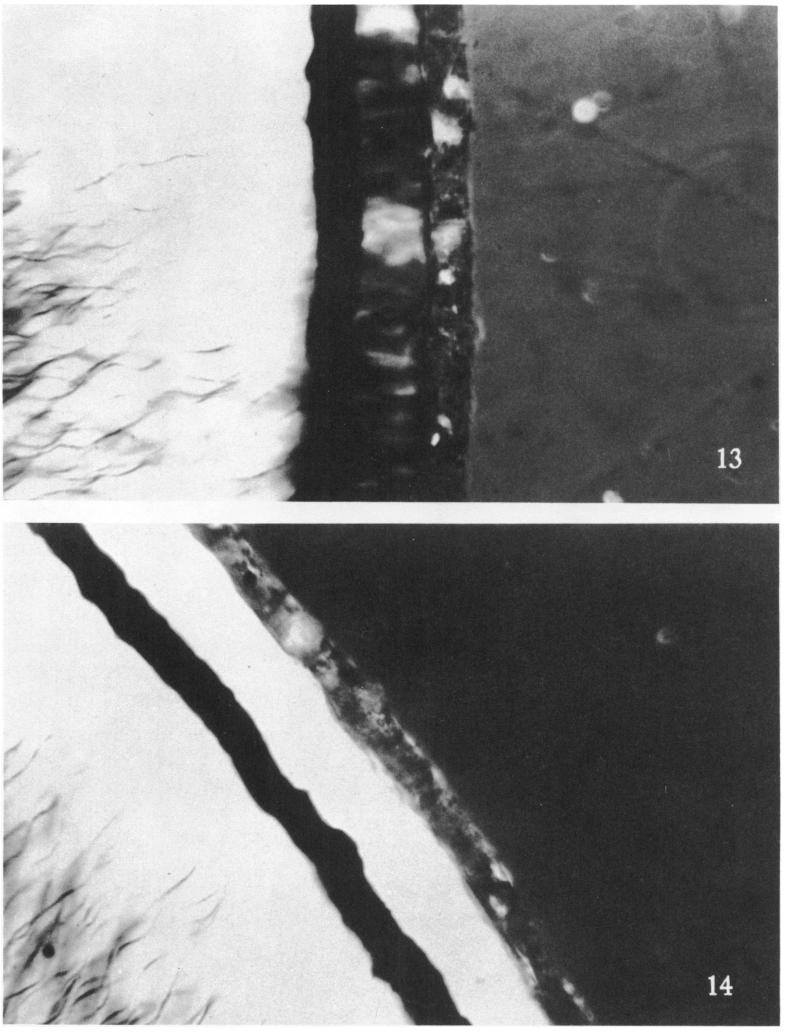
FIG. 12. The same section shown in figure 11 has been rotated slightly clockwise. The cuspally directed banded appearance is now well seen. Note the non-congruence of band and "tubule" directions.

middle of the enamel layer. The inner layer has bands directed somewhat cuspally, but in the outer enamel layer the continuation of these bands is directed so that their long axes lie normal to the outer enamel surface (fig. 9). Careful focusing through the thickness of the section with crossed nicols suggests a possible decussating arrangement of the enamel bands. This section is unusual also in that I was able to detect some indication of these vertical bands with plane polarized light (Poole, 1956).

Meniscoessus: The continuous enamel of this late Cretaceous multituberculate has well-marked "tubules." In the rather thick specimen studied, their spiral-like course is easily observable (fig. 11). The enamel, as a whole, has three distinct layers. The innermost is the thickest and contains the "tubules." The thinnest is an intermediate dark-stained layer the structure of which is completely obscured (figs. 11–14). The outermost layer is totally without tubular inclusions. In this enamel we again observe a change in direction of the alternating banded appearance. In the inner layer the bands (about 10 μ wide) incline cuspally (fig. 12), whereas in the outer layer the bands are normal to the outer enamel surface (figs. 13, 14).

The section of this tooth was fortuitously prepared in such a manner that the enamel of some areas can be observed in cross, oblique, and longitudinal section, because of the coronal morphology. In cross section, under crossed nicols, a series of alternating rows of hemispheres is seen (cf. Poole, 1956). The position of these hemispheres alters as the section is rotated, and is accompanied by simultaneous changes in colors when observed with first order red. In general, these hemispheres are red and the intervening areas yellow when the hemispheric base faces cervically. Rotation of the section causes the hemispheric bases to shift to the left, as the section is rotated clockwise, while at the same time formerly yellow areas become successively red and then blue. These changes, in sum, support my impression that a gradual transition of preferential *c*-axis orientation is being observed, and not an abrupt change, as would be the case in discontinuous, prismatic enamels. These data fully support, and extend, those of Poole (1956) who observed similar, but not identical, structures in synapsid enamel.

Cimolodon (LATE CRETACEOUS): This enamel is structureless in transmitted light and with phase optics. Tubules are present, but not in great numbers, nor are they readily apparent. The now typical banded appearance (6.6 μ wide) is seen under crossed nicols (fig. 15). This is most marked when the section is roughly parallel to the major polarization axes, but does not disappear completely when the enamel is placed



FIGS. 13, 14. 13. The outer layer of the enamel of *Meniscoessus* (uncatalogued) has a banded appearance which lies at an angle to the thicker inner layer, i.e., the former lies normal to the outer enamel surface. 14. Note the abolition of their appearance when the enamel layer is placed in a diagonal position.

diagonally; some dark bands remain. The bands, in general, incline somewhat toward the cusp tips and do not always extend to the surface of the tooth, traversing about four-fifths of the enamel thickness. The upper fifth shows another series of bands, running normal to the outer

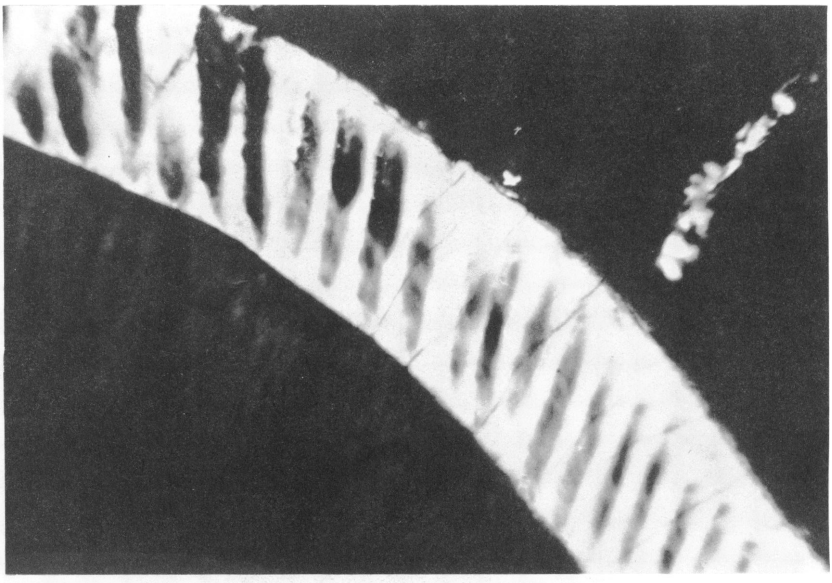


FIG. 15. The enamel of the late Cretaceous multituberculate *Cimolodon* (uncatalogued) demonstrates the typical banded appearance of continuous, nonprismatic enamel.

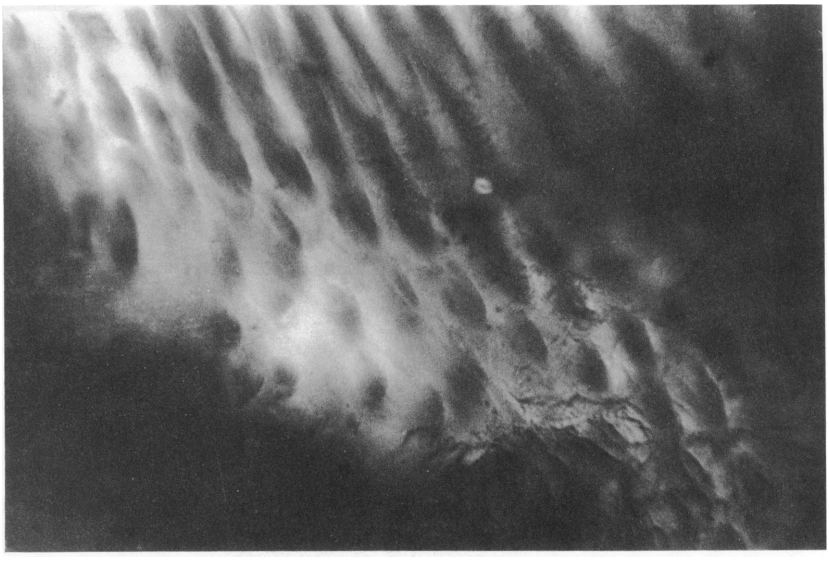


FIG. 16. An enamel fragment of *Taeniolabis taoensis* (Y.P.M. No. 14452), an early Paleocene multituberculate. This oblique section seems to show both cross and longitudinal profiles of banded structure.

FIG. 17. The enamel of a lower premolar of an unidentified mid-Paleocene multituberculate (uncatalogued), showing the large number of enamel "tubules" present. Some "tubules" show the presence of presumably intrusive particulate matter.

enamel surface. Examination with first order red shows the typical alteration of colors reported above. These data indicate once more that a continuous enamel is present, of which the preferential crystallite direction varies continuously from essentially normal to the enamel surface to an orientation that is cervically directed (fig. 3).

Taeniolabis taoensis (EARLY PALEOCENE): Unfortunately, only an enamel fragment was available for study. In this fragment no tubules are observed. The banded appearance of this continuous enamel is the most impressive of the series presently studied. These bands (8 μ in width) are observed arrayed both longitudinally and obliquely (fig. 16).

MULTITUBERCULATE (MID-PALEOCENE): We were fortunate to obtain both an incisor and premolar tooth of this otherwise unidentified form. The continuous enamel is tubular in both teeth, and in many places the presumptive intrusion of geologically derived matrix into the tubules is observed (fig. 17). The tubules of the premolar enamel tend to run without significant curvature from the dento-enamel junction to the outer enamel surface. In the incisor, however, the tubules are sharply angled toward the incisal edge. Band width in the premolar is about 4.4 μ, and averages 6.5 μ in the incisor.

Ectypodus (EARLY EOCENE): In this youngest multituberculate in our

series, we have two teeth for study, an incisor and a premolar. The continuous tubular enamel seen in both teeth does not differ significantly from that observed previously. In the incisor there is some indication of a possible decussation of tubules, as well as an indication that the tubules have a sinusoidal path. The tubules run normal to the dento-enamel junction for a short distance, then incline sharply cuspally, and finally bend again to terminate normal to the outer enamel surface. Band width is about 5.0 μ.

Monotremes

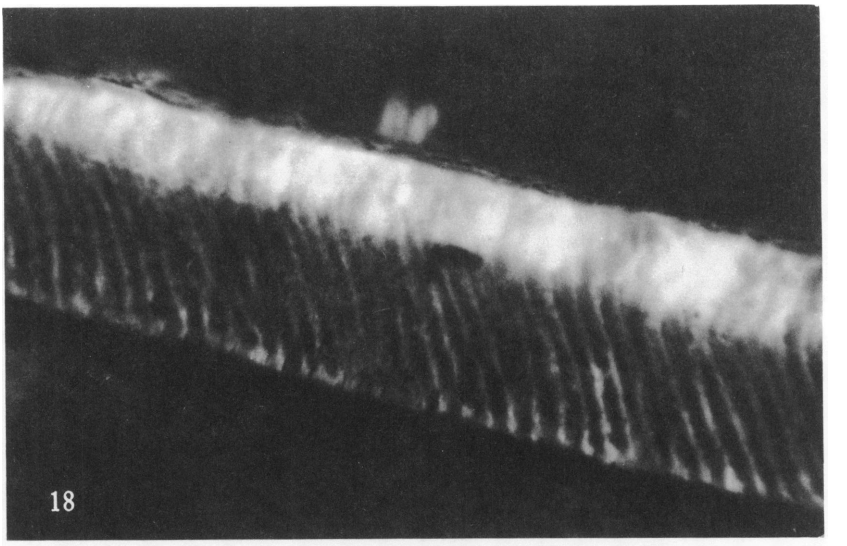
Ornithorhynchus: The rudimentary, fetal teeth of this Recent form pose a problem. We restrict our present remarks to the enamel, and shall report on the unusual histology of this tooth as a whole at another time. The enamel is thin, having a maximum thickness of 0.04 mm., and appears to be tubular. It is positively birefringent. There are indications of horizontal striae in the enamel. It is my opinion that this enamel is continuous, or non-prismatic, in structure on the basis of presently available material. In general the enamel gives maximal brightness in the diagonal positions with crossed nicols, and maximal darkness when parallel with the two polarization axes, although there is some indication of a crystallite orientation that is not observed in the other nontherians but is seen in the synapsid reptiles, and is most noticeable when a first order red plate is in place. A color sequence of yellow-red-blue-red-yellow is observed when the enamel is placed in the extinction positions. The band width observed is very irregular; that is, the alternating light and dark bands do not run in an uninterrupted course through the enamel. A rough average band width is about 5 μ.

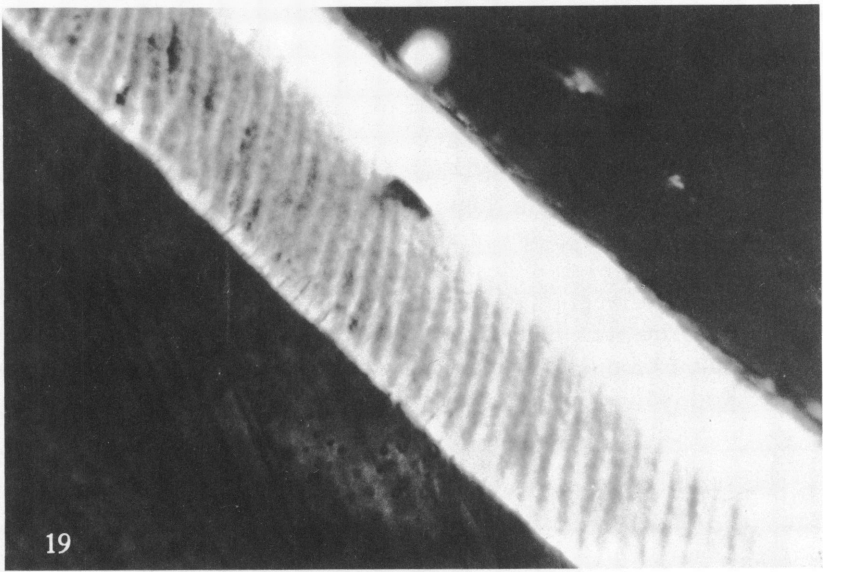
Therian Enamels

Pappotheriidae: Lower molar, Trinity Type 5, early Cretaceous, Albian, Texas (see Slaughter, 1965).

Therian: From the early Cretaceous, Forestberg, Texas (see Patterson, 1956).

True discontinuous, prismatic enamel is found for the first time in the two early Cretaceous therian teeth mentioned above. The enamel as a whole is divided into three zones: (1) a narrow inner zone of continuous (non-prismatic) enamel in which the crystallite *c* axes lie normal to the dento-enamel junction; (2) a thick intermediate zone of "prisms" which are cuspally directed, and in which the "prisms" are seen to be separated by narrower bands of what has previously been termed "inter-





FIGS. 18, 19. The enamel of a lower molar (Trinity Type 5) of *Pappotherium* (uncatalogued), an early Cretaceous therian. This is the earliest therian specimen in our series to demonstrate discontinuous, prismatic enamel.

prismatic" enamel; and (3) an outer zone of non-prismatic enamel, the crystallite orientation of which differs from that of the subjacent pris-

matic zone by being normal to the outer enamel surface (figs. 18, 19).

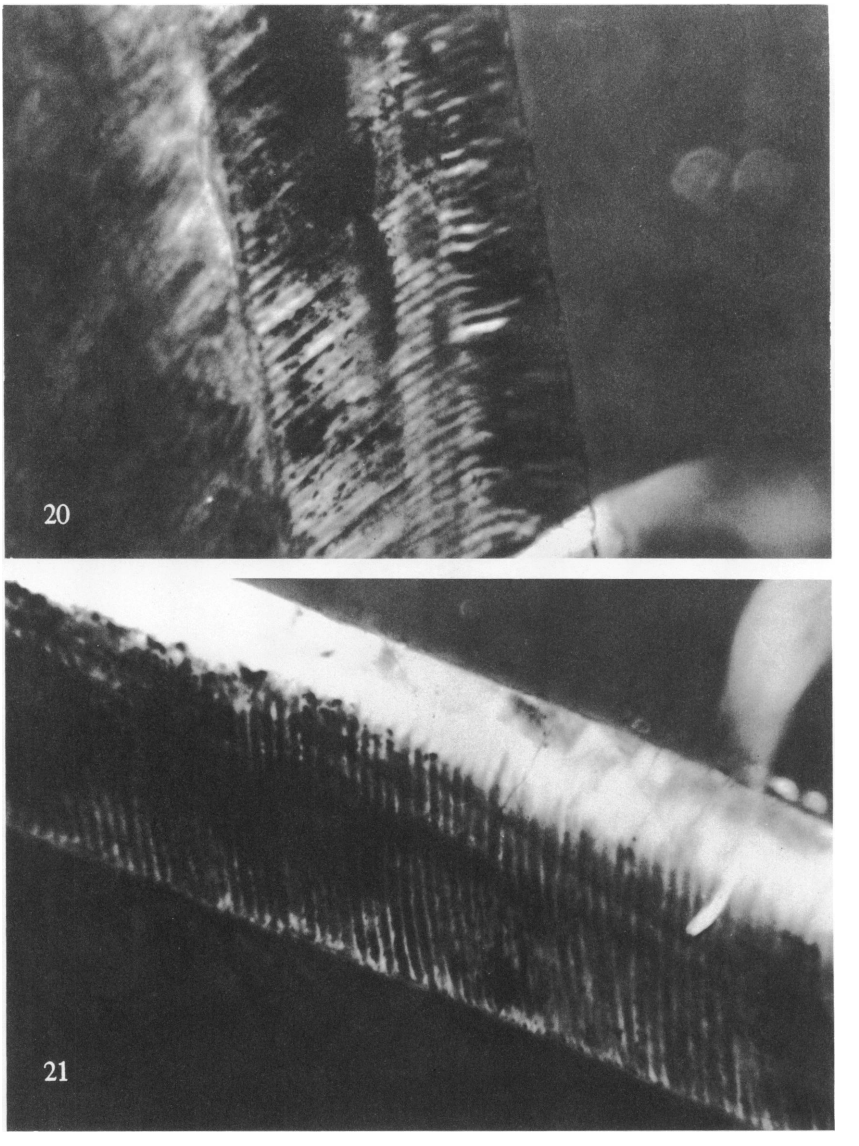
The identification of prismatic and non-prismatic structure is based on the optical properties discussed above. Prism borders are observed faintly but positively in the middle zone with transmitted light, and with greatly increased visualization in phase and plane polarized light. With crossed nicols this middle zone never exhibits a rotation position in which the prisms are not visualized, i.e., the pattern of thick prisms separated by thin interprismatic bands is constant. In other words, the boundary marked by a sharp discontinuity of preferential *c*-axis crystallite orientation is always seen.

The inner and outer zones of continuous enamel have markedly different optical properties from those of the middle zone, in all ways similar to those described above for the other non-prismatic enamels. The now typical banded appearance, with crossed nicols, is most clearly seen when these two layers parallel either major polarization axis, and is lost when these layers are in a diagonal position (figs. 18, 19). Both the bands and prisms have a mean width of 5.0 μ.

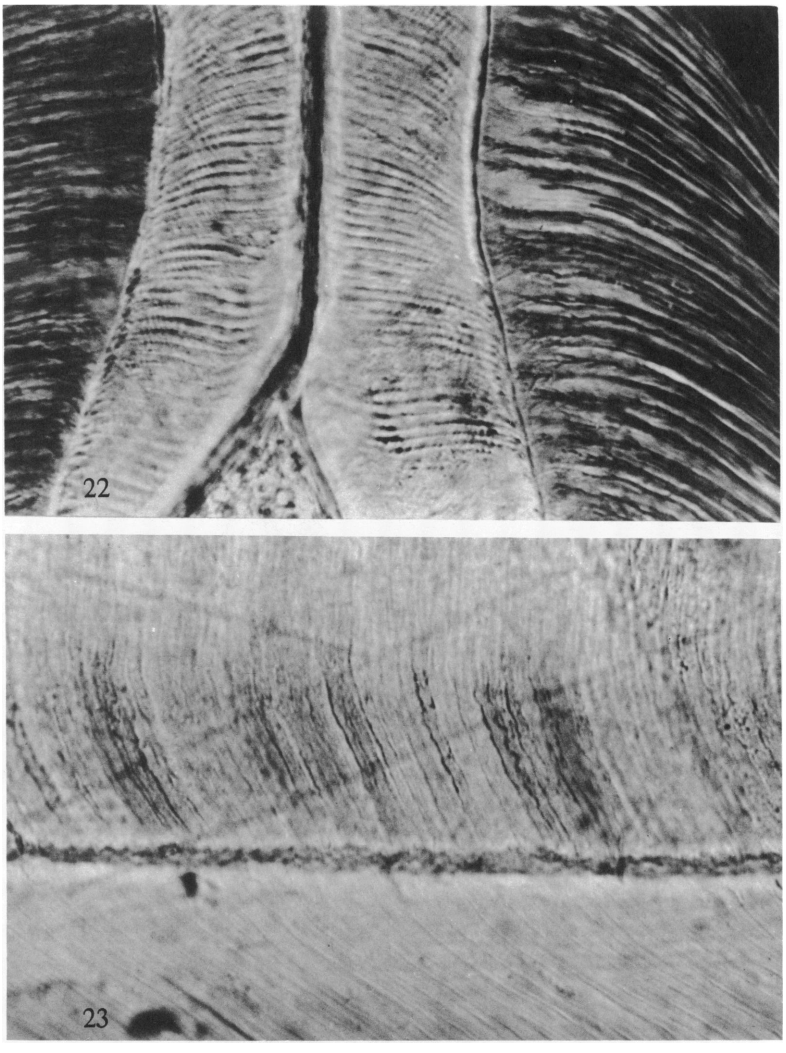
PLACENTALS, *Gypsonictops* (LATE CRETACEOUS): The tooth of this genus, and all other placental teeth, contain discontinuous (prismatic) structure. This late Cretaceous enamel differs in one significant way from that of the other Cenozoic placentals presently studied in that the former enamel has a relatively thick outer zone (one-third of the thickness) of non-prismatic enamel (figs. 20, 21). In this respect it closely resembles the early Cretaceous teeth, although I could not definitively establish microscopically the presence of an innermost zone of continuous enamel in *Gypsonictops*. Here again the prismatic layer is cuspally directed, whereas the outer non-prismatic layer is essentially normal to the outer enamel surface, with respect to its over-all crystallite orientation. As in other mammalian continuous enamels, a gradual change in crystallite orientation is observed within the prism, with the first order plate, which varies from a cervical inclination at the cervical side of the prism to one perpendicular to the outer enamel surface at the cuspal side of the prism (figs. 20, 28).

A fairly extensive series of fossil and Recent placental enamels were examined. Three illustrations are included, showing the appearance of enamel prisms in transmitted light in both late Paleocene and Recent placental enamels (figs. 22–24). Apart from the fact that no significant zones of continuous enamel structure are observed in any of these teeth, nothing of significance for the present paper need be reported.

MARSUPIALS: Prismatic enamel is not an exclusive attribute of placentals; it is found in all the Recent and late Cretaceous marsupials



FIGS. 20, 21. The enamel structure of a late Cretaceous placental, *Gypsonictops* (U.C.M.P. No. V5711). The inner two-thirds of the enamel is prismatic. 20. The outer layer has a banded appearance. 21. The banded appearance is lost when the enamel layer is placed diagonally.



FIGS. 22, 23. The enamel of molars. 22. *Mus musculus*. 23. *Tupaia glis* (uncatalogued).

I have examined. In addition to having a discontinuous structure, marsupial enamel is characterized generally by the presence of "enamel tubules." As is reported above, "tubules" appear independent of the type of enamel structure (i.e., in the multituberculates).

Sections of Recent marsupial enamels (mounted as noted above) differ

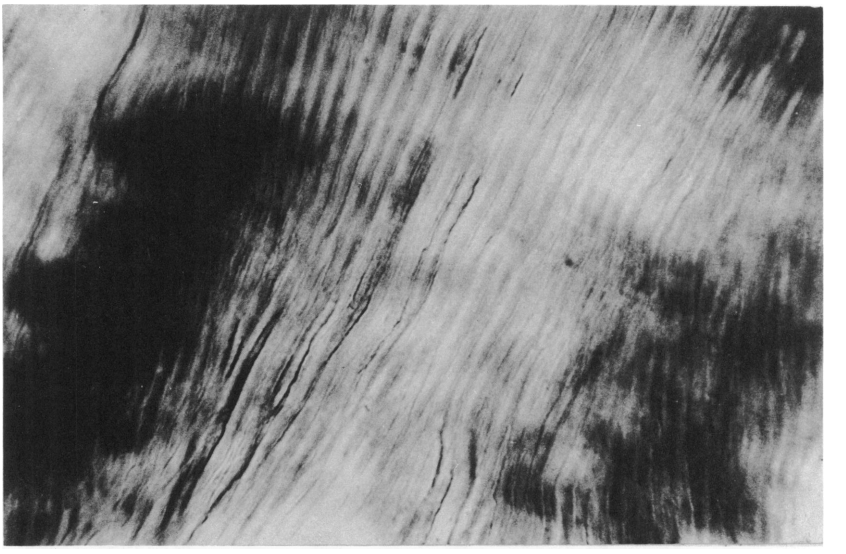


FIG. 24. Enamel of an incisor of a late Paleocene carnivore (uncatalogued).

dramatically from fossil marsupial enamels in the sign of their birefringence, the Recent forms being positive and the fossil forms being negative with respect to prism length. An extensive investigation of Recent marsupial enamel in this laboratory has established that this anomalous positive sign in Recent marsupial enamel is a "form" birefringence, owing to the presence of spaces between the rodlike crystallites which are filled with a substance of which the refractive index differs from that of enamel. It has also been shown that this effect is due primarily to the uncalcified-enamel organic matrix which normally fills the "tubule" space. These data are reported elsewhere. The negativity of fossil marsupial enamels is attributed to a filling of these now empty spaces by intrusive materials, thus permitting the demonstration of the intrinsic negative birefringence of the apatite crystallites.

Some specific comments concerning the individual fossil specimens are pertinent.

MARSUPIAL (LATE CRETACEOUS, CAMPANIAN): The prisms of this specimen are well marked by a series of horizontal striae, easily seen in transmitted light (fig. 25). Prism width averages 5.0 μ. In some areas a dark particulate filling is seen within the "tubular" spaces. Tubules, on the whole, are only sparsely present in this tooth.

DIDELPHID (LATE CRETACEOUS): Prism width averages 5 μ in this

tooth. "Tubular" spaces are much more abundant than in the previous specimen, and the degree of "tubular" filling with intrusive material is also more apparent (fig. 26).

Pediomys (LATE CRETACEOUS): This tooth well demonstrates a general property of most marsupial enamels: cervical enamel is in most cases almost totally free of "tubules." Prism width averaged about 3.3 μ.

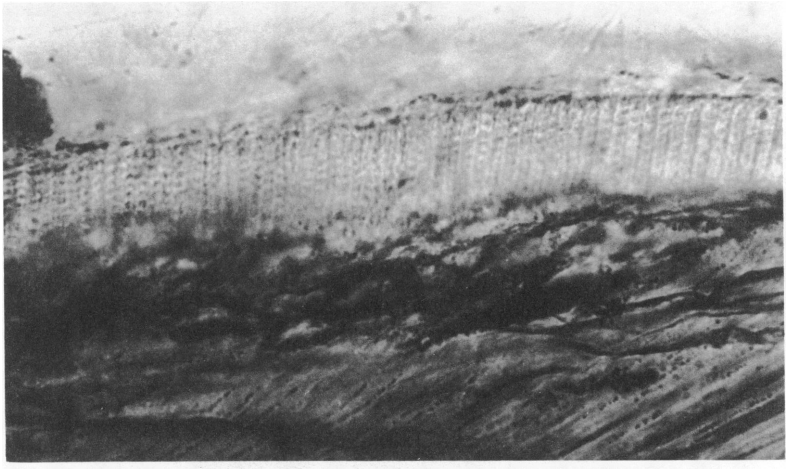


FIG. 25. Marsupial enamel (A.M.N.H. No. 59696), from the late Cretaceous (Campanian). A sparsely tubular enamel, in which both the prismatic structure and horizontal striae are well seen. This figure was taken in transmitted light.

Alphadon (LATE CRETACEOUS): Prism width again averaged 3.3 μ in this discontinuous enamel. Figure 27 clearly illustrates "tubular" filling by intrusive materials. All four fossil marsupial enamels have a negative birefringence.

DISCUSSION

OPTICAL BEHAVIOR AND CRYSTALLOGRAPHIC STRUCTURE OF ENAMEL

ENAMEL PRISM STRUCTURE: The structure of dental enamel in Recent mammals is described as prismatic. Prisms are observed in ground sections studied with ordinary transmitted light. Recent studies demonstrate that the perception of prisms under these circumstances is due in all cases to abrupt discontinuities of the preferential *c*-axis orientation of the apatite crystallites in adjacent enamel areas. These optical discontinuities produce diffraction, reflection, and refraction of light, the sum

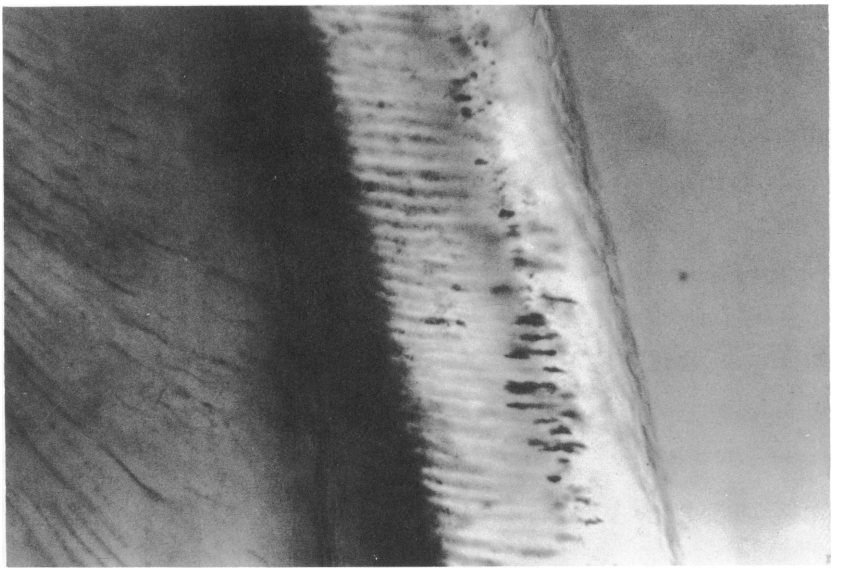


FIG. 26. The intrusive filling of the "tubules" in the discontinuous enamel of a late Cretaceous didelphid marsupial (uncatalogued).

of which causes the phenomenon of a prism border. The prism border is the quivalent of what has been termed the "prism sheath" (Meckel *et al.*, 1965a, 1965b; Boyd, 1965; Carlström, 1965; Rönnholm, 1962a, 1962b, 1962c). The observed width of a prism is the distance between any pair of such borders.

The structure of the mammalian enamel prism has been clarified by recent investigations. There is general agreement that in cross section, in man at least, the prisms are not complete in the sense of being round or hexagonal, as had been suggested in the older literature. It is now suggested that the prism is so constructed that in frontal section it resembles a "keyhole," with a nearly round head facing cuspally and a biconcave, tail-like extension projecting cervically, which fits between the heads of the next lower row of prism heads (Meckel *et al.*, 1965a, 1965b; Hinrichsen and Engel, 1966). The extension of this observation leads to the further conclusion that human enamel is "a virtual continuum" since "the prisms are not closed units having insides and outsides" (Carlström, 1964). Accordingly, interprismatic enamel, as such, is said not to exist in man (see Boyd, 1965, for a partially alternative viewpoint).

The orientation of crystallites within an enamel prism also has been

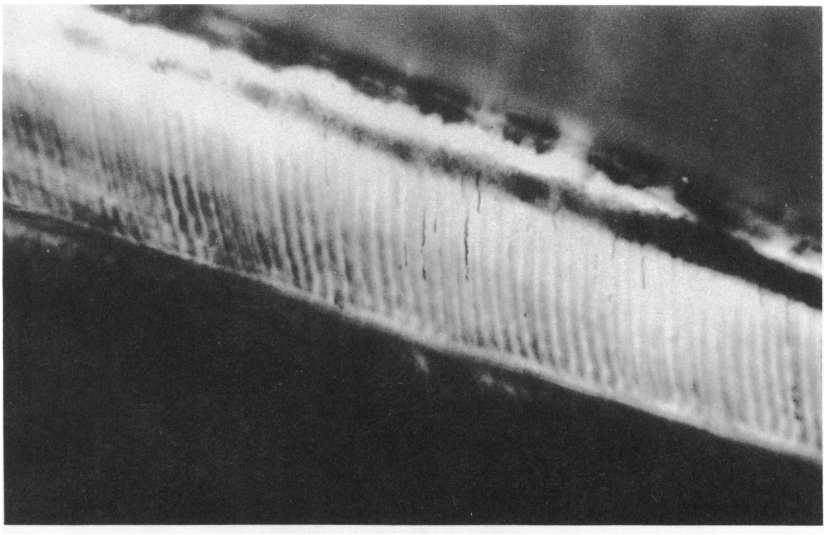


FIG. 27. The enamel of *Alphadon* (U.C.M.P. No. V5711), a late Cretaceous marsupial, demonstrates the filling of several of the "tubular" spaces.

clarified by the use of electron microscopy and X-ray diffraction. In a typical case, it is now established that, in longitudinal section, the cuspal end of a prism has a mean preferential orientation of the *c* axes of the crystallites that is parallel to the prism long axis, i.e., normal both to the outer enamel surface and to the dento-enamel junction. As we progress cervically within any given prism, this means preferential orientation of the crystallite optic axes gradually changes to a direction that is virtually perpendicular (normal) to the prism long axis (Meckel *et al.,* 1965a, 1965b; Poole and Brooks, 1961; Glas, 1962; Rönnholm, 1962a, 1962b, 1962c; Glas and Nylen, 1965). When any two enamel prisms are considered in a longitudinal section, it is obvious that, between the cuspal portion of the more cervical prism and the cervical portion of the next immediately cuspal prism, a sharp discontinuity exists in preferential crystallite orientation (fig. 28). Such is the optical basis for the observation of prisms in transmitted light. It is permissible to speak of this type of enamel structure as crystallographically discontinuous.

Not all mammalian enamels have identical prismatic structures. Again, basing his ideas on patterns of crystallite orientation, Boyd (1965, MS) suggested four different types of structural organizations in recent Mammalia, all of which are, nevertheless, prismatic. In some of these types "interprismatic" enamel must exist. Shobusawa (1952) further suggested

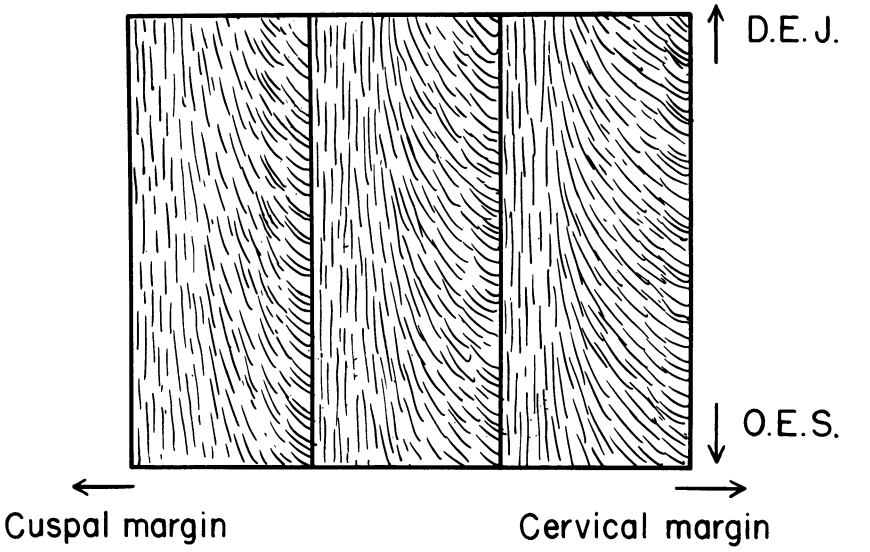


FIG. 28. A graphic representation of the mean preferential orientation of the *c* axes of hydroxyapatite crystallites in discontinuous (prismatic) enamel. Although this *c* axis direction is parallel with the long axis of the "prism" in the cuspal portion, there is a marked divergence of *c* axis direction in the cervical portion of this same "prism." The region of sharp discontinuity between any two such areas produces the optical phenomenon of a prism boundary.

Abbreviations: D.E.J., dento-enamel junction; O.E.S., outer enamel surface.

that all recent mammalian enamels have structural patterns of prism arrangement that are species specific, a point not yet confirmed.

The cytological processes underlying the production of prismatic enamel apatite crystallites have been demonstrated recently (Rönnholm, 1962a, 1962b, 1962c; Boyd, 1965). In essence they depend on a single fact, i.e., that all enamel crystallites are formed in such a manner that their *c* axes are essentially normal (perpendicular) to the related portion of the distal ameloblastic plasma membrane. This relationship is significant when coupled with the observation that more than one ameloblast is involved in the formation of a single prism. Figure 29, adapted from electron photomicrographs originally published by Rönnholm (1962a, 1962b), clearly demonstrates these points (cf. Boyd, 1965, MS). A single ameloblast, in the plane of section illustrated, has a distal plasma membrane that is parallel to the length of cuspal prism, as well as normal to the length of the next cervical prism. The *c* axes of mineralizing crystallites lie normal to both portions of the plasma membrane;

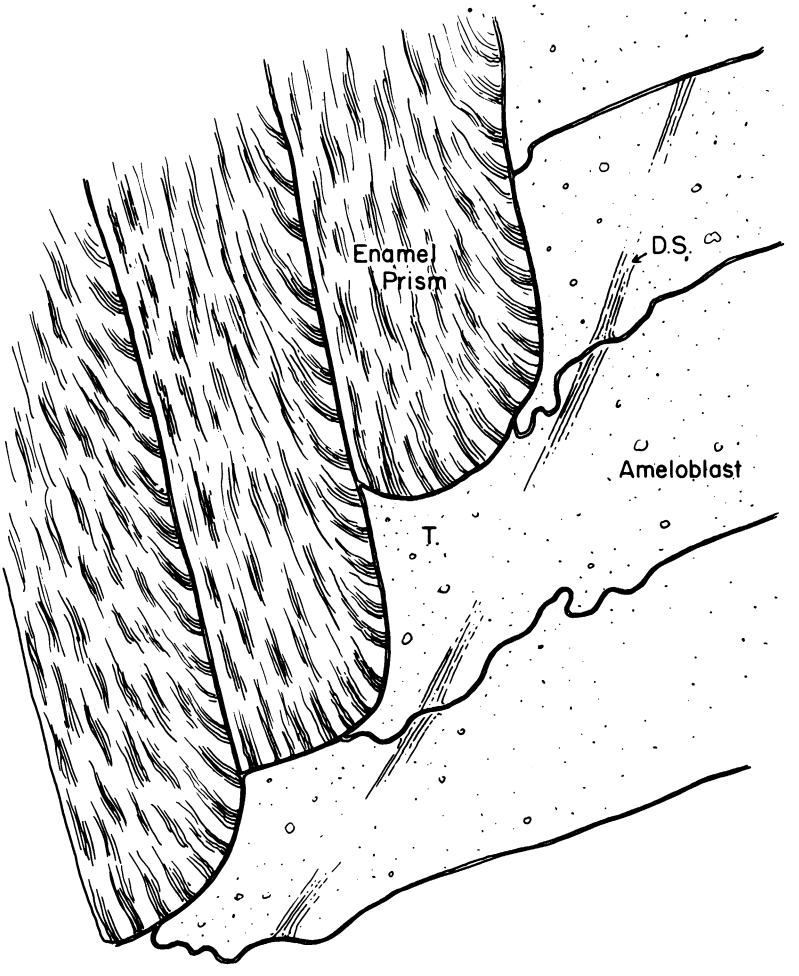


FIG. 29. The formation of discontinuous enamel. Note that the distal plasma membrane of any single ameloblast is related to the formation of more than one "prism." The *c* axes of the hydroxyapatite crystallites within the enamel are seen to arise perpendicular to the distal plasma membrane immediately adjacent to them. The cuspal portions of the "prisms" lie to the right of this figure, and the cervical portions to the left. Compare with figure 28. Adapted from Rönnholm (1962a).

Abbreviations: D.S., distal septum; T, Tomes process.

accordingly this single ameloblast gives rise to crystallites the mean preferential orientations of which are strikingly discontinuous. Boyd

(1965, MS) suggested that the mode of "packing" of ameloblasts is related to the four different types of enamel he observed, a subject beyond our present scope. In summary, available data provide an adequate morphological description of the development of prismatic enamel in mammalian teeth.

CONTINUOUS (NON-PRISMATIC) ENAMEL: When enamel structure is classified on the basis of preferential crystallographic orientation, the term "discontinuous" is a proper synonym for prismatic structure. Accordingly, we suggest that continuous enamel is adequately descriptive for the non-prismatic enamels of the early mammalian teeth.

Actually, continuous enamel is found in human teeth in several normal and pathological conditions. Rushton (1964) described a homogeneous, non-prismatic enamel in hereditary enamel hypoplasia. The same paper cited the apparently spontaneous appearance of continuous enamel in the teeth of Musschenbroek's palm civet. One need not, apparently, seek such rare instances. Ripa and his co-authors (1966) reported that "prismless" enamel is present in the outer enamel layer of all deciduous human teeth and in 70 per cent of the permanent human teeth they had examined. These authors considered this to be a normal feature of human enamel. They attributed this continuous enamel, correctly it would seem, to a "loss of the staggered or step-like arrangement of adjacent ameloblasts." Their further suggestion that the resultant linear ameloblastic orientation is a result of reduced functional activity is discussed below. That the *c* axes of the crystallites in the outermost enamel layer are perpendicular to the surface has been shown by Lobjoie (1965) and by Baud and Lobjoie (1966). Rönnholm (1962b) noted that in the first enamel formed in human teeth, up to a thickness of about 1.5 μ, "there are no indications of subdivision of the enamel into rods or prisms." At this early stage of amelogenesis, the distal surfaces of the ameloblasts are perpendicular to the long axis of the ameloblast; the change in topography to an oblique orientation occurs later, coincidently with the first appearance of prisms.

EVOLUTION OF CORONAL MORPHOLOGY

It is pertinent to note in the recent statement of Mills (1964) that the earliest stage of therian dentition occurs in the symmetrodont molars of the latest Triassic. This apparently is identical to Kermack's "unnamed Welsh pantothere." Whatever the nature of the undoubted genetic factors underlying this alteration in gross coronal morphology, and all subsequent ones, they were all brought about by homologous ontogenetic

processes within the enamel organ. Whether the primary genetically influenced change occurred in the ectomesenchyme of the presumptive dental papilla, or resided in the basal layer of the topographically related oral ectoderm, or, indeed, was the result of the interaction between the two is beside the point (Lyne and Short, 1965, gave a stimulating review of this general problem). What is important is the fact that the well-known series of sequentially interrelated inductive sequences associated with odontogenesis could, and did, evolve so as to produce a recognizably therian crown form. This gross morphological evolutionary change is independent of the crystallographic structure of the enamel so produced, which implies that the spatial orientation of functioning ameloblasts, with respect to the developing enamel, is independent of the total form of the mammalian enamel organ of which they are a part, and, further, that neither the size nor the shape of the mammalian tooth crown is correlated necessarily (causally) with the crystallographic orientation of the enamel. Finally, it appears that tooth function is similarly independent of enamal crystallite organization.

Evolution of Enamel

We note above that the origin of enamel in vertebrates remains a point of controversy. There is no question about the true ectodermal origin of the enamel of reptilian and mammalian teeth; the older concept of Marcus (1931), that dentin gave rise to enamel phylogenetically, has been rejected. We note the recent summary statement of Carlström (1964), "that dental enamel from varying sources may exhibit considerable variations both with regard to morphology and histology, but the underlying ultrastructural patterns remain surprisingly much the same throughout the whole subphylum of vertebrates." The implication is clear that we are concerned with evolutionary changes that simply rearrange essentially identical ultrastructures.

This point is emphasized by the study of Poole (1957) on the organic matrix of reptilian tooth enamel, in which he stated, "the process of enamel function in reptiles is essentially the same as the corresponding process in mammals." Poole believed that two "important changes" mark the evolutionary step from reptilian to mammalian enamel. Of course, we must be aware that Poole assumed that prismatic enamel appeared in the earliest mammals, and judge his statements accordingly. He noted: (1) that reptilian enamel organic matrix is "continuously fibrous," whereas the mammalian matrix is "broken up into units," and (2) that "the second important change in the evolution of prismatic

enamel was the production of a more refined and delicate matrix instead of the coarse, fibrous type characteristic of reptiles." In other words, qualitative and spatial alterations of the enamel matrix mark the origin of discontinuous enamel. Because we cannot recover the organic matrices of fossil mammalian teeth, or observe their amelogenesis, this concept must remain theoretical. To the extent that Poole's speculations are correct, we would amend them by stating that these changes did not occur until the early Cretaceous in therians, and not at all in non-therians.

The evolutionary change of enamel from a continuous to a discontinuous structure is the result of a change in orientation of the functioning ameloblasts in relation to the enamel front. In the former the long axes of the ameloblasts are perpendicular to this front; in the latter the ameloblastic long axes are inclined toward the cervical and angulated to the front of the developing enamel.

Subsequent Evolution of Prisms

Post-Jurassic therian enamels are prismatic. We note above a great variation in prism pattern in the teeth of fossil and Recent marsupials and placentals. This phenomenon, together with enamel prism formation, is completely accounted for by postulating specific topographic relationships between functioning ameloblasts and forming enamel. Boyd (1965, MS) presented a full account of these developmental relationships and their consequences for crystallographic orientation in a series of Recent marsupials and placentals. It is entirely reasonable to assume that homologous relationships existed in the post-Jurassic fossil forms. It is not the purpose of the present paper to consider in detail the subsequent stages of prismatic enamel evolution.

We wish, however, to emphasize the retention, in man at least, of continuous (non-prismatic) enamel layers, in the first and last enamel formed. Our data suggest that the acquisition of discontinuous enamel was a gradual process, with the continuous enamel very much in evidence in the outer layers of the Cretaceous forms. We speculate that in post-Cretaceous enamels the amount of continuous enamel is only gradually reduced. Although a comprehensive study of the innermost and outermost layers of recent therian enamels remains to be made, it is likely that all Recent therian enamel has some continuous layered component. Accordingly, we suggest that the acquisition of discontinuous enamel has been a gradual, and incomplete, evolutionary change.

The reader may have assumed tacitly that all aspects of enamel prism evolution are genetically (intrinsically) determined. In this regard it is pertinent to note the interesting, but yet unconfirmed, report of Helmke

(1962) on the structural pattern of the incisor enamel of the mouse (*Mus musculus*). This enamel is normally prismatic, with its prisms arranged to produce what Helmke termed an interlayered "plywood" pattern. When incisor tooth buds in mice are implanted intracerebrally they produce teeth with a normal external shape; however, the alternating "plywood" pattern is lost. Helmke (1962) believed that "since the final structure of enamel is the result of the reciprocal interaction between the secretory power of the ameloblasts on one hand and the spatial conditions in the alveoli on the other," environmental (extrinsic) factors must play an important role in ameloblast orientation in this tooth. The possible extension of the influence of similar extrinsic alveolar factors to the problems of continuous and discontinuous enamel structure are intriguing, but speculative. For example, Glasstone (1954) noted that mammalian tooth germs grafted onto the chorio-allantoic membrane of the chick produce prismatic enamel, whereas when such tooth germs are grown *in vitro* non-prismatic is produced.

Two other points have a possible relation to enamel crystallite orientation. The first is the crown size of a tooth, and the second is the rate of enamel formation. We sectioned two very small Recent teeth, the maxillary third molar of a mouse (*Mus musculus*) and the maxillary third molar of *Microgale cowani.* Both enamels are discontinuous in structure, with prisms clearly visible. Accordingly, we believe that size *per se* is not a determining factor in ameloblastic orientation. The second point is more difficult to assess. It is possible theoretically that crystallite orientation, in terms of continuous or discontinuous structure, is related to the rate of formation. There are data indicating that the beginning and end of amelogenesis, when continuous enamel is formed in human deciduous teeth at least, occur at slower rates than does the formation of the main body of the enamel. Kraus (1959) indicated that a significant curvilinear regression, "not unlike the typical sigmoid growth curves of postnatal development," is found when calcification rates are determined. Kraus's paper also gave some quantitative data for human amelogenesis, but similar data do not exist for reptilian teeth (Edmund, 1960, 1962). By extension these data suggest that continuous enamels may arise in all mammals when amelogenesis is "slow." Unfortunately, we can give no valid meaning to the term "slow" as a rate, and we are not able to estimate the critical rate of amelogenesis associated with discontinuous structure, if such a relationship in fact exists. A more critical objection to a rate-related explanation is given below in the paragraph headed Tubular Enamel.

Enamel Inclusions

A number of structures are customarily described as normal inclusions in human enamel: tufts, lamellae, and spindles. Other optically observed structural arrangements of enamel include the striae of Retzius and the bands of Hunter-Schreger (see Hinrichsen and Engel, 1966, for a recent review of the structural bases for these). With the exception of the striae of Retzius, which are observed as noted in the descriptions of the individual sections, I am impressed by the lack of enamel inclusions in fossil enamels. An adequate study of this question requires significantly larger samples for each species than could presently be obtained. Nevertheless, the phylogeny of enamel inclusions is worth further study. Such structures are to be found in Recent alligator enamel (Kvam, 1959).

Tubular Enamel

So-called tubular enamel is found in many of the non-therian teeth, as well as in the marsupials. Tubular enamel structure is not correlated with either a continuous or a discontinuous enamel structure, amending the statement of Poole (1957) that "tubular enamel possesses both prisms and tubules." Tubular enamel is a misnomer, because the "tubules" do not consist of cell processes of any sort, but rather represent areas of uncalcified enamel organic matrix. Their visualization in ground sections is, in fact, an "artifact" of preparation (Moss and Applebaum, 1963), a view supported by Boyd (MS). Moss and Applebaum suggested that such areas of uncalcified enamel matrix might reflect the relative rapidity of amelogenesis in marsupials. If so, we may conclude that the rate of amelogenesis plays no causal role in enamel crystallite orientation in the prismatic enamel of marsupials, and, further, that similarly rapid amelogenesis may have occurred in the fossil non-therian forms with tubular enamel. Such a conclusion remains speculative.

SUMMARY

A polarization microscopic study of evolutionary changes in mammalian dental enamel structure is reported. An extensive series of fossil and Recent teeth were studied. The data show that the enamel of the earliest true mammals was non-prismatic (continuous), that true prismatic (discontinuous) enamel structure first arose in the early Cretaceous (Albian) therians, that in placentals prismatic enamel only gradually became the predominant structural type, and that non-therians did not evolve prismatic structure at any time.

A discussion of current theories of amelogenesis and its relationship to the orientation of the *c* axes of the enamel crystallites suggests that the nature of the evolutionary change in enamel structure is an alteration of the orientation of the ameloblasts in relation to the developing enamel front.

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