

The Enamel Microstructure of the Early Eocene Pantodont *Coryphodon* and the Nature of the Zigzag Enamel

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An additional method for the investigation of the microstructure of enamel is described using the teeth of *Coryphodon*, *Uintatherium*, *Entelodon*, and *Crocota*. Under low magnification natural surfaces or sections of teeth display details of the enamel microstructure when the light guide effect of prisms is used. Under the same low magnification even more details were obtained from sputter-coated surfaces of sections. The method is of particular significance for the investigation of large teeth with thick enamels when structures are somewhat irregular. The new method provides a better general survey, where scanning electron microscope images often show confusing details. The enamel of *Coryphodon* shows oblique lines of nested chevrons that are similar, to some degree, to the zigzag enamel in *Crocota*, but a distinct asymmetry between ascending and descending lineaments was observed. This specific *Coryphodon*-enamel was also found in *Uintatherium* and *Entelodon*. This enamel type, which evolved several times in parallel, cannot be attributed to a specific diet, but must be regarded as one of the several ways to strengthen the enamel against breakage.

KEY WORDS: *Coryphodon*, *Uintatherium*, *Entelodon*, enamel microstructure, zigzag enamel, Hunter–Schreger bands.

INTRODUCTION

Tooth enamel microstructure provides a number of detailed characters very useful for phylogenetic and functional interpretation. Since enamel microstructure is well preserved in the fossil record it is possible to trace the evolution of the different enamel types and their spatial combination in the schmelzmuster.

Among the extant larger placental mammals transverse Hunter–Schreger bands (HSB) are the most common specialization for strengthening the enamel. Many large herbivores of the early Tertiary, however, show quite unique enamel structures (Fortelius, 1985; Pfretzschner, 1994; Koenigswald, 1997). Most of these lineages are extinct, only

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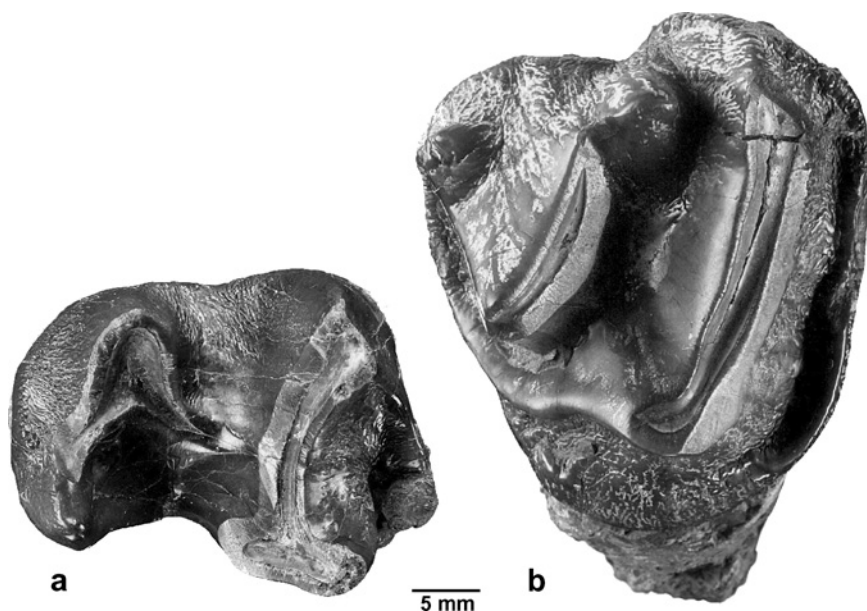


Fig. 1. Lower and upper molars of *Coryphodon* sp. (a, left m3, USNM 488343; b, right M2, USNM 488344), Wasatchian, Willwood Formation, Bighorn Basin, Wyoming. The sharp shearing facets characteristic of a herbivore are clearly visible. The enamel surface in the unworn parts shows the distinctive wrinkles oriented more or less vertically.

rhinoceroses, which show vertical HSB (Rensberger and Koenigswald, 1980), having survived to the present day.

This study focuses on one of the biggest herbivores from the early Tertiary, the pantodont *Coryphodon*, the largest species of which probably weighed 600–700 kg (Uhen and Gingerich, 1995). *Coryphodon* is the most common large mammal in the latest Paleocene and early Eocene (Clarkforkian–Wasatchian) of western North America, and is also known from the early Eocene (Ypresian) of Eurasia. The abundance of *Coryphodon* teeth (Fig. 1) in the Eocene of Wyoming facilitated this study.

Large teeth with a complex enamel structure cause some problems when studied with conventional methods. Therefore we demonstrate here the method of reflecting light images under low magnification as an additional tool which has been used so far only sporadically (Fig. 2a–c).

Bill Clemens has always shown a deep interest in the evolution of early mammals. He has always welcomed new methods for providing additional characters for phylogenetic analysis. Therefore it is a pleasure to dedicate this paper to him.

MATERIALS AND METHODS

Coryphodon tooth samples used in this study derive from collections made over many years by the U.S. Geological Survey and Johns Hopkins University expeditions in the Bighorn Basin, Wyoming, conducted by T. M. Bown and K. D. Rose. All are from lower Eocene (Wasatchian) strata of the Willwood Formation (Bown *et al.*, 1994).

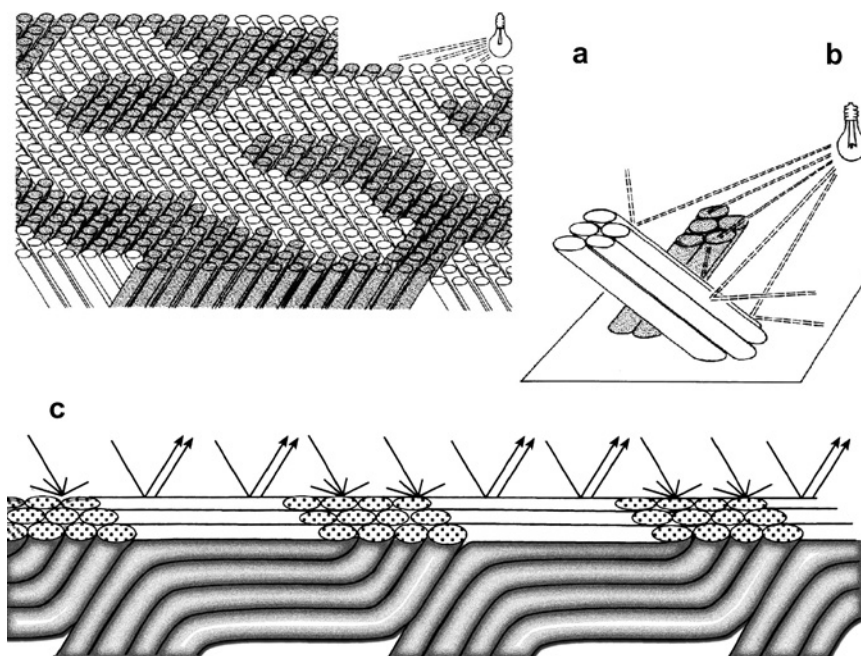


Fig. 2. (a) The light-guide effect of enamel prisms is due to the subsurface microstructure. In Hunter-Schreger bands one set of prisms appears dark since the light is guided away by the prisms; in the other set oriented at an angle the light is reflected from the outside of the prism. This optical effect becomes relevant only when the effect is multiplied by several parallel prisms (from Koenigswald and Pfretzschner, 1987). (b) Model of the light guide effect. Light is reflected from the side of prisms but vanishes within the prisms when it meets the cross-section (from Koenigswald and Pfretzschner, 1987). (c) The reflected light pattern of etched and sputter-coated enamel sections is a surface phenomenon. The coarse cross-sections of the intersected prisms scatter the light and appear dark while prisms exposed more or less parallel to their long axis reflect the light.

Enamel sections from lower incisor, canine, premolar, and molar, as well as upper molar, were examined (KOE 1019, 1302, 3676–3684). For comparison several enamels from different mammals were examined, especially *Crocota spelaea*, from the Upper Pleistocene, Germany (KOE 62), *Uintatherium* sp., from the Bridgerian of Wyoming (YPM 11204–KOE 2783), and *Entelodon* sp. from the White River Oligocene of western Nebraska (KOE 1989).

The method of investigating enamel microstructure has been described mostly for small teeth (Koenigswald, 1980; Martin, 1992; Kalthoff, 2000). The investigation of large teeth like those of *Coryphodon* required some modifications. Teeth were cut into pieces before imbedding them in epoxy resin, taking care to note the direction of the occlusal surface, so that the desired section (tangential, longitudinal, or transverse) could be placed parallel to the resin surface. Thus flat tooth areas were selected for ease of preparing tangential sections, and horizontal and vertical cuts were made in other pieces to facilitate preparation of transverse and longitudinal sections. It saves time if it is decided in which direction a tooth fragment will be investigated before imbedding it. The proposed section can be oriented parallel to one of the sides of the resin block.

The imbedded fragments are sectioned in the selected way and then ground in three steps. Initial grinding to the enamel surface was done on the wheel (grit 250), followed by hand grinding on fine wet sandpaper (grit 400) wrapped around a glass plate, and then on fine powder (grit 1000) in water on a glass plate. Polishing is not needed. The ground surfaces were rinsed off, cleaned in an ultrasonicator, blown dry, and etched with 10% hydrochloric acid (2 normal HCl (about 10% HCl) for about 2–5 s. Experience shows that etching with a strong acid for a short time produces a strong profile, useful to investigate the prism orientation. Etching with a weak acid for a longer time might reveal the crystallites in more detail, but the general structure is more difficult to investigate. There is no optimal time for etching since slight differences in the fossilization may cause different results. Therefore sections may be easily reground and etched again if the result is not satisfactory. Usually the etched surface is sputter coated and investigated in the scanning electron microscope (SEM).

In the longitudinal sections of teeth of most larger or medium-sized mammals structures such as HSB regularly repeat at relatively short distances, and are visible at the same magnification that reveals prisms (roughly at a magnification of 200× or at lower magnification under the binocular microscope).

Fragments of larger teeth or thick enamels can cause a problem, however, since at a magnification at which the prisms are clearly visible the larger structure might not be evident any more. In the longitudinal section of *Coryphodon* we detected some structures that did not show a distinct repetition of the pattern. A transverse and somewhat oblique section perpendicular to the crenulations on the surface of a premolar showed a repeating pattern caused by different prism orientation, when an area of about 24 adjacent SEM images were compiled.

The mosaic measured about 1.5 m in length, exceeding any publishable scale. To document these major structural elements in thick enamel, all prisms visible for more than 10–15 μm were marked manually with color in order to differentiate them from those exposed in cross-section. Figure 4b shows this mosaic reduced for publication, with the colored areas shown in white, while the cross-sections of prisms appear gray.

To study the tangential sections we turned to another way of investigation, the analysis of reflecting light under low magnification which uses the light-guide effect of the enamel prisms (Koenigswald and Pfretzschner, 1987). If light meets an enamel prism approximately perpendicular to its long axis, the light is reflected and the prism appears light. If the light hits a prism parallel to its long axis, the light disappears into the prism and the prism appears dark (Fig. 2a and b). This effect is only visible at relatively low magnification (approximately 10–50 times) when several adjacent prisms are oriented in the same way so that the optical effect is multiplied. Already over two centuries ago Hunter (1778) and Schreger (1800) depicted these light and dark bands in enamel, but not until much later did Preiswerk (1894) relate the light and dark bands to orientation of the enamel prisms. Many teeth show such light and dark bands under a binocular microscope when they are illuminated from one side. Since the light summarizes an effect of different depth the bands are usually not very sharp and it is very difficult to focus on them. This effect can be used on unprepared teeth as well as on sections. A very similar effect is shown by etched sections when they are sputter coated, but here the reflection comes from the surface only, so the picture may be more focused. The coarse cross-sections of intersected prisms scatter the light and appear dark, while the prisms exposed more or less parallel to their long axis for some distance reflect the light like a mirror (Fig. 2c).

Since the reflection depends on the direction of the incoming light and the prism orientation, the image changes when the light is moved. Therefore we mounted the sections under a binocular microscope and rotated the light source around the specimen to observe the changing pattern of reflection. To get reproducible results we mounted the section in such a way that the occlusal surface is upwards. We rotated the light source from directly above (0°) clockwise to 90° , 180° , and 270° , or sometimes intermediate angles.

We follow the specific terms used for the description of enamel microstructure that were defined by Koenigswald and Sander (1997).

RESULTS AND DISCUSSION

Description of the Enamel of *Coryphodon*

The enamel is discussed in the various levels of complexity proposed by Koenigswald and Clemens (1992).

Crystallites

The crystallites forming the prisms and the interprismatic matrix (IPM) are visible at magnification about 2000 times as fine needles less than $0.5 \mu\text{m}$ in diameter (Fig. 3a and b).

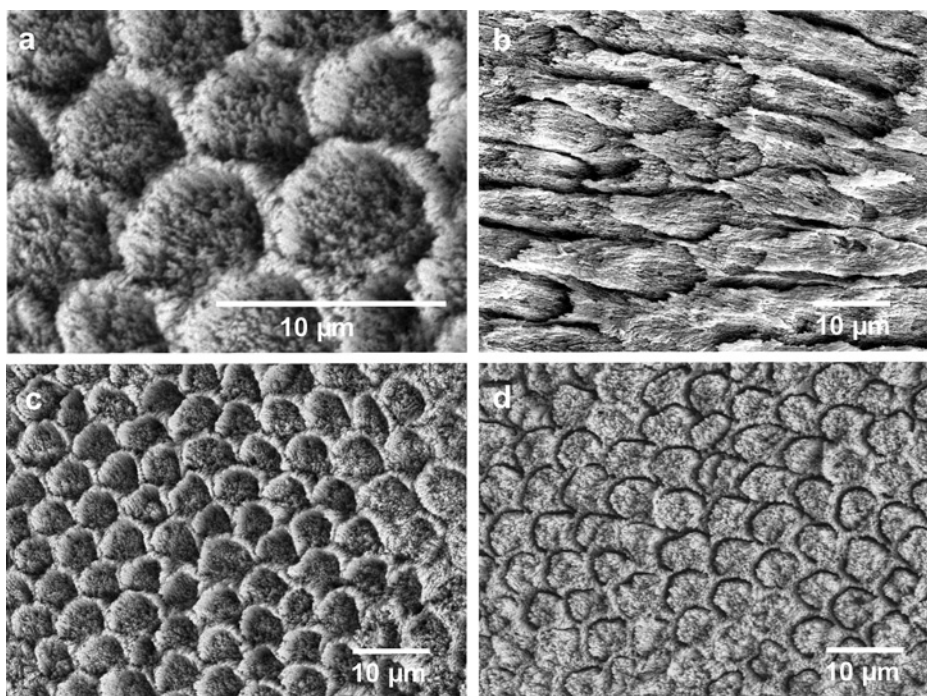


Fig. 3. Crystallites and prisms in the enamel of *Coryphodon* sp. (KOE 3678, 3679). SEM-images. (a) Cross-section of prisms showing crystallites. (b) Crystallites of prisms and interprismatic matrix seen in side view. (c) Prisms in cross-section with an open prism sheath. The prism sheath appears as a positive wall. (d) Prisms in cross-section with an open prism sheath. The prism sheath is etched away and appears as a trench.

The length of these needles cannot be estimated from our images. Most of the crystallites are truncated by the section plane. Even if the crystallite is seen almost tangentially its end may be etched away, thus the ends are usually artifacts. Daculsi *et al.* (1984) indicated that the length of the crystallites is more than 100 μm , consequently they are more than 200 times longer than thick. It is important to note that the individual crystallites are easily visible, since that is the evidence that any diagenetic modification of the enamel microstructure is minimal.

Prisms

The prisms are rounded and the prism sheaths are generally open to one side. Thus in the cross-sections they appear roughly horseshoe-shaped. They are closely packed but the prism-sheaths do not touch each other (Fig. 3c and d). This prism type is widely distributed and has been classified as prism type 3 by Boyde (1976). In some areas the prisms are arranged in horizontal rows and some prisms even show the keyhole pattern, a special form of the prism type 3, common in higher primates. In the tangential section, where the prism cross-sections are best seen, the open side generally points toward the root or somewhat to the sides. The thickness of the prisms is about 4–6 μm . In some prisms tubules are present.

Between the prism-sheaths of adjacent prisms some IPM is present (Fig. 3d). The IPM consists of apatite crystallites like the prisms, but in the IPM the crystallites are not bundled. If the crystallites of the IPM are oriented at an angle to the prisms, as in most more derived enamels, the IPM can be readily discerned. If the IPM is almost parallel to the prisms it is difficult to distinguish it from the crystallites of the prisms, as in *Coryphodon* (Fig. 3b).

In the tangential section neighboring areas sometimes show the prism sheath variously as a reflecting wall or as a dark deep trench (Fig. 3c and d). The SEM-image reflects the topography of the etched surface, and thus it may be related to a variable reaction to the etching by crystallites near the prism sheath, resulting from differences in prism orientation, diagenesis, or unknown factors.

Enamel Types

At the level of enamel types in *Coryphodon*, some radial enamel is present, in which prisms are parallel to each other. Dominant, however, is a very complex enamel, which shows intensive prism decussation, but without HSB. Thus sometimes it resembles irregular enamel (Fig. 4a), which is enamel with decussating prisms which otherwise lacks regular structure (Koenigswald and Sander, 1997). Irregular enamel is poorly understood. The complex enamel in *Coryphodon*, however, shows a repeated pattern not yet described in mammalian enamel and is described in the next section.

The Schmelzmuster

Stefen (1999) states that *Coryphodon* has radial enamel and HSB. The schmelzmuster of the various molar fragments is characterized by the dominance of a very complex enamel of decussating prisms. Near the enamel-dentine junction (EDJ) a thin zone of radial enamel occurs, but even in this zone some prisms group together with a somewhat different orientation. The decussation of the prisms in the middle zone (at least three-fourths of the

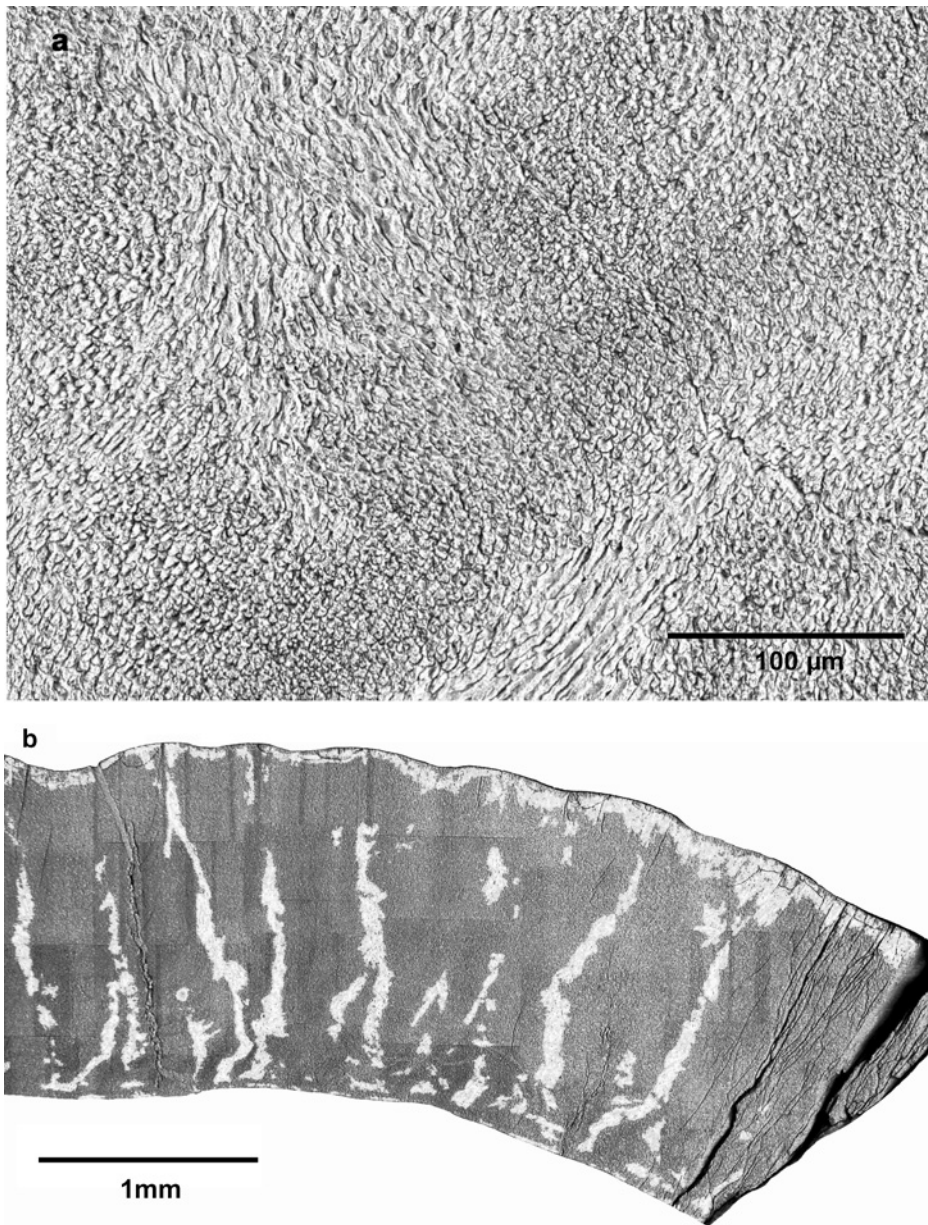


Fig. 4. Enamel of *Coryphodon* sp. (KOE 1919A). (a) Transverse section perpendicular to the slightly oblique ridges on the enamel surface of a premolar. SEM image showing a complex arrangement of prisms intersected at various angles. The section is too limited to recognize the overall pattern. (b) Reproduction of a mosaic of 24 SEM-images which provides the basic pattern of the enamel in *Coryphodon* (same specimen as Fig. 4a). In gray areas prisms are seen in cross-sections at various angles. The areas where prisms are seen more laterally and are visible for more than 10 μm are shown in white. The inner half of the enamel is more complex. In the outer half of the enamel the gray fields indicate the stripes, while the lineaments are white.

total enamel thickness) is reduced toward the outer enamel surface (OES), where a thin outer zone of radial enamel may be present. The thickness of the zones of the inner and the outer radial enamel varies widely (Fig. 4b).

In the middle zone groups of decussating prisms are visible in longitudinal and transverse sections. They cannot be described as HSB, since their occurrence is very irregular and difficult to interpret. The clue to the structure of this middle zone derives from the tangential section. The reflected light images were studied at much lower magnification (about 10–40 \times) under the binocular microscope and illuminated at a low angle.

When the tangential section was illuminated from the lower right (about 130 $^\circ$) a conspicuous pattern of obliquely oriented, undulating stripes emerged (Fig. 5a). The margins of these stripes are not straight but somewhat feathered, the stripes resembling slightly wavy, sometimes bifurcating lines of nested chevrons pointing obliquely upward toward the tooth crown. Since these prisms are reflecting light from the lower right, they are somewhat inclined upwards. These broad, light stripes are separated by similar, narrower dark stripes. However, when the section is illuminated from the opposite direction (about 310 $^\circ$), only very fine lineations reflect in the middle of the formerly dark field (Fig. 5b). In combination with the SEM pictures this indicates that these prisms are perpendicular to the OES. Those remaining dark when illuminated from either side have an intermediate direction.

The SEM study of the tangential section did not present a clear picture of the general structure. The structure was even obscured since most prisms were seen in cross-section. Their slight differences in angle were hardly detectable. At least some diagonally oriented narrow lineaments were visible and, between them, broad fields of prisms organized in groups of somewhat different orientation. Based on our observations under the binocular microscope these fields are the broad stripes with their feathered margins and include that part of the dark field in between that did not belong to the narrow lineaments.

The interpretation of the longitudinal and transverse sections was much more complicated since most sections cut through the oblique structure at an unfavorable angle. As a general pattern, the inner part of the middle zone appears to be extremely complex. Groups of prisms decussate in various directions. This inner part may cover one-third or one-half of the enamel thickness. Based on examination of the tangential section under low magnification, in this area close to the EDJ the feathered ends of adjacent stripes tend to share the same prism orientation, so that they shine under the same angle of illumination (either from about 40 $^\circ$ or 220 $^\circ$). This aspect resembles the zigzag enamel of hyaenid carnivorans (Stefen, 1997).

When transverse sections were oriented perpendicular to the somewhat oblique structure a more regular pattern could be seen in the remaining part of the middle zone. Striking are narrow lineaments of prisms that are seen almost in full length and therefore are running almost parallel to the OES (Fig. 4b). These lineaments are rooted in the inner part and show an intensive folding for short distances close to the EDJ.

Between these lineaments much wider stripes are present in which the prisms are seen in cross-section. The angle at which the prisms are truncated differs throughout the stripe.

The most significant characteristics of this enamel type are vertical or oblique structures in which the prism orientation is not symmetrical. That is, the stripes reflect light when illuminated from one side but the spaces in between are much thinner and appear only as a thin lineament when illuminated from the opposite direction.

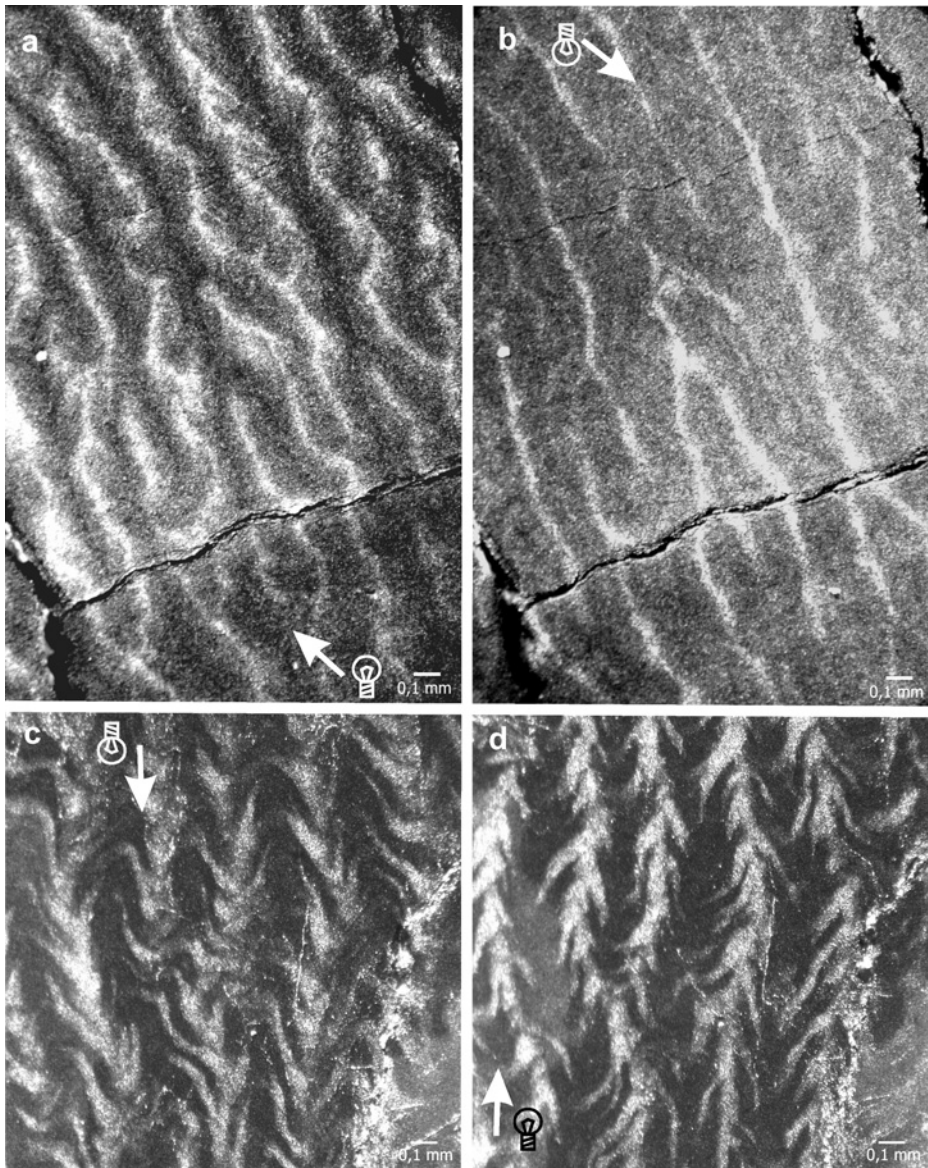


Fig. 5. (a) and (b) Reflected light images of tangential sections of *Coryphodon* sp., (tooth fragment, lower Eocene, Wyoming KOE 1302) illuminated from opposing sides. The arrows indicate the direction of the incident light. Broad stripes are visible when illuminated at 130° (a), but from 310° (b) only discontinuous thin lines are visible. This asymmetry is typical for the enamel type here called “*Coryphodon*-enamel.” (c) and (d) Reflected light images of tangential sections of *Crocuta spelaea*, (lower premolar, Upper Pleistocene, Germany, KOE 62). Note that the light and dark patterns complement each other when the light is turned from 0° (c) to 180° (d).

This is a new enamel type, which is here designated as “*Coryphodon*-enamel.” It will be compared with other enamel types, such as zigzag enamel, in a later section.

Dentition Level

The schmelzmuster may change within the dentition. This is very common if the teeth are very different in shape, as in rodents. In *Coryphodon* the various tooth positions examined—incisors, canines, premolars, and upper and lower molars—show a very similar schmelzmuster, with the “*Coryphodon*-enamel” in the middle zones and much thinner outer and inner zone of radial enamel.

It is notable that the outer enamel surface of the cheek teeth of *Coryphodon* exhibits distinct, more or less vertically arranged ridges and wrinkles. The outer radial enamel appears to be reduced in these wrinkles. The width and the orientation of the wrinkles show a close relationship to the stripes of the *Coryphodon*-enamel seen in the tangential section, but they are not precisely equivalent (Koenigswald, 2001).

On the shearing crest of the molars the broad stripes form ridges (Fortelius, 1985, Fig. 36), similar to those formed by vertical HSB in rhinoceroses, but the structure in *Coryphodon* definitely differs from vertical HSB.

Comparison of the “*Coryphodon*-enamel” with Other Enamel Types with Vertical Elements

A similar complex structure as in the pantodont *Coryphodon* was found in the dinoceratan *Uintatherium*. This genus was investigated by Fortelius (1985), who listed it as having vertical but irregular HSB. Pfretzschner (1994) classified its enamel as irregular. We observed the “*Coryphodon*-enamel” with bright stripes and narrow lineaments in the tangential section of *Uintatherium* (Fig. 6c and d).

The *Coryphodon*-enamel resembles to some degree the zigzag enamel described for specialized carnivores, like *Crocota* (Fig. 5c and d). Stefen (1995, 1997) analyzed the modifications of the transverse HSB in carnivores and demonstrated an increased folding from slightly undulating HSB to a zigzag enamel. In its most derived stage, as in *Crocota*, the chevrons unite to form vertical elements. A somewhat similar structure was found in *Coryphodon* in the very complex part of the middle zone near the EDJ. However, the *Coryphodon*-enamel differs distinctly from the zigzag enamel in tangential view, when illuminated from opposing sides. In *Crocota* both sets of vertical elements complement each other and are symmetrical (Fig. 5c and d). That is, both elements are of similar thickness. In contrast, in *Coryphodon* the stripes form broad fields while the lineaments are less than half as wide.

Stefen (1995) mentioned that the zigzag enamel was found in some entelodontids. According to our observations in *Archaeotherium* transversely oriented HSB are well developed in the molars and in the lower parts of the canines, but in the tip of the canine zigzag enamel was found. In the robust conical premolars zigzag enamel dominates. Thus in entelodontids (Fig. 6a and b) the transformation of transverse HSB to zigzag enamel is documented again. In tangential light, however, entelodontids show a similar pattern to that in *Coryphodon*. Illuminated from about 160° broad stripes with feathered margins were visible, while at about 340° thin lineaments appeared.

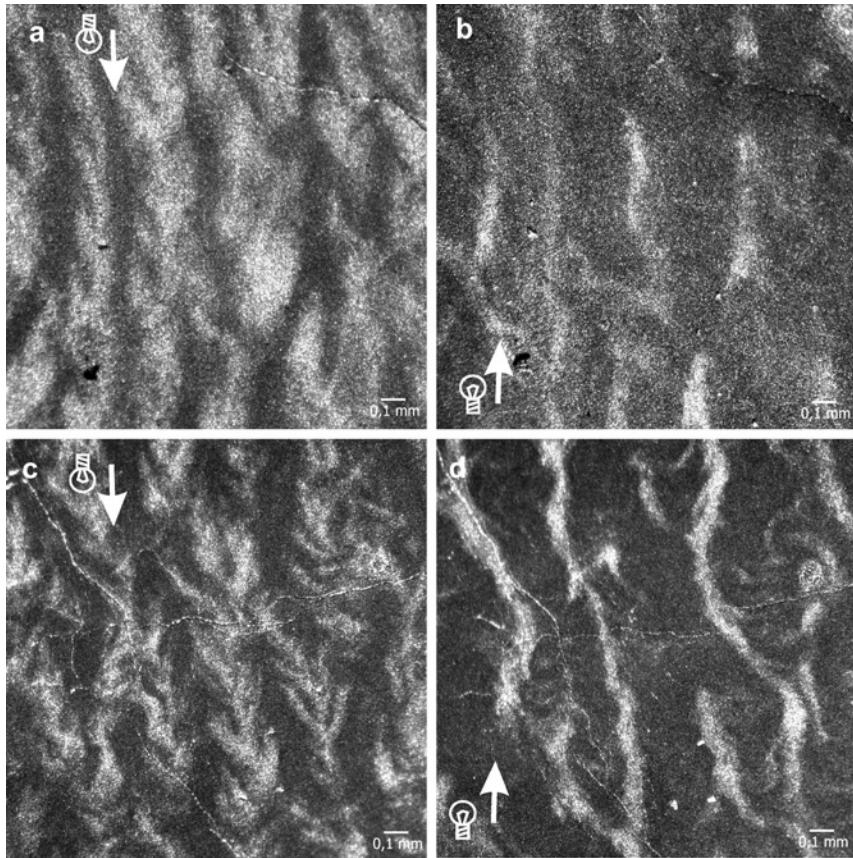


Fig. 6. (a) and (b) Reflected light images of tangential sections illuminated from opposing sides in *Entelodon* sp. (Oligocene, Nebraska, KOE 1989). Tangential section of a premolar illuminated from 0° (a) and 180° (b). In molars and the lower parts of the canine *Entelodon* shows transversely oriented and undulating HSB. (c) and (d) Reflected light images of tangential sections illuminated from opposing sides in *Uintatherium* sp. (fragment of a lower molar, Eocene, Wyoming, KOE 2783). Illuminated from 0° (c) and 180° (d).

In *Crocota* the vertical elements were interpreted as a specific adaptation to cope with the high stresses occurring during bone crushing. Entelodontids are regarded as omnivorous and occasional hard-object feeders. It has been suggested that they could have been carnivorous, scavengers, or bone crushers (Joeckel, 1990). Thus a correlation of zigzag enamel with high stresses during mastication seems likely. But *Coryphodon* and *Uintatherium* (Fig. 6c and d) were clearly herbivores with transverse shearing facets on all molars (Fig. 1), indicating that there may be different reasons why the vertical structures that characterize the zigzag enamel evolved. So far, particular enamel-types have not been convincingly correlated with specific diets. The organization of prisms in HSB instead should be regarded as a general adaptation to protect the enamel from being cracked by high tension-forces. The decussation of prisms is a crack-stopping device (Pfretzschner, 1988, 1994; Koenigswald *et al.*, 1994).

The occurrence of the zigzag enamel in small groups of Carnivora, Artiodactyla, Dinocerata, and Pantodonta indicates that this enamel type evolved several times independently. It is not even clear whether the zigzag enamel in Dinocerata and Pantodonta developed from transverse HSB. Thus the occurrence of similar enamels in *Coryphodon* and *Uintatherium* is not necessarily homologous.

Ways to Modify the Orientation of HSB

Structural elements of decussating prisms are usually organized transversely in mammalian enamel, like the HSB of most herbivores and carnivores. This orientation seems to be optimal to compensate for transverse tension forces originating from vertical pressure (Pfretzschner, 1988; Koenigswald *et al.*, 1994). Nevertheless several modifications of this orientation have been observed.

Besides the alteration into zigzag enamel or *Coryphodon*-enamel with its vertical elements, the transverse HSB may incline their lateral margins to intersect the occlusal surface, where abrasion forms tiny ridges and valleys according to the prism direction. This has been observed in Brontotheriidae, Chalicotheriidae, and Tapiridae (Fortelius, 1985; Koenigswald, 1994, 1997). In Rhinocerotidae and Astrapotheriidae the HSB are even oriented vertically forming similar ridges and valleys (Rensberger and Koenigswald, 1980; Fortelius, 1984; Koenigswald, 1994; Pfretzschner, 1994). The combination of the enamel structure with vertical HSB and abrasion by food form a sequence of small valleys and ridges, similar to those found in *Coryphodon*. We assign no special functional significance to this wear pattern. Some rodent taxa show in their incisors a similar modification of the transverse HSB. For example, vertical HSB have been found in certain eomyids (Wahlert and Koenigswald, 1985), myomorphs (Martin, 1997; Kalthoff, 2000), and the theridomyid *Patriotheridomys* (Martin, 1999).

Pantodonta, Dinocerata, and Carnivora followed another pathway. Stefen (1995, 1997) showed that in Carnivora the transversely oriented HSB are not absolutely straight but undulate slightly. During the subsequent differentiation the undulation increased. Passing through a stage of "HSB with acute angles" the zigzag enamel was formed, characterized by its vertical elements (according to the definition by Stefen 1997, 1999). Stefen (1995) and Rensberger (1995, 1997, 2000) observed this structure and its attainment through a phyletic transition from folding of the primarily transverse HSB in Carnivora. The zigzag enamel results from the uniform prism direction in the synclines and anticlines of the zigzag structure. In Carnivora the upward and downward oriented elements have opposing feathered margins that complement each other. Both are of equal size as can be seen by illuminating the tangential sections from opposite sides (Fig. 5c and d).

Our small sample of entelodontids showed a similar transition from transverse HSB to zigzag arrangement resulting in vertical elements (Fig. 6a), but here the vertical elements are not of equal size. As in the "*Coryphodon*-enamel," broad stripes contrast with thin lineaments.

At present the difference between the zigzag enamel and the *Coryphodon*-enamel is difficult to interpret. It is most unlikely that the zigzag enamel passed through a stage like the *Coryphodon*-enamel. The opposite might be more likely, but cannot be demonstrated, although the transition in enamel structures seen in entelodonts suggests this possibility.

A dichotomy from a stage with acute-angled HSB to zigzag enamel on the one hand and *Coryphodon*-enamel on the other is possible as well.

Probable ancestors or sister groups of *Coryphodon* and *Unitatherium* will need to be examined to investigate how their complex enamel types evolved. At this stage we can only postulate that transversely oriented HSB antedated these specific enamel types.

The application of the use of reflected light images of the enamel under low magnification facilitated investigation of the complex enamel structures not easily recognized by SEM study. Previously these have been regarded as irregular enamel. This technique is a promising approach for the investigation of “irregular enamel” in larger teeth, such as those of Proboscidea, Lagomorpha, or others.

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