

Functional and phylogenetic interpretation of enamel microstructure in rhinoceroses

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Abstract.—Worn enamel surfaces of the cheek teeth in fossil and recent rhinoceroses are characterized by fine, parallel ridges aligned perpendicular to the enamel-dentin interface. We show that these ridges result from an unusual enamel ultrastructure in which a primitively horizontal layering of the prisms has become vertical. The new structure apparently appeared between early and middle Eocene, at the time when the superfamilies of perissodactyls were rapidly diverging. Similar modifications of the enamel structure occurred in certain parts of the cheek teeth in tapiroids, chalicotherioids and brontotherioids, but hardly at all in the equids. The modified enamel structure, where it occurs in groups other than rhinocerotoids, is associated with lophes but not cusps. Experimental evidence shows that the modified enamel is more resistant to wear than the unmodified enamel. The consistent association with thin lophes rather than cusps suggests that the modified enamel evolved to prolong the life of the lophes, where occlusal pressures are highest and attrition greatest. The dominance of modified enamel in rhinocerotoids correlates with the higher degree of compression of the cusps and extreme lophodonty in this group. The absence of modified enamel structure in the equids, even in the ectoloph, correlates with the lesser importance of the ectoloph in equids relative to brontotherioids, chalicotherioids and rhinocerotoids.

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Introduction

The chewing surfaces of the cheek teeth in most herbivorous mammals are characterized by smooth facets worn into the enamel. These planes of wear may be tangent to the enamel surface, or they may cut through the enamel to intercept and expose the dentin. In either case, the worn surface of enamel in most taxa is either smooth or marked by irregular striae produced by abrasion.

In the rhinoceroses, however, the worn surface of enamel often exhibits a rather remarkable pattern of regularly spaced ridges aligned perpendicular to the adjacent outer surface of the tooth (Figs. 1A, 2). These ridges may be prominent enough to be detected by the unaided eye and often may be felt by running a fingernail along the surface.

We had independently commenced studies of the nature and origin of these unusual patterns of wear in rhinocerotoids and the possible re-

lationship to the enamel structure several years ago. When we discovered our mutual interest in this problem, we decided to combine our efforts.

The purposes of this paper are to describe the enamel prism arrangement in the cheek teeth of representatives of the family Rhinocerotidae, to show how this structure relates to the unusual pattern of wear, and to describe evidence suggesting how and why this specialization may have arisen. The results show that the occlusal ridges are caused by a rather profound restructuring of the enamel tissue in the early Eocene in association with the appearance of lophodonty.

Previous work.—It is known that gross occlusal morphology in molars has evolved in response to selective advantages related to chewing activity, and some of these advantages have been identified. Enamel on the downstroke (see General Structural Relationships) side of the

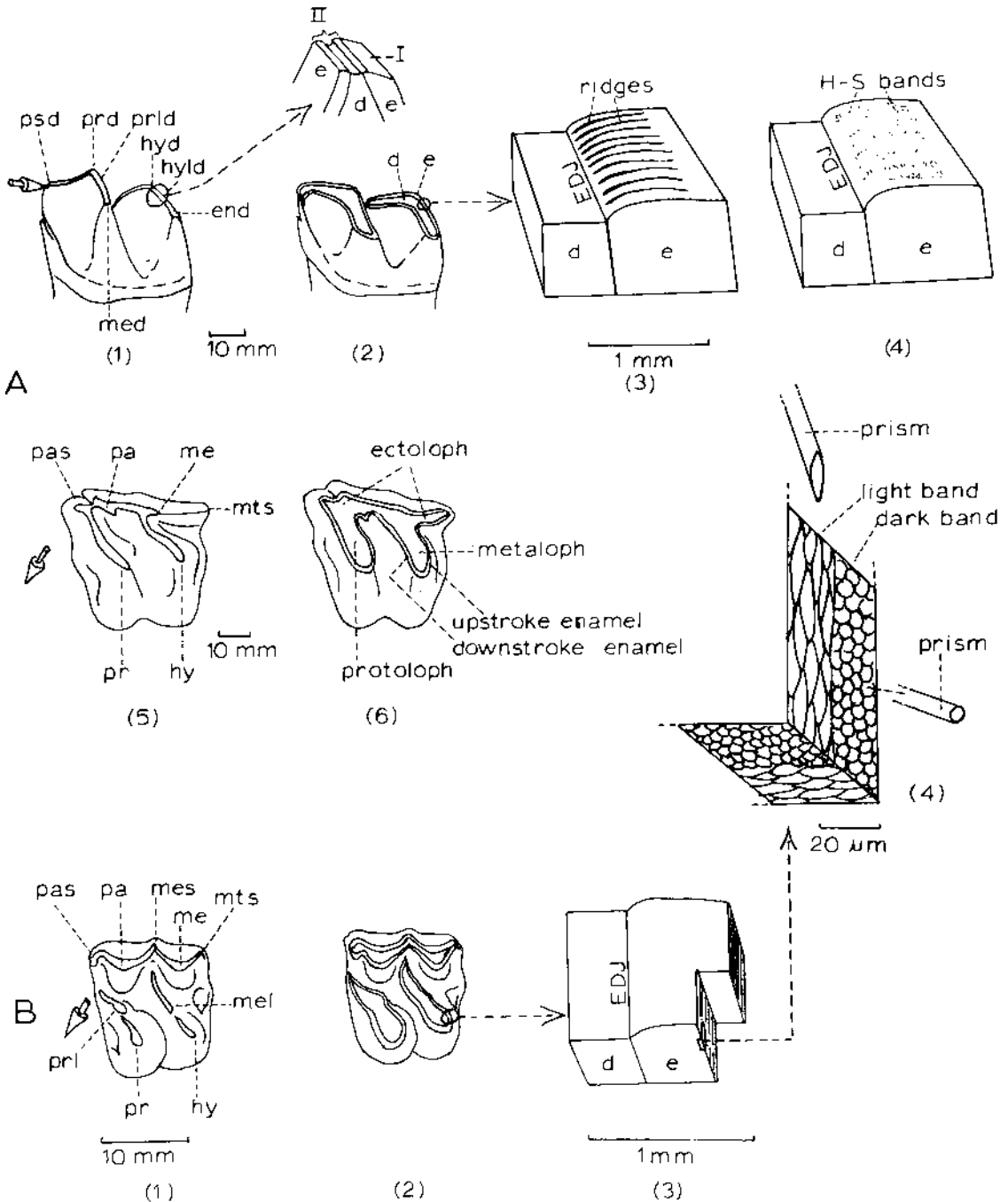


FIGURE 1. Occlusal and enamel structures in perissodactyls. A, *Rhinoceroidea*: (1), little worn right lower molar, obliquely lingual view; (2), same, moderately worn; (3), enlarged view of segment of occlusal surface of posterior enamel and dentinal platform from hypolophid of (2), showing enamel ridges; (4), same, showing Hunter-Schreger bands; (5), little worn left upper molar, occlusal view; (6), same, moderately worn. B, *Mesohippus*: (1), little worn left upper molar; (2), same, moderately worn; (3), enlarged view of segment of posterior enamel and dentin from hypocone of (2), showing horizontal Hunter-Schreger bands in cut-away section; (4), further enlarged view of cut-away section in (3), showing prism attitudes in Hunter-Schreger bands. Abbreviations: d = dentin; e = enamel; EDJ = enamel-dentin junction; pr = protocone; hy = hypocone; prl = protoconule; mel = metaconule; pas = parastyle; pa = paracone; mes = mesostyle; me = metacone; mts = metastyle; psd = parastyloid; prd = protoconid; med = metaconid; prld = protolophid; hyd = hypoconid; hyld = hypolophid; end = entoconid; I = phase I facet; II = phase II facet; H-S = Hunter-Schreger. Solid arrows represent direction of relative motion of opposing tooth during chewing stroke.

chewing platform is usually thicker than the enamel on the upstroke side in many forms because the former is the side where the greatest amount of food (and detritus) is carried and wear is most intense (Rensberger 1973). Continued response of this sort has led to the eventual loss of enamel in tracts on the sides of the tooth which are 90 degrees opposed to the direction of masticatory motion, where little food is masticated.

The microscopic structure of the enamel itself has been known to differ from taxon to taxon. Some of the most pronounced differences (and most complex structures) occur in the incisors of the rodents (Tomes 1850; Korvenkontio 1934; Wahlert 1968; Warshawsky 1971; Boyde 1978). Kawai (1955) showed that the enamel structure of the cheek teeth differs between orders of mammals as well as between taxa of some individual orders. Yet the functional reasons for these differences, if any, have only recently been studied. It has been found (v. Koenigswald 1977, 1980) that the enamel in the cheek teeth of arvicoline rodents may differ regionally in a single tooth in a fashion related to the direction of the chewing stroke, suggesting an adaptive response to some function of the stress produced by the masticatory force. Rensberger (1978) figured SEM micrographs of worn occlusal surfaces of arvicoline molar enamel in which opposite edges were characterized by different patterns of breakage associated with the direction of occlusal stress.

Unusually regular furrows and ridges were observed on the naturally worn surface of the enamel in the arvicoline, *Microtus* (Rensberger 1978) and it was suspected that these structures are related to the enamel prism structure because the spacing is the same as that of the prisms. Walker, Hoek and Perez (1978) observed naturally worn enamel surfaces in the hyracoid *Procavia*, in which the outlines of enamel prisms tended to be etched into relief by food eaten during the dry season but obscured by more abrasive opaline phytoliths during the wet season when the diet favored grasses. These examples suggest that differences in resistance to abrasion exist within the enamel structure and raise the question whether in some mammals microstructural evolution may not have taken advantage of this characteristic.

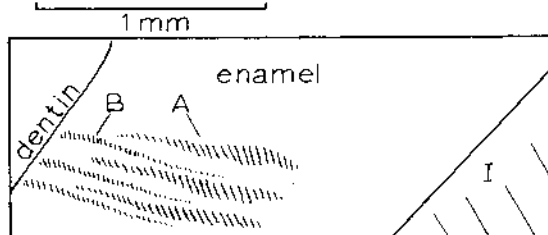
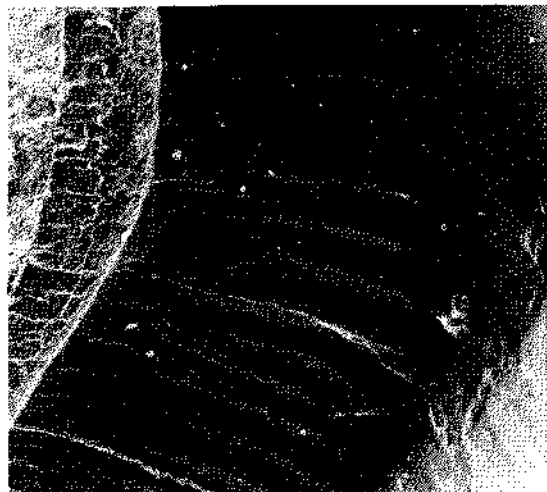


FIGURE 2. Naturally worn occlusal surface of enamel from the hypoconid of *Subhyracodon*, middle Oligocene, North America. A = ridge formed by prisms of type A (see text); B = ridge formed by prisms of type B; I = phase I wear facet containing striae gouged by contact with ridges on opposing enamel.

Materials and Methods

We examined enamel from fossil cheek teeth of various taxa of the Rhinocerotidae as well as other families of perissodactyls under scanning electron microscopy (SEM) and/or low magnification light microscopy (Appendix). The specimens viewed under the light microscope were examined untreated or in some cases after coating with ammonium chloride or a very thin layer of magnesium oxide (by burning a strip of magnesium ribbon). Owing to the transparency of the enamel, the white coating was found to be almost essential in order to clearly show the ridge patterns and in establishing their relationship to the Hunter-Schreger bands.

The SEM specimens were coated with 100 angstroms of gold in a vacuum evaporator, usually after etching the enamel surface in a dilute acid for between a few seconds and one minute. The SEM equipment included a Japan

Electron Optical Laboratory model JSM U3 and a Cambridge Instruments S150.

Differential resistance to abrasion was determined by cementing fragments of enamel together, grinding them to a single flat surface and subjecting them simultaneously to a uniform jet of fine, 10–50 μm abrasive powder propelled by compressed air (90 psi). An S. S. White Industrial Abrasive unit was used to provide the abrasive jet.

General Structural Relationships

Describing the microstructure of enamel in rhinoceroses presents severe problems of scale. The study itself is tedious because only fragments of these large teeth may be properly inserted in the SEM stage. We shall initially illustrate the entire tooth in unworn and worn conditions and compare them to those of the equids, in which the microstructure remained most primitive among the perissodactyls. Sketches showing the coarse scale relationships of prisms and Hunter-Schreger bands on the tooth are provided. The reader may refer back to these diagrams as needed when studying the small areas represented by the SEM micrographs and drawings in later descriptions.

Cusps, lophs and wear.—The unworn upper molar in primitive (hyracotheiine and anchitheriine) perissodactyls bears six major cusps, paracone, metacone, protocone and hypocone (Fig. 1B). The paracone and metacone are each strongly convex lingually and flattened labially. After the early Eocene a mesostyle, parastyle and smaller metastyle are joined to the apices of the paracone and metacone by a crest, the ectoloph. The protocone and protoconule (paraconule), although joined to form a protoloph, remain distinct but somewhat compressed. In advanced forms the hypocone and metaconule become somewhat more compressed and difficult to distinguish on the metaloph.

The upper molar of the rhinocerotoids (Fig. 1A) is similar to that of the anchitheriines only in the directions and proportions of the major crests because the cusps are much less prominent. In the late Eocene and Oligocene hyracodontids and rhinocerotids, the unworn occlusal edges of the lophs are almost knife-edged, with no indication of the positions of the primitive cusps. The styler cusps of the ectoloph have no

labial processes such as are present in the equids, and the ectoloph is relatively flat walled. The positions of the paracone and metacone in labial view are slightly higher than other parts of the crest but are much less prominent than in other perissodactyls.

The lower molar in the primitive equids is dominated by V-shaped lophids joining the protoconid and hypoconid to the lingual cusps. In *Mesohippus* the parastylid, protoconid, and hypoconid are compressed, but the metaconid, metastylid and entoconid are distinctly subcylindrical. The basins of the trigonid and talonid are relatively shallow so that the inner walls of the bordering lophids are gently sloping and the lophids therefore thicken rapidly with wear.

In the rhinocerotoids (Fig. 1A) the lophids of the lower molar bear steeper interior walls which descend almost to the base of the crown, much deeper than in the primitive equids. The lingual cusps are more fully compressed and merge with the rest of the lophid. The lophids are oriented more nearly perpendicular to the direction of occlusal motion of the opposing tooth than in the primitive equids.

The direction of occlusal motion of the lower cheek teeth during the power stroke is anterolingual and the relative motion of the uppers is posterolabial (solid arrows in Fig. 1A). In the early phase (phase I of Kay and Hiiemae 1974; = buccal phase of Mills 1955, 1967), the direction of the occlusal stroke is upward as well as anterolingual. Consequently, during this phase contact is initially made along obliquely vertical facets (I in Fig. 1A). The labialmost structure of the upper molars (the ectoloph) and the lingualmost structures of the lowers (metaconid, metastylid and entoconid) contact the opposing tooth only in phase I. In other positions there are usually both phase I and phase II facets. Because the phase I facets are made during an early part of the stroke, the total area of contact is not as great as when the teeth are more fully occluded, and occlusal pressure on these contacts is correspondingly high. Because of this, phase I surfaces more often fully penetrate the food, make intimate contact with the opposing surface, and are flat, sharply bounded facets in the true sense. On the other hand, phase II facets most often do not make intimate contact with opposing surfaces and tend to be convex,

smoothly polished by food abrasion, and poorly defined. The ridges (Fig. 1A[3]) found on the worn enamel of rhinocerotoid cheek teeth are most prominently developed where food abrasion dominated and consequently are more often seen on phase II facets. In later stages of wear of the protoconid, hypoconid, protocone, and hypocone, phase II facets become progressively more dominant.

In order to determine the relationship between the ridges of the enamel surface and the structure of the enamel, it has been necessary to take into consideration the effects of the direction of the masticatory force. The terms upstroke and downstroke (Fig. 1A[6]) are useful in distinguishing the enamel plates on opposite sides of a loph or lophid. The leading or upstroke enamel is that which occurs on the side of the dentinal platform toward the source of relative movement (solid arrows in Fig. 1A) of the opposing masticatory surface. The downstroke or trailing enamel is on the opposite side of the loph. Similarly, the enamel plate itself has a leading and a trailing edge with respect to the direction of opposing masticatory motion. The masticatory force vector is the direction and magnitude of the force exerted by the muscles in producing the power stroke. When food is being compressed between facets, the masticatory force is transmitted through the food and the abrading force is approximately that of the masticatory force. We have used the line of intersection of the phase I facets as a guide in making a rough estimation of the direction of the abrasive vector.

Enamel prisms.—Enamel is composed of prisms (rods), which appear as bundles of crystals (crystallites) of hydroxyapatite. The prisms are first formed at the enamel-dentine junction (EDJ in Fig. 1B[3]) and grow in the general direction of the outer surface of the tooth. Individual prisms therefore extend through the entire thickness of the enamel although they seldom run in a straight line. In the descriptions which follow, we refer to "descending" and "rising" directions of prisms, using the direction of growth as a means of describing prism directions. Thus, "descending" means running downward from the EDJ, etc.

Hunter-Schreger bands are light and dark bands of enamel seen under light microscopy.

These bands are a phenomenon of the variation in the reflective property of sets of prisms, depending upon the direction of the prisms with respect to the source of light. In most mammalian orders, alternating sets of prisms begin growing in different directions a short distance beyond the EDJ. When the sets are many prisms thick, alternating light and dark bands may be seen under low magnification (Figs. 1A[4], 1B[3-4]). Therefore, the bands are, in a strict sense, merely optical phenomena of two dimensions. However, in a broader sense, they identify three-dimensional layers of prisms of alternating directions, and we use the term Hunter-Schreger (H-S) band to describe both aspects. In the equids and most other mammals, the H-S bands are seen on the sides of the teeth and represent horizontal layers perpendicular to the vertical axis of the tooth (Fig. 1B[3]). However, in rhinoceroses the H-S bands are seen on both the occlusal surfaces (Fig. 1A[4]) and the sides of the tooth and represent layers oriented parallel to the vertical axis of the tooth.

Results

Wear surfaces.—The ridge system of the worn enamel surface varies in prominence and spacing within a single tooth. The number of ridges per millimeter along a single enamel edge is often 5 to 6, but, where a full complement (described below) of major and minor ridges is developed, is usually 9 or 10.

The ridges are typically developed on the inner one half to two thirds of the enamel (side closest to the EDJ) and tend to fade away at some point between the middle of the enamel plate and the outer surface (Fig. 2). The point at which the ridges disappear varies within a single tooth, but usually a distinction between inner and outer enamel is apparent.

Sets of double ridges occur in certain positions of the tooth. Each set consists of a narrow ridge which is highest nearest the EDJ and a wider ridge which is highest near the center of the enamel plate (Fig. 2). The narrow ridge arises abruptly very near the EDJ and tapers in width and height outward. The wider ridge arises more gradually near the center of the enamel, then tapers in width and height toward the EDJ. Thus only one ridge (the narrow one)

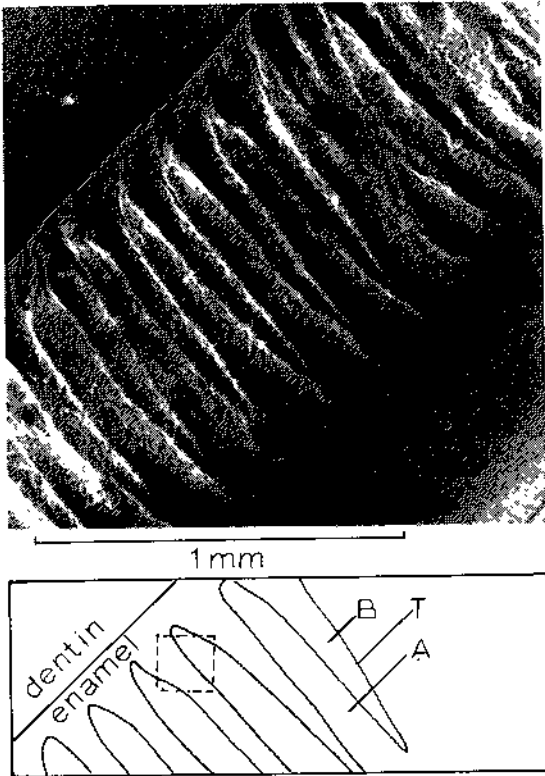


FIGURE 3. Etched occlusal surface of enamel on hypoconid of *Subhyracodon*, same individual as in Fig. 2. A = zone containing prisms of type A; B = zone containing prisms of type B; T = prisms transitional between A and B. Prisms A and B, with axes directed toward surface, etch more rapidly than horizontal prisms of T. Dotted rectangle is area of Fig. 4.

is distinct near the EDJ and only one (the wide one) near the center of the enamel. Double ridges are most commonly found on the enamel around the protocone and hypocone of the upper teeth and around the protoconid and hypoconid of the lowers. Where the double set of ridges is not present, the structure seems to be one in which a single member of the couplet is dominant because careful searching will frequently reveal faint development of the second ridge, sometimes at an extreme position on the margin of the enamel plate. Where doublets are present, the ridges are packed twice as densely as otherwise. Although these ridges are produced by food abrasion, not by contact with the enamel of the opposing tooth, another type of more or less regularly spaced furrow was frequently observed. These occur on flat facets, especially the facets resulting from phase I of

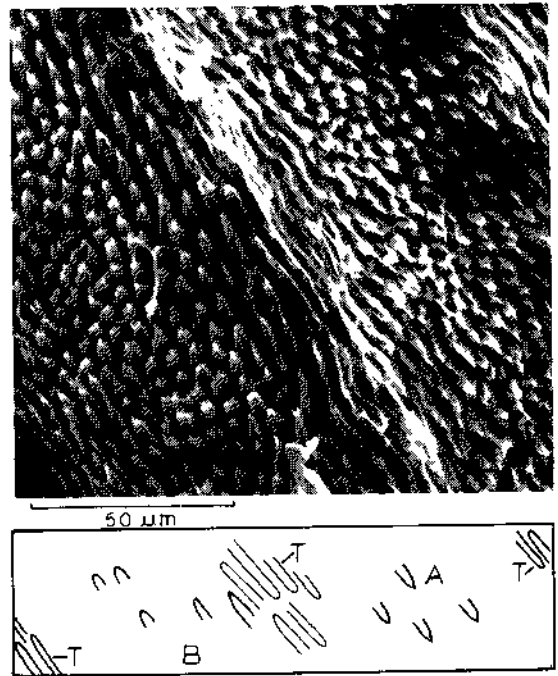


FIGURE 4. Portion of Fig. 3, enlarged (enamel-dentin junction toward upper left). Horizontal prisms of transitional zone (T) bordering obliquely rising prisms of reversed orientations (A and B).

the masticatory stroke. These structures are not directly related to the underlying structure of the enamel, are usually longer, and seem to be striae produced by the regular sets of ridges on the worn surface of the opposing enamel. A set of such striae can be seen on the phase I facet in the lower right corner of Fig. 2.

Enamel structure.—The pattern of abrasion ridges is related to the underlying structure of the enamel. In order to explain this relationship, it is necessary to first describe the enamel structure. Etched surfaces of enamel which conform to the horizontal wear plane, that is, which lie more or less perpendicular to the vertical axis of the tooth, show a series of transitions in prism direction under the SEM (Figs. 3–5). Two distinct prism directions occur in alternate tracts along the enamel (Figs. 4–6). In one set (B) the prisms descend from the occlusal surface and the EDJ. In the second set (A), the prisms rise toward the occlusal and outer enamel surfaces. Between these two sets is a narrower transitional zone (T), represented by a set of prisms lying parallel to the occlusal surface (Figs. 4–6).

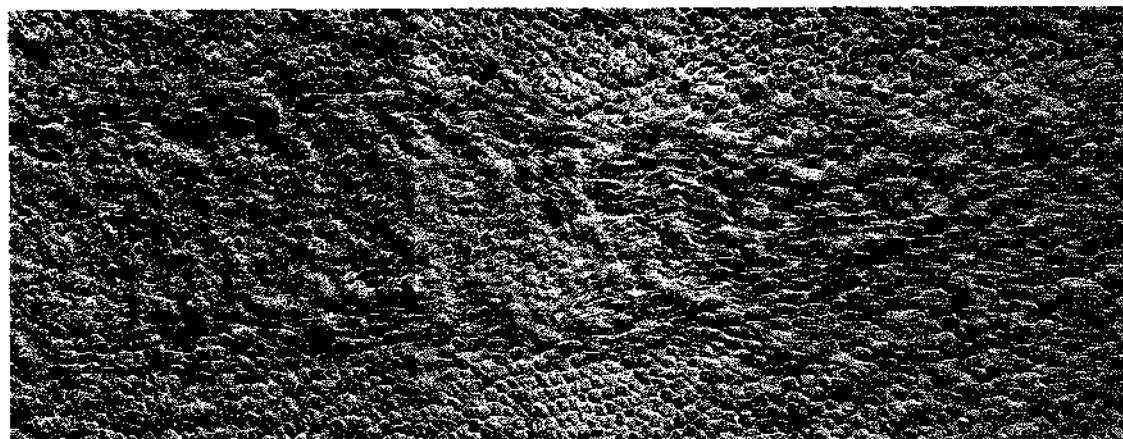
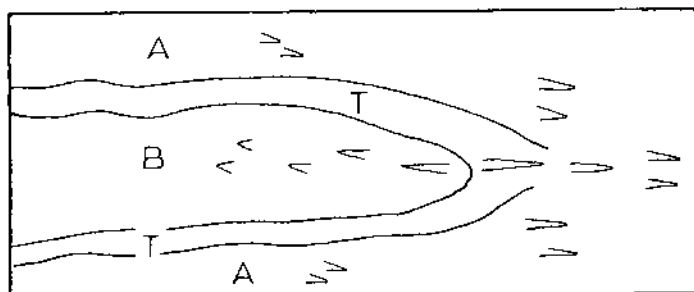
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FIGURE 5. Polished and etched section of inner enamel, parallel to occlusal surface, from *Coelodonta antiquitatis*, Pleistocene, southern Germany. Wedge shaped zone (B) of prisms descending from left, bounded above and below by prisms of zone A rising toward right. Transitional horizontal prisms (T) separate types A and B. Outer enamel begins at right side of micrograph.

In vertical sections, sets of prisms at different angles may be seen to continue at some depth without change in attitude (Figs. 7–10). At certain points of depth one set is replaced by another of opposing prism attitude, owing to the fact that the vertical section crosses now and then from one set to the next.

Because of differential reflectance of light by adjacent sets of prisms, individual sets (H-S bands) can be viewed under a low power dissecting microscope from the outer surface of the enamel. The sets thus viewed can be seen to be essentially vertical, parallel but occasionally branching, and often individually continuous to great depth.

Where the enamel is moderately thick, distinct inner and outer zones are evident (Figs. 7, 9). The inner enamel is characterized by layers with alternate prism directions, whereas the outer enamel is characterized by prisms of one direction only. The prism direction in the outer enamel either almost corresponds to that of one

(A) of the inner sets or is intermediate between the directions of the two inner sets (A and B). In *Dicerorhinus* the inner prisms of layer B, that is, those which descend from the EDJ, become abruptly horizontal at the middle of the enamel and then swing sharply upward to complete a 90 degree bend and become almost parallel to those of layer A. Prisms of layer A continue outward with a slight bend toward the outer enamel. In *Subhyracodon* the prisms of inner layer B are seen to bend into a horizontal attitude but no farther, and the prisms of inner layer A converge upon this same direction, so that the direction of all prisms in the outer enamel is horizontal. Analogous differences between inner and outer enamel have been described for the incisors of many genera of rodents (Tomes 1850; Korvenkontio 1934; Wahlert 1968; Warshawsky 1971; Boyde 1978), and for the molars of arvicoline rodents (v. Koenigswald 1977, 1980).

Relationship of prism tracts and ridges.—De-

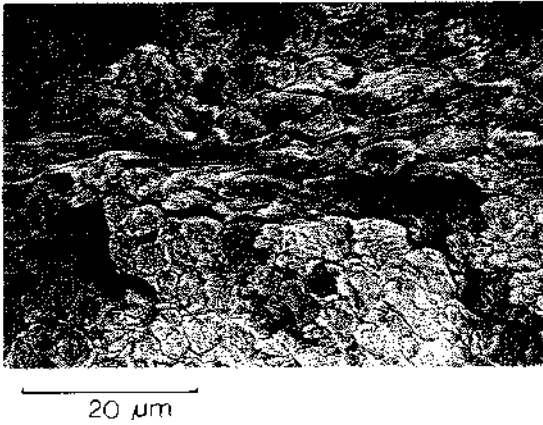


FIGURE 6. Portion of Fig. 5, enlarged, showing elongate sections of horizontal transitional prisms above center, bordered by more nearly oval sections of prisms of zone A below and B above. Crystals of individual prisms visible, with axes approximately parallel to prism axes.

termination of which set of prisms forms the ridges is difficult because the prisms cannot be seen on the unaltered three-dimensional wear surface of enamel which simultaneously shows the ridges. When the surface is etched with acid to reveal the prism structure, the transitional zones of horizontal prisms form ridges (Figs. 3, 4) and the other two sets of prisms form valleys. It can be seen that the transitional zones form a continuous zig-zag ridge which does not closely resemble the isolated fingerlike ridges of the naturally abraded surface. However, the valleys separating the ridges on those worn surfaces in which double sets of ridges are formed (Fig. 2) trace an outline which closely matches that of the etched ridges of the transitional zones. This suggests that the double sets of natural ridges are formed by the two zones of obliquely vertical prisms (A and B). When light strikes the enamel surface parallel to the long axes of the prisms, maximum absorption occurs and the zone appears dark. When the light strikes the enamel surface perpendicular to the prism axes, maximum reflectance occurs and the zone appears light (Fig. 11). Thus it is possible to differentiate the layers of differing prism direction under the low magnifications of dissecting microscopes.

Rhinocerotoid enamel shows alternating light and dark H-S bands distributed along the occlusal edge of the enamel and perpendicular to the EDJ (Fig. 12). Rotation or shifting of the

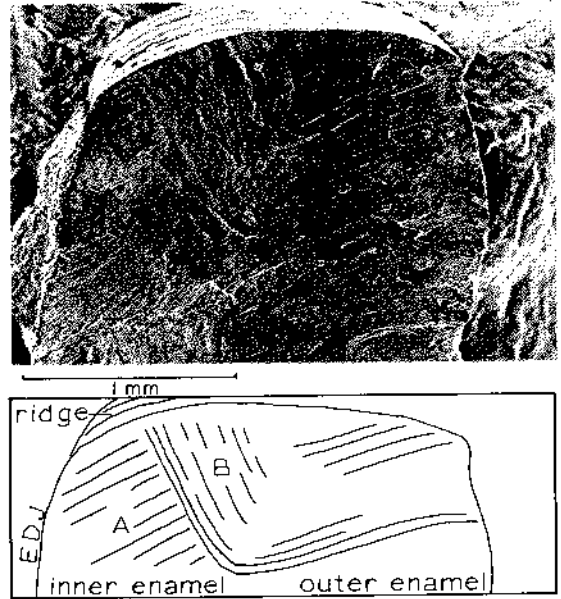


FIGURE 7. Unetched broken vertical section of enamel perpendicular to surface of EDJ, from *Dicerorhinus* sp., Pleistocene of Sangiran, Java. Naturally worn occlusal surface at top, bearing ridges. A = prisms of type A, rising toward outer surface of enamel; B = prisms of type B, descending from left. Inner enamel defined by layers of prisms with reversed direction. Broken surface transgresses from one layer to next, exposing both A and B in single section. Prisms of outer enamel with single direction, almost parallel to axes of A.

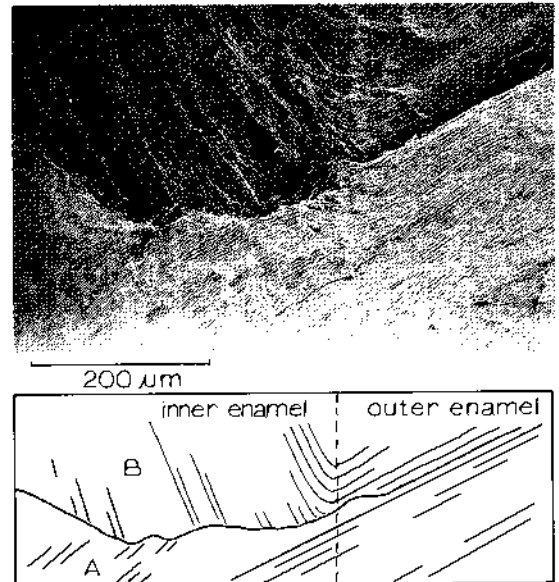


FIGURE 8. Etched, enlarged area from Fig. 7. Prisms of descending layer B turn sharply upward in outer portion of enamel. Rising prisms of layer A turn slightly downward in outer enamel to parallel those originating from layer B.

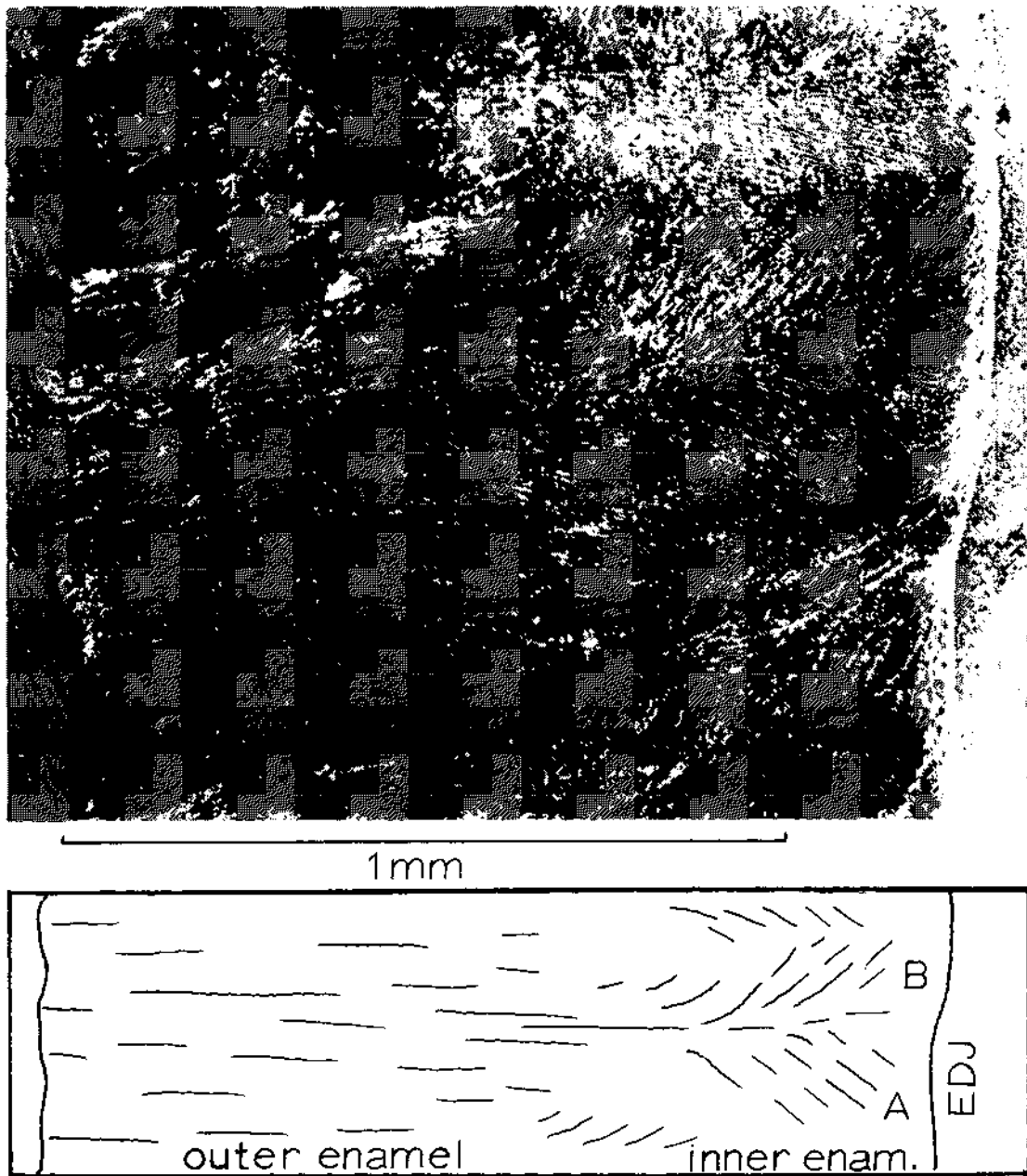
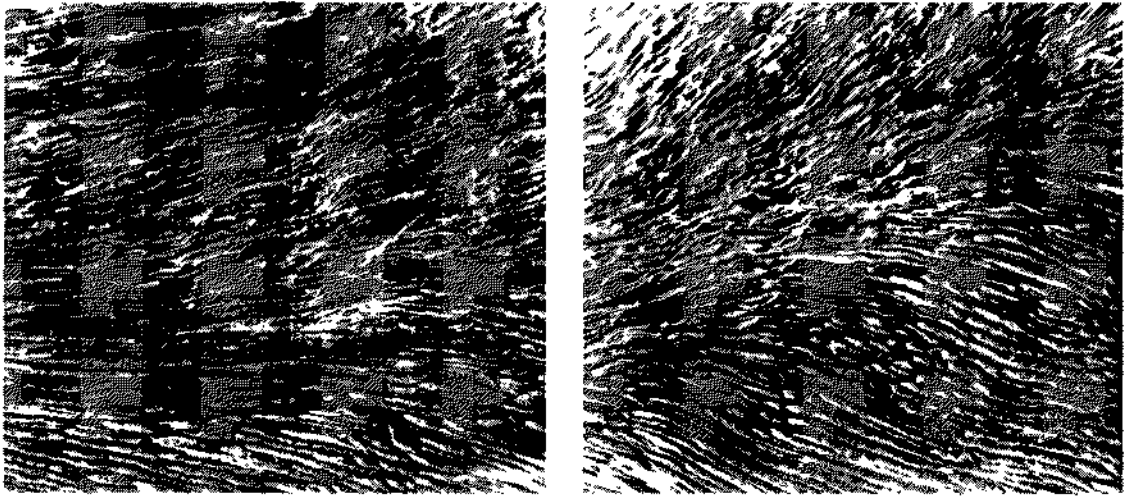


FIGURE 9. Etched, broken vertical section of hypoconid enamel, perpendicular to surface of EDJ, from *Subhyracodon*, middle Oligocene, North America. Outer enamel containing prisms perpendicular to outer surface, inner enamel containing layers of prisms either declining from EDJ (set B) or rising toward outer surface (set A). A and B layers alternate due to slightly oblique vertical attitude of broken surface.

specimen under a fixed source of illumination causes the dark bands to become light and the light bands to become dark (Fig. 11). Between these areas a thinner, often lighter trace is visible, representing the transitional zone, in which the prisms are horizontal.

Using these clues, one can see that at least one of the sets of obliquely vertical prisms forms ridges (Fig. 13). When only one set forms ridges, there are only half as many ridges as there are major prism sets, discounting the transitional zone. Where ridge doublets occur, both dark



100 μm

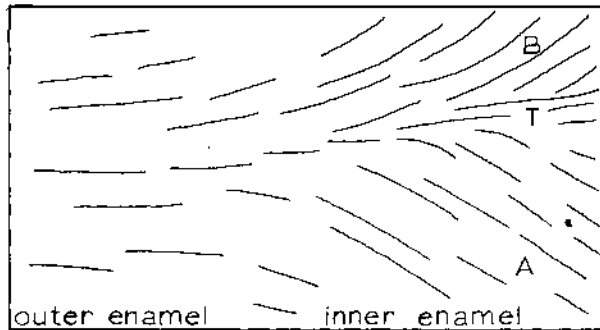


FIGURE 10. Enlarged portion of Fig. 9, showing prisms of layer B descending from upper right, bending to become horizontal in outer enamel; prisms of layer A rising from lower right, bending to parallel others of outer enamel.

and light prism tracts can be seen to form ridges, but the position of maximum prominence of the ridges alternates along the enamel plate (Fig. 14). This alternation in position of

prominence is related in part to the different positions of maximum angle between the prisms and the occlusal surface (Figs. 13, 14) and in part to the difference in direction of the abrasion vector, that is, the direction in which force is

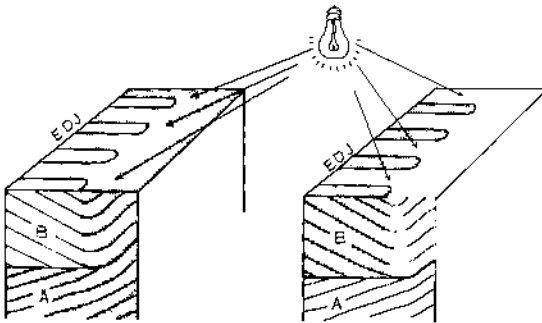


FIGURE 11. Relationship of light direction, reflectance, and prism direction in enamel of rhinocerotoids. A = prisms of inner enamel rising toward outer enamel surface; B = prisms of inner enamel descending from EDJ. Prisms with axes perpendicular to light source reflect light; those parallel to light source absorb light.

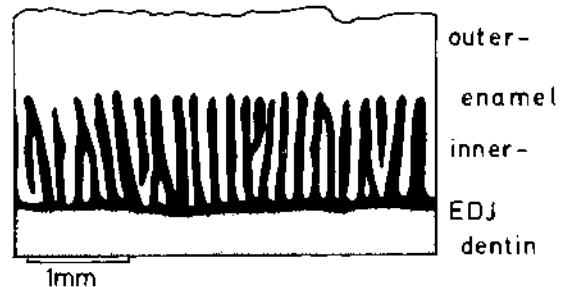


FIGURE 12. Section parallel to chewing surface of enamel in *Coelodonta antiquitatis*, late Pleistocene, Urspringhohle, Lonetal, southern Germany, showing light and dark bands with illumination from below. In this example dark bands correspond to ridges but this can be reversed by changing light source.

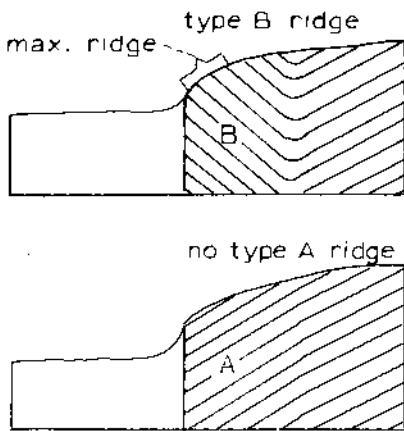
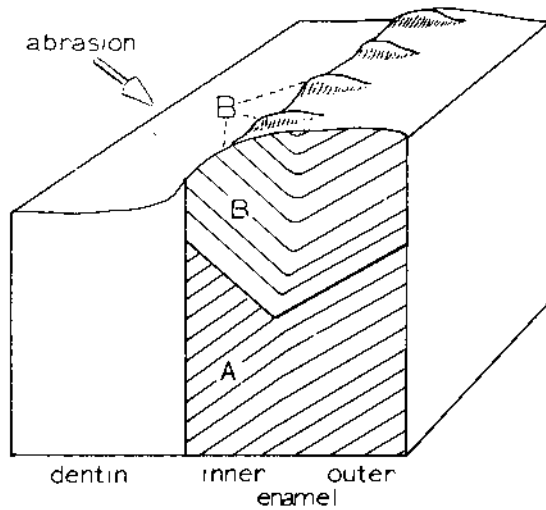


FIGURE 13. Relationship of enamel ridges, prism direction and attitude of food abrasion vector. Ridges formed only by type B prisms.

exerted by food being pressed against the surface. The phase II facets on the hypoconid, for example, are more nearly perpendicular to the abrasion vector than are the phase I facets of the ectoloph of the upper molar. The ectoloph therefore tends to exhibit only one set of ridges; for example, the downstroke enamel of the ectoloph may exhibit the relationship shown in Fig. 13, in which type B ridges alone are commonly evident. The downstroke enamel of the hypoconid, on which the surface and abrasion vector shown in Fig. 14 are common, may have both type A and B ridges almost equally developed, or elongate type B ridges with short type A ridges, or long type A ridges with short type

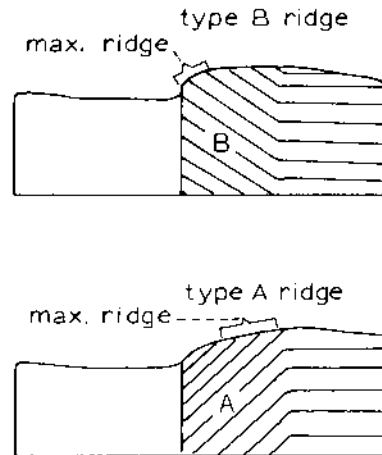
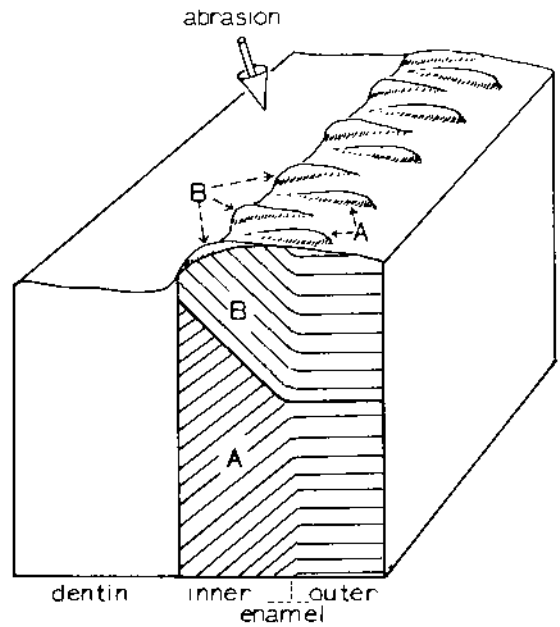


FIGURE 14. Double sets of enamel ridges, as related to prism direction and food abrasion vector. High angle of abrasion vector (arrow) causes both A and B type prism layers to form ridges.

B ridges (the latter is illustrated in the SEM micrograph of Fig. 2).

Single lochs tend to exhibit ridges formed by opposite sets of prisms (Fig. 14). Enamel bordering the downstroke side or trailing edge of the dentinal platform (abrasion vector emanating from the direction of the EDJ) tends to develop type B ridges rather than type A ridges, whereas enamel bordering the upstroke side or leading edge tends to develop type A ridges,

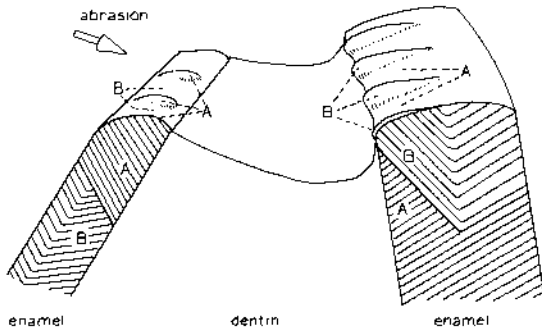


FIGURE 15. Ridges formed by opposite prism types on opposing enamel layers of single cusp. Prisms with axes most nearly parallel to abrasion vector offer maximum resistance to wear.

frequently in the absence of type B ridges (Fig. 15), although other variations may occur.

Causal relationships.—The outer enamel, where prisms of both types A and B become parallel, varies in thickness from region to region in a single tooth. It may represent as much as half the total thickness of enamel, or it may be of negligible thickness. Where it occurs, ridges do not develop. This and the fact that either type A or type B prisms of the inner enamel may form ridges suggests that the ultimate determining factors are simply the relative attitudes of the prisms and the direction of the abrasive vector. The prisms seem to exhibit maximum resistance to wear when the prism axes are aligned parallel or nearly parallel to the abrasive vector and minimum resistance when the axes are aligned perpendicular to the abrasive vector.

This postulated relationship explains all of the ridge phenomena described above. It accounts for the joint occurrence of both type A and type B ridges of phase II surfaces because the angle of the abrasion vector tends to be relatively high and thereby forms minimum angles with the axes of both sets of prisms. In this case the food vector is nearly perpendicular to the prisms of the transitional zone, which therefore defines the valleys (Fig. 16 top). The situation in which only one set of ridges is developed is always one in which the axes of one prism set (A or B) are more nearly parallel to the food vector, and therefore that set, being the more resistant, forms the ridge. In this case the prisms of the transitional zone and the other oblique

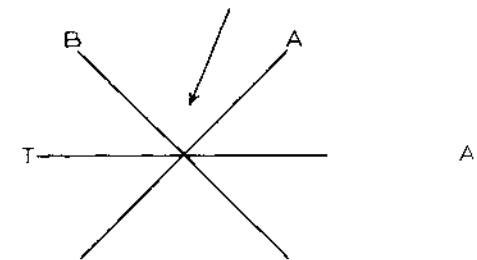
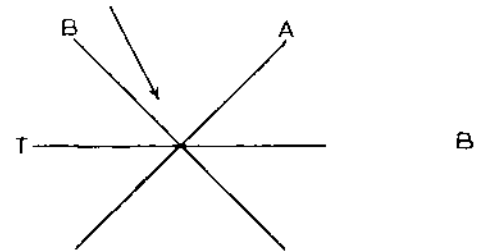
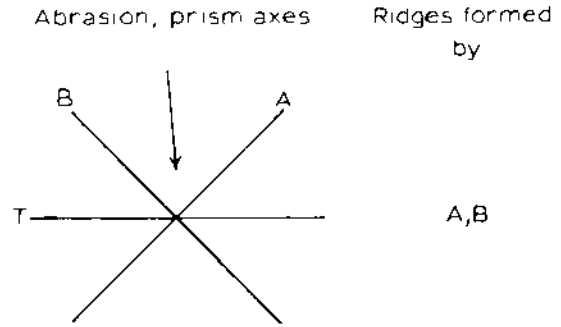


FIGURE 16. Model explaining ridge "preference" for particular prism layer. A = axis of prisms of type A, B = axis of prisms of type B, T = axis of transitional prisms. When abrasion direction is within this range, T direction always forms valleys, but A or B or both may offer maximum resistance to wear, depending on attitude of abrasion vector (arrow) with respect to axis of prisms.

set form subequally greater angles with the food vector than the set forming the ridge (Fig. 16 center and bottom), and therefore only one set of ridges is formed.

Phyletic origin.—The occurrence of optically light and dark H-S bands and corresponding ridges on the occlusal surface in the Rhinoceroidea extends as far back as the middle Eocene (Bridgerian). In the early Eocene peris-

sodactyls *Hyracotherium*, *Homogalax* and *Lambdaotherium*, H-S bands are evident in the cheek teeth but lie in horizontal planes, that is, planes perpendicular to the vertical axis of the tooth. This is the condition in other orders of mammals in which H-S bands are present, according to Kawai's (1955) survey and must be the primitive condition for the perissodactyls. Although Kawai did not observe that the H-S bands in the Rhinocerotidae are vertical rather than horizontal, he apparently had only a single fragment for examination and may have been unable to determine the orientation owing to the unusual direction of the bands. The successive stages in which the attitude of the H-S bands in rhinocerotoids became vertical is suggested by transitional conditions in Eocene and Oligocene brontotherioids and tapiroids. In middle Eocene to early Oligocene brontotheres, layers of reflective and absorptive enamel are horizontal near the centers of the major cusps of the ectoloph, but bend toward the occlusal edges of the loph (Fig. 17C). The appearance of the layers on the worn surfaces of the loph resembles that in the rhinocerotoids in both differential reflectivity and differential wear. In the early Eocene to early Oligocene tapiroids, the layers tend to be horizontal near the subcylindrical cusps but moderately to strongly vertical along the occlusal edges of the lophs and lophids, with individual layers traceable between the two areas (Fig. 17A, B). As particularly shown by the ectoloph of brontotherioids, where the edge of the occlusal surface of the loph is not horizontal, the H-S bands still tend to rectangularly intersect that surface. These conditions in the brontotherioids and tapiroids form intermediate stages of specialization between the completely vertical attitude in the rhinocerotoids and the completely horizontal attitude in the primitive hyracotheriines. These intermediate stages are suggestive of a transitional structure which may have occurred as the rhinocerotoids diverged from the primitive morphology. This transition appears to have occurred rapidly because we have not seen an indication of change in the perissodactyls examined before the later early Eocene at Lysite, yet in the middle Eocene of the Bridger Formation the rhinocerotoid condition is fully developed, with vertical H-S bands on all parts of the tooth.

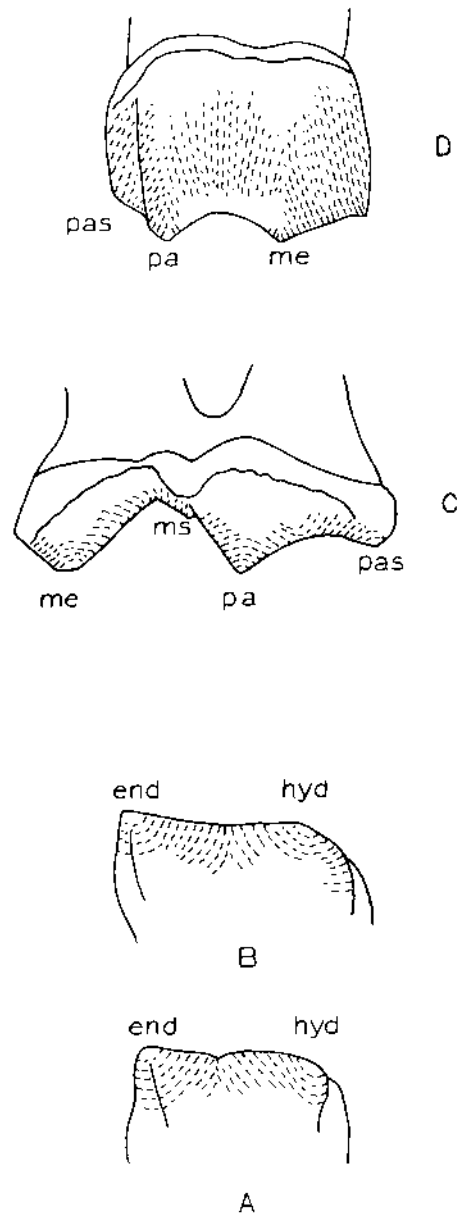


FIGURE 17. H-S bands (dashed lines) in tapiroids, brontotherioids and rhinocerotoids. A = molar hypolophid, middle Eocene (Bridger Fm.) tapiroid, anterior view; B = molar hypolophid, early Oligocene, N. America (McCarty's Mtn.), tapiroid, *Colodon* sp., anterior view; C = molar ectoloph, middle Eocene (Bridger Fm.) brontotherioid, labial view; D = molar ectoloph, middle Oligocene (lower Brule Fm.), rhinocerotoid, *Hyracodon nebraskensis*, labial view; end = entoconid, hyd = hypoconid, me = metacone, ms = mesostyle, pa = paracone, pas = parastyle. H-S bands tend to be perpendicular to chewing surface in areas of crests (tapiroids, brontotherioids), or in areas of both crests and cusps (rhinocerotoid). Structure in the European tapiroid *Lophiodon lautricense* is very similar to that shown for the North American tapiroids.

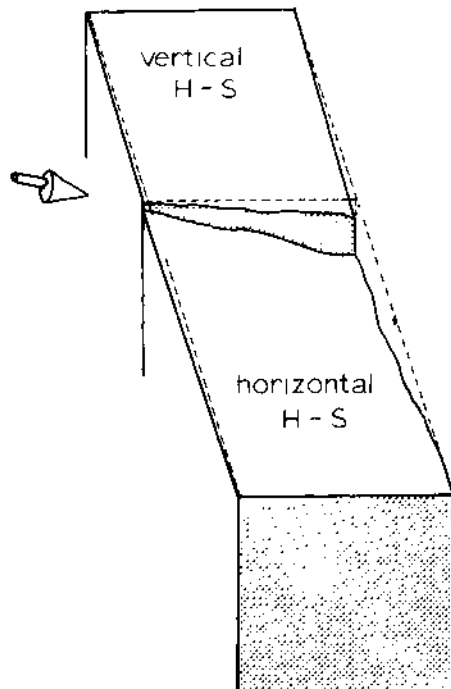


FIGURE 18. Sketch of surfaces of enamel of *Subhyacodon*, differentially worn owing to artificially reversed directions of H-S bands. In experiment, two samples from same cusp were cemented together with reversed polarity of H-S layers and subjected to abrasive jet (arrow). Original surface shown by dashed line.

Wear resistance.—The fact that the H-S bands in the perissodactyls, where modified, tend to intersect wearing surfaces at high angles, and the tendency for ridges to appear where sets of prisms intersect wearing surfaces at different angles, together suggest that the vertical H-S bands may cause the enamel to exhibit a different degree of resistance to wear than horizontal H-S bands. In experiments, the enamel with vertical H-S bands in rhinocerotoids does provide greater resistance to wear than that with horizontal bands. By using fragments of enamel of identical thickness taken from the same cusp of the same tooth of a single individual and cementing the pieces together with the attitudes of the H-S bands 90 degrees opposed to one another, the relative resistances of the two orientations were tested. The spliced pieces were ground to form a single flat plane, and this composite surface was then abraded by dolomite dust. The results (Fig. 18) indicate considerably more rapid wear on the surface with horizontal H-S layers than on the surface

with vertical H-S bands. The experiment was performed several times on rhinocerotid enamel with the same results. A differential response to abrasion was exhibited in these tests by the inner and outer enamel. The outer enamel of the fragments with the vertical H-S bands wore at a rate about 60% of that with horizontal H-S bands. The inner enamel with vertical H-S bands wore only 35% as rapidly as that with horizontal bands. The overall rate of wear of the vertical H-S bands would be about 40–45% of the rate of the horizontal H-S bands.

Similar results were obtained for a late Eocene brontothere with differences of only slightly smaller magnitude. It was more difficult to obtain perfect 90 degree rotation of the H-S bands in the brontotheres, owing to the curvature of the bands, and some of the horizontal bands tended to intersect the surface at low angles. Wear to the vertical set was less regular than in the rhinocerotoids, which correlates with a lesser regularity in arrangement of the bands.

Functional significance.—Two important questions are raised by the occurrence of vertical H-S bands in the rhinocerotoids. The first issue is whether the altered structure evolved by random processes alone or whether it exhibited some functional attribute which made it susceptible to selection. The second question is, if the structure had a nonrandom origin, what caused it?

Two relationships suggest that the changes were functional. One is the persistent tendency for the H-S bands to bend in both the rhinocerotoids and the tapiroids in such a way as to maintain a high angle of intersection with the occlusal surface. The other is the association with lophs (Fig. 17). These observations suggest that a functional relationship between occlusal aspects of the masticatory process and the attitude of the layers exists. An increased degree of bending toward the base of the tooth in some brontotherioids corresponds with the flattening of the occlusal angles in later stages of wear so that a high angle of incidence is maintained. Furthermore, the long retention of vertical H-S bands in the rhinocerotoids from middle Eocene to present is suggestive of stabilizing selection for a functional structure.

From the fact that enamel with vertical H-S

bands offers greater resistance to wear than that with horizontal bands, it may appear that simply this was the selective advantage. However if that were true, one would expect many other hypsodont mammals to have vertical H-S bands, which is not the case. Several possible functional explanations for the occurrence of vertical H-S bands in rhinocerotoids are suggested by the nature of the resulting occlusal surface. The ridges themselves might serve in several ways: sharpening of the edge by concentrating contact (and stress) in narrow areas in the fashion of crenulated edges in saber cat canines, shark teeth and theropod teeth; holding vegetation between the teeth and thus increasing tension on the fibers as it is cut. One very important function seems to be that the altered structure of the enamel provided differential resistance to wear at the time that it arose.

Differential resistance to wear.—The function involving altered resistance of the enamel merits special attention. Such a function would explain why the phenomenon is associated with lophos rather than cusps in the transitional stages. Lophos in tapiroids and rhinocerotoids are narrow structures which are subjected to high occlusal pressures because of the small size of the contact area. In lophodont systems of mastication, wear is most rapid in areas of highest pressure, which are also the areas of greatest cutting efficiency (Rensberger 1973). Consequently, with the appearance of lophos, which must necessarily be narrow for maximum efficiency, a problem of differential wear is presented, with the areas of maximum efficiency tending to be worn away first. In the early stages of its phyletic appearance, a loph may commence as a ridge which emerges from the side of a cusp. This in fact appears to be the origin of the lophos in tapiroids, as evidenced by both North American (Fig. 17) and European tapiroids. In the early stage (Fig. 19), the descending surfaces of such incipient ridges intersect the horizontal H-S bands at oblique angles. If the rate of wear of enamel is dependent upon the steepness of the angle of incidence between the H-S bands and the wearing surface, this initial stage in the acquisition of lophos would begin to offer differential resistance to wear on the occlusal surface. The enamel of the incipient lophos would be more resistant than the enamel

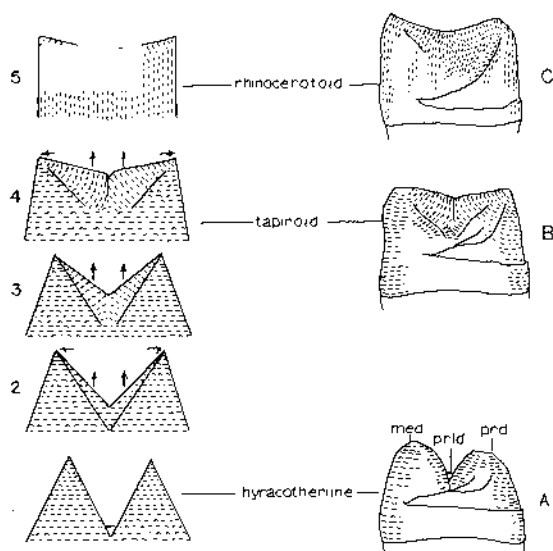


FIGURE 19. Hypothesis for evolution of vertical H-S layers in rhinocerotoids, assuming passage through Eocene tapiroid condition. (1) Cusps moderately appressed. (2) Cusps wider, crests forming on sides of cusps, H-S bands horizontal but intersecting chewing surfaces of crests. (3), (4) Crests elevated, H-S bands bending upward to maintain attitude with respect to edge of crest. Had H-S bands remained horizontal, crests would have worn more rapidly than cusps. (5) Cusps compressed to form part of crest, H-S bands of cusps vertical, equalizing wear along crest. A, *Hyracotherium* protolophid, anterior view; B, middle Eocene (Bridger Fm.) tapiroid protolophid, anterior view; C, middle Eocene (Bridger Fm.) rhinocerotoid protolophid, anterior view. med = metaconid, prld = protolophid, prd = protoconid.

at the apices of the cusps. Consequently the tendency for greater wear on the lophos, as they formed narrow edges where pressures were highest, would have been minimized by the harder enamel. But as the lophos became elevated until the occlusal edges were nearly horizontal, as in stage 4 of Fig. 19, unless the H-S layers had bent in the occlusal direction, the ridges would no longer have intersected the H-S bands and would have lost the attribute of differential hardness. The bending of the H-S bands toward the occlusal surface at the edges of lophos in the forms with less extremely modified structure, the tapiroids and brontotheroids, is strongly suggestive of such a response. In the tapiroids the H-S bands lack vertical attitude at the bases of the lophos where the latter broaden (Fig. 19). In later stages of wear, when the lophos are broad, they are no longer subject to more rapid wear than the regions of the cusps and in

these basal positions the teeth therefore do not require enamel with different characteristics of wear.

However, if the wear hypothesis is correct, it must also be consistent with the advanced condition in the rhinocerotoids, in which the H-S bands are vertical throughout the tooth. At this stage the function can no longer be differential resistance to wear. The explanation would seem to depend upon consideration of the way in which the conditions arose, and upon a difference in gross morphology of the occlusal surface in the rhinocerotoids on the one hand and the tapiroids and brontotheres on the other. In the rhinocerotoids the occlusal surface is extremely lophodont (see General Structural Relationships), whereas in the other groups the major cusps remain distinct. If vertical H-S bands in rhinocerotoids first occurred in lophs between the cusps, as the cusps later became compressed until indistinguishable from the lophs, either the lophs would have had to lose the vertical H-S bands or the cusps would have had to gain them. Selection in that case is more likely to have extended the vertical bands throughout the tooth than to have eliminated them, because of the advantage of overall wear resistance offered by the vertical condition. An analogous situation prevails with respect to hypsodonty in mammals. Among the numerous occurrences of hypsodonty in mammals, we know of no documented instances in which an increase in crown height has been reversed.

Resistance to breakage.—An alternative function is suggested by the structural nature of the H-S bands. The reversed attitudes of the prisms in adjacent zones may serve to strengthen the enamel against fracturing. In primitive herbivores chewing with a dominantly vertical masticatory motion, stress tends to be applied to the cusps at a high angle and to cause vertical compression. The cylindrical shapes of the cusps and the almost vertical direction of stress would make the most likely lines of fracturing vertical. The evolution of lophs would allow a new lateral direction of bending and increase the likelihood of horizontal lines of fracturing. A change of emphasis from a tendency for vertical to a tendency for horizontal fracturing would represent a rotation of 90 degrees in the

same plane as the 90 degree change in attitude of the H-S bands of rhinocerotoids.

The empirical evidence supporting resistance to breakage as a cause for the evolution of vertical H-S bands is the observation that fractures in broken pieces of mammalian enamel which run in oblique directions with respect to the planes of the H-S bands tend to follow the planes for short distances before jumping across from one band to the next. However, we have frequently seen fractures which run perpendicular to the planes of the H-S bands and these tend to be relatively flat. Straight fractures running parallel to the vertical axis of the tooth may be no more common in broken fragments of fossil rhinocerotid teeth than in hypsodont equine teeth, in which the H-S bands are horizontal. The evidence for the existence of a change in direction of maximum resistance to fracturing as a result of change in direction of H-S bands is therefore not yet as convincing as the evidence for a difference in resistance to abrasion, but further investigation is needed.

Other Perissodactyla.—Brontotheres and chalicotheres show some degree of modification of the attitudes of the H-S bands in the region of the ectoloph, but not in the regions of the protocone, hypocone and conules. In the horses, the H-S bands remain horizontal almost throughout the teeth. The absence of modification in the equids and the differential modification in the brontotheres and chalicotheres is consistent with the hypothesis that the modification is related to functional aspects of lophodonty. The absence of modification in the regions of the protocone, hypocone and conules in all these forms correlates with the absence in those areas of a narrow loph comparable to the protoloph and metaloph in the tapiroids and rhinocerotoids.

The degree of modification of the attitude of the H-S bands in the ectoloph of the perissodactyls varies in accordance with the degree of emphasis of that structure in the occlusal apparatus. The ectoloph is more compressed in the rhinocerotoids than in any of the other perissodactyls and bears the most highly modified H-S bands. In the tapiroids the ectoloph is divided complexly into cusps and crests, and the attitude of the H-S bands varies over the ecto-

loph. Among the brontotherioids, chalicotherioids and equids, in which a W shaped ectoloph is present, a correspondence exists between the relative size of the ectoloph and degree of upward bending of the H-S bands. The ectoloph is anteroposteriorly longer than the width of the molar in the brontotheres and chalicotheres and the H-S bands bend to meet the edge of the crests at a high angle. In the equids the length of the ectoloph is less than the width of the tooth and the H-S bands do not bend toward the occlusal edge. Function in brontotheres and chalicotheres, unlike function in the equids, seems to occur dominantly in the ectoloph, which may attain considerable wear when the protocone is still little worn. In certain though not all later rhinocerotids, for example *Diceros bicornis* and *Dicerorhinus*, the upper molars actually rotate lingually during the life of the individual in order to compensate for excessive rates of wear on the ectoloph (Fortelius, in press). This seems to illustrate the functional importance to lophodont taxa of maintaining uniform rates of wear. Thus it probably can be said that the raising of the attitude of the H-S bands was in general a correlate of the concentration of masticatory function on narrowed lophs. Groups such as equids and artiodactyls, in which selenodonty evolved, did not experience the same selective pressure, probably because of lesser differential wear over the occlusal surface in early stages of divergence.

Discussion

Adaptive evolution in mammalian teeth at the ultrastructural level is not unexpected, considering the extensive modifications of the occlusal surfaces that have occurred during the Cenozoic, at least some but perhaps most of which is surely adaptive. The full 90 degree reorientation of the H-S bands in the rhinocerotoids is nevertheless an unexpectedly profound change to the enamel structure, and even after recognizing that it has occurred, one has difficulty visualizing how it happened without seeing the intermediate conditions in the tapirids and brontotherioids.

These results, together with the observation of correlation between enamel structure and direction of masticatory movement in arvicoline

rodent molars, suggest that the phyletic history of mammalian enamel ultrastructure may be as instructive as that of the gross morphology of the tooth. The potential for diversity in the ultrastructure is perhaps as great as that of the occlusal surface, for different combinations of occlusal structures, directions of movement and occlusal pressures should be reflected by different patterns of stress and wear. For example, the relatively simple rodent incisor contains exceedingly complex prism patterns which may prove to be solutions to problems of strain involved in producing the high occlusal pressures needed in gnawing.

A knowledge of the ultrastructure of enamel may be necessary in accounting for a given particular gross configuration of enamel. Most mammalian teeth, even brachyodont ones, probably depend upon at least some degree of wear to hone edges and produce functionally adequate surfaces, and also upon resistance to breakage in areas of high stress. Thus, the configuration of the occlusal shape, which determines the attitudes of the various wear facets as well as stress concentrations, may in a given case be influenced or limited in some way by the directional properties of wear and resistance to breakage.

Conclusions

1. Worn occlusal edges of enamel in the cheek teeth of rhinocerotoids exhibit one or two sets of macroscopic ridges. The ridges correspond to positions of intersection of the surface with tracts of enamel prisms.

2. The ridges are caused by the differential resistance of enamel prisms to abrasion, depending upon prism attitudes. Prisms with long axes aligned parallel or nearly parallel to the abrasion vector are most resistant to physical abrasion, and those perpendicular to the abrasion vector are least resistant.

3. The sets of prisms producing ridges contain either one or both of two types of prism directions. In one type (B) the prisms, as they grow from the EDJ, decline obliquely from the occlusal plane and the EDJ. In the other type (A) the prisms rise obliquely toward the occlusal surface and the outer enamel surface. The two sets are separated by a transitional zone of hor-

horizontal prisms running perpendicular to the EDJ.

4. Prism sets A and B are usually confined to the inner part of the enamel. The outer enamel consists of parallel prisms derived from both inner sets A and B by a bending of those of one set or both near the center of the enamel. Prisms of the outer enamel trend outward and often, though not always, at a moderate angle upward.

5. Prisms of type A tend to form ridges where the abrasion vector trends toward the EDJ from the direction of the outer enamel surface. Prisms of type B tend to form ridges when the abrasion vector trends in the reverse direction. Prisms of type A and type B together form a double set of ridges when the food vector is at a high angle, as for example, on the phase II wear facet of the hypoconid.

6. The prisms of type A and type B differentially reflect light, depending upon whether the light enters the prisms along the long axis (poor reflectance) or perpendicular to the long axis (high reflectance).

7. Because of the differential reflectivity and the large number of prisms forming a single tract, the tracts can be identified under low magnification light microscopy.

8. The vertical tracts of reversed prism direction are homologous with the horizontal H-S bands of other mammals.

9. Transitional conditions of H-S bands in fossil tapiroids and brontotheres show that the change from horizontal to vertical attitude was functionally associated with the evolution of lophs in these groups and occurred between early and middle Eocene.

10. The vertical H-S bands in rhinocerotoids are more resistant to wear than horizontal layers because with this attitude a high percentage of the prisms are directed toward the occlusal surface and the source of abrasion.

11. Selection initially favored upturned H-S bands on the lophs rather than the cusps because the lophs were narrowly crested and subject to more rapid wear. Later, in rhinocerotoids alone, continued equalization of wear as cusps became compressed caused vertical H-S bands to extend to all parts of the tooth. The advantage of enhanced cutting and holding ability of the tiny occlusal ridges also may have

been involved. Whether upturned H-S bands affected the tendency of the enamel to fracture is not yet clear.

12. The dominance of vertical H-S bands in the rhinocerotoids and lesser development in other perissodactyls is associated with the more extreme development of narrow lophs early in the history of the rhinocerotoids.

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Hispanotherium grimmi, late Mioc., Turkey.
Diceros neumayri, Pontian, Turkey.
Subhyracodon occidentalis, middle Olig. (Orellan), N. Am.
 Equidae
Mesohippus sp., Brule Fm., middle Olig. (Orellan), N. Am.
Orohippus sp., Bridger Fm. (B), middle Eocene, N. Am.
Equus (domestic).

Under light microscope only

Rhinocerotoidae

- Diceratherium* sp., John Day Fm., Oligo-Mioc., N. Am.
Hyrcodon nebraskensis, Brule Fm., middle Olig. (Orellan), N. Am.
Hyrcodon sp., Clarno Fm., late Eoc., N. Am.

Tapiroidea

- Hyrachyus cf. modestus*, early Eoc. (Wasatchian), N. Am.
Colodon sp., early Olig. (Chadronian), N. Am.
Lophiodon lauricensis, Eoc., France.
 Other tapiroids, Bridger Fm., middle Eoc., N. Am.

Brontotherioidea

- Early Olig. (Chadronian), N. Am.
 Late Eoc., Clarno Fm., N. Am.
 Middle Eoc., Bridger Fm. (B), N. Am.
Lambdatherium sp., early Eoc. (Wasatchian), N. Am.

APPENDIX

Taxa Examined

Under SEM and light microscope

Rhinocerotidae

- Dicerorhinus* sp., Pleist., Sangiran, Java.
Coelodonta antiquitatis, Pleist., southern Germany.