Scanning Microscopy

Volume 1 | Number 2 Article 19

2-17-1987

Cracks in Fossil Enamels Resulting from Premortem vs. Postmortem Events

John M. Rensberger
University of Washington

Recommended Citation

Rensberger, John M. (1987) "Cracks in Fossil Enamels Resulting from Premortem vs. Postmortem Events," *Scanning Microscopy*: Vol. 1 : No. 2 , Article 19.
Available at: https://digitalcommons.usu.edu/microscopy/vol1/iss2/19

Scanning Microscopy, Vol. 1, No. 2, 1987 (Pages 631-645)
Scanning Microscopy International, Chicago (AMF O'Hare), IL 60666 USA

0891-7035/87$3.00+.00

CRACKS IN FOSSIL ENAMELS RESULTING FROM PREMORTEM VS. POSTMORTEM EVENTS

John M. Rensberger

Department of Geological Sciences
and Burke Memorial Washington State Museum,
University of Washington DB-10
Seattle, Washington 98195
Phone no. 206-543-7036

(Received for publication May 9, 1986, and in revised form February 17, 1987)

Abstract

Vertebrate enamel preserves a record of fracture-producing strain. Fracturing during the life of the individual is potentially a source of selection for stronger enamel in the course of evolution. To determine if it is possible to recognize such fractures in fossil enamel, cracks in a variety of fossil materials, including enamel-covered holostean scales, crocodilian teeth, theropod and hadrosaurid dinosaur teeth, and mammalian teeth were examined. Cracks that occurred during the life of the individual could be recognized by abrasive wear on edges exposed at the surface of the enamel in areas worn by oral or locomotor abrasion. Certain distinctive crack patterns were identified as results of specific stress states occurring during life. Transverse cracks on the anterior parts of *Lepisosteus* scales were probably caused by external loading. Hertzian cracks and shallow, arcuate, lateral cracks on the occlusal edges of tooth enamel appear to be caused by stress concentrating impacts. Horizontal cracks arranged asymmetrically on the sides of conical teeth were reproduced in models subjected to bending stresses. Oblique cracks near the tips of conical fossil teeth were produced in models by oblique loads near the tip. Vertical cracks around cylindrical or conical tooth surfaces may be caused by several different sources of stress, including lateral "wind" loads and vertical "snow" loads. Of the postmortem causes of fracturing of fossil enamel, drying cracks seem to be the most important. Experimental drying produced from 25% to 50% of the cracks in dry teeth.

Key Words: Enamel fracturing, teeth, scales, fossils, stress, *Lepisosteus*, crocodilians, theropods, hadrosaurs, mammals.

Introduction

Teeth have exhibited perhaps the greatest evolutionary change of any skeletal elements in the mammals. Modifications of the gross form of mammalian teeth fall into several categories: addition, repositioning, reduction or loss of cusps; narrowing of cusps to form lophs or sharp carinae; folding of the surface to form inflections; and hypsodonty (lengthening of cusps or crown, sometimes accompanied by addition of cementum to the crown and loss of roots). Except for the development of tusks or canine sabers in some forms, the most extensive modifications have occurred in the cheek teeth, which frequently have attained great surface complexity (or have reversed that trend). These changes have been so pervasive throughout mammalian history that usually the most discriminating information about the taxonomy of fossil taxa comes from the dentition.

Because the teeth have as their main function the grasping and processing of food, many of these evolutionary changes are related somehow to changes in diet (Kay, 1978) or improved efficiency in the processing of food (Rensberger, 1973). However, the gross dental form is a resultant of other factors as well, particularly the selection for toughness.

Teeth are mechanical devices that concentrate masticatory force in complex stress distributions at the chewing surface where food is compressed and sheared. For example, the teeth in hypsodont mammals contain structures that increase chewing pressure locally to very high values at specific moments during the power stroke (Rensberger, 1975). The variety of the dental architectures that can be utilized is constrained by the strength of the structure and the materials. For example, sharp enamel edges may be optimal for cutting tough fibers, but when maximized for that factor alone, the resulting thin dental structures would be impractical because the tooth would rapidly disintegrate under the high occlusal pressures that are generated.

It is therefore probable that a significant amount of the structure of molariform teeth in mammals results from the need to maintain a rigid surface that is resistant to the occlusal stresses that are required to subdivide food of a given toughness or hardness. When stress exceeds the strength of a dental structure, failure leads to the loss of part or all of that structure. The loss may be through abrasion, in which breakage is inflicted on a very fine scale to the enamel crystallites on the surface, or through spalling fractures that penetrate the enamel deeply and that may cause the loss of a major structure. Enamel failure at the fine scale of wear and at the larger scale of macroscopic cracking are probably related. The finer scale flaws of abrasive wear are very likely to be nuclei or precursors of the larger cracks in many instances.

The toughness of enamel to resist fracture is related to the microstructure of the material. Mammalian enamel tends to fracture parallel to prism boundaries (Powers, et al, 1973; Boyde, 1976; Rasmussen, et al., 1976; Hassan, et al, 1981) and in humans has been observed to fracture preferentially parallel to Hunter-Schreger bands (Powers, et al, 1973). There is evidence now that the microstructure of enamel has evolved in mammals in relationship to directions and intensities of chewing stresses. In arvicolid rodents, where the direction of chewing motion across a loph is from the outer side of the enamel toward the enamel-dentin junction (EDJ), the enamel exhibits a certain sequence of microstructures across its thickness from the EDJ to the outer surface (v Koenigswald, 1980). On the opposite side of the loph, where the direction of the chewing stress is reversed, the sequence of microstructure is also reversed in some arvicolids, indicating that the microstructural sequence functions to resist chewing stress in a complex fashion that is not fully understood. In tapiroids, where stresses vary along a loph as it becomes narrow near its center, the Hunter-Schreger bands, that is, the sheets of decussating prisms, become tilted vertically to almost 90°. The high angle bands are more resistant to wear (Rensberger and v Koenigswald, 1980), owing to the larger percentage of prisms that have their axes perpendicular to the wearing surface and the anisotropism of hydroxyapatite crystallites which have their C axes roughly parallel to the long axes of the prisms. In rhinocerotids, in which the entire lophs are compressed, vertical Hunter-Schreger bands occur throughout the lophs. Similar modifications occur in other ungulate orders (Rensberger, 1983; Fortelius, 1985).

Crack patterns are a potential source of information about the nature of the stresses to which teeth and dental structures have been subjected. Cracks propagate perpendicular to the direction of tension. In fossil bones, because most of the cracks formed during life will have healed before death, almost all observed cracks have been acquired after the animal died. Unlike bone, enamel preserves cracks as long as the enamel itself survives, so the cracks are a complete record of the stresses that have exceeded the strength of the material, including postmortem stresses. However, it is the enamel failure occurring during the life of the individual that influences the structural evolution of teeth. This is not meant to imply that the total abundance of cracks, including those that occurred after death, might not be a source of information about different strengths of teeth in different taxonomic groups. Yet, to maximally utilize the information from fossil cracks, we need to find ways to identify their causes and whether they occurred during the life of the individual.

Materials and Methods

This study was undertaken to determine the feasibility of distinguishing premortem from postmortem cracks. Initially about ninety dentitions and teeth from a variety of fossil and Recent ungulates and carnivores were examined with light microscopy at 10X to 40X magnification. The teeth were searched for crack patterns that repeated from specimen to specimen or group to group, and for directional characteristics suggestive of premortem stresses. In order to eliminate the possible effects that complex surfaces might have on crack patterns, lower vertebrates with simple enamel shapes were examined as well as mammals.

Fresh cracks in enamel have very sharp edges. Rounded edges are evidence that abrasion of some kind has been superimposed after the crack formed. Abrasion that has been caused by chewing action is therefore a potential means of identifying a crack occurring during the life of the individual. For example, chewing in ungulates produces abrasive wear that is concentrated in areas near the occlusal surface. Chewing effects in crocodilian teeth include polishing at worn tips of the crowns and patterns of striae on the sides of the crowns. Another source of abrasion is that produced by streams and rivers into which teeth may fall before being eventually buried in sediment. Stream abrasion is usually distinguishable because it is evenly distributed over the specimen whereas chewing abrasion is consistently restricted to specific areas of the crown. Many bodies of fossiliferous rock do not represent stream deposits and contain no stream-abraded teeth or bones. In this study, specimens from high energy deposits (stream channel deposits) were excluded, and all specimens were individually screened for absence of stream abrasion and presence of chewing abrasion. The qualifying specimens were examined for abrasion to crack edges in worn areas of the tooth under light microscopy and a subset of those was subjected to scanning electron microscopy (SEM).

Two types of models of simple conical teeth were constructed. One type consisted of thin glass shells filled with epoxy (simulating enamel and dentin). The other consisted of resin covered epoxy casts of teeth. These models were then subjected to a variety of loads. Models with glass shells were inserted in a sand-filled chamber with a piston at one end and compressed in order to test the effects of burial on teeth.

Models with glass and resin shells ranging from sharply conical to low hemispheric shapes, including casts of crocodilian and mammalian teeth, were subjected separately to vertical compressive and bending loads until fracturing occurred.

To test the effects of drying on teeth, the total lengths of cracks in a sample of extracted human teeth that had been preserved in formalin were measured. The teeth were then dried and remeasured. Drying was done at 38° C for 72 hours, with examination at 8 to 12 hour intervals. This time period proved to be ample because most of the new or lengthened cracks appeared within the first 8 hours of drying.

Results

Lepisosteus scales.

The scales of these holostean fishes (gars) have a moderately thick layer of an enamel-like material called ganoine overlying dentinlike cosmine and a heavy substrate of bonelike material. These specimens were examined because ganoine is relatively flat, in contrast with the enamel of teeth, and the crack orientations are therefore less influenced by the shape of the object. The pattern of cracking is expected to be a rather simple reflection of the applied load.

Examination of many scales from different localities revealed a consistent pattern of cracks at the anterior end of the scale, the end anchored to the integument. In that area a few widely spaced cracks tend to be aligned transverse to the longitudinal axis of the scale (fig. 1). When only a few cracks are present, they usually occur in this area. Sometimes a number of cracks occur in the posterior half of the scale, but these are less consistent in direction.

The parallel cracks at the anterior end of the scale were produced by tension acting parallel to the longitudinal axis of the scale. The source of this tension will be discussed after the crack patterns in the other animals have been described. The cracks in the underlying bone generally are short and

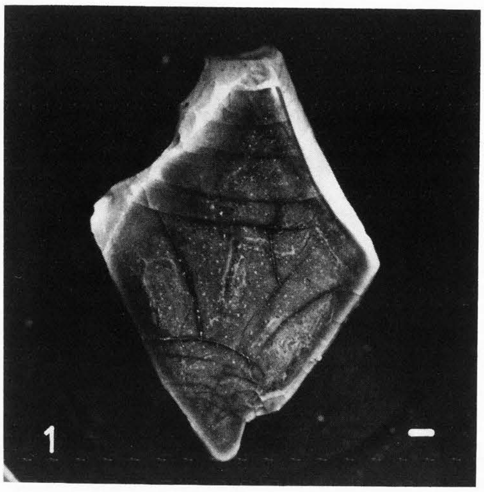


Figure 1. *Lepisosteus* scale, UWBM 59434a, external view; early Paleocene (Puercan), Nacimiento Fm., New Mexico. Ganoine dark; dentin and bone like material light, beneath ganoine. Anterior end, where scale was attached to integument, at top. Bar = 1 mm.

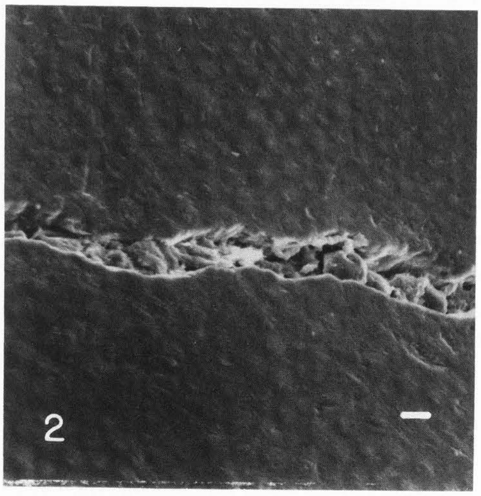


Figure 2. *Lepisosteus* scale, UWBM 59434b, external view, anterior at top; early Paleocene (Puercan), Nacimiento Fm., New Mexico. Micrograph of ganoine surface showing transverse crack (perpendicular to anteroposterior direction) near anterior end of scale. Edges of crack slightly worn. Papillae ranging over entire surface. Bar = 10 µm.

perpendicular to the margins of the scale, clearly suggesting shrinkage as a cause rather than external loading. Few of these cracks are continuous with those in the ganoine and the directional patterns are unrelated. In a number of specimens the marginal underlying cracks are randomly shaped and bend to intersect adjacent cracks perpendicularly, like drying cracks. Short marginal cracks with no connection to the overlying ganoine can be seen in the margin of the underlying tissue of the scale in figure 1.

To determine the timing of fracture in the ganoine, specimens were examined under light microscopy and under SEM for evidence of abrasion that could be attributed to life events. Evidence of abrasion to the edges of certain of the parallel anterior cracks could be seen under the light microscope. Under SEM it is evident that this abrasion occurred during life. For example, the edges of the crack in figure 2 appear to be slightly rounded, suggesting light abrasion. However, the edges of the same crack at a different position across the scale shows much greater rounding (fig. 3). In this latter area, the papillae of the surface are almost obliterated by wear, whereas in figure 2, where the crack is less worn, the papillae are only slightly worn. Had the abrasion been due to fluvial activity after death of the individual, abrasion would have been evenly distributed over the surface. Small parallel scratches could be seen on the surface of the ganoine in many scales. Because these scratches are not random and are absent on the recessed ganoine near the margins of the scales, the cause must have been abrasion during locomotion, not fluvial activity. The superposition of this abrasion on the edges of the crack definitely indicate that the crack was present while the fish was living.

Crocodilian teeth.

Crocodilian teeth have a simple conical shape and thin enamel of relatively uniform thickness. Most of the teeth examined are narrow cones with a relatively smooth or slightly rugose enamel surface (fig. 4). The cone is usually bent, making the lingual surface concave. The anterior and posterior surfaces in these teeth have a carina (the dark vertical stripe to right of center in figures 4 and 10; the light streak near the center of figure 8, and the light streak near the left margin of figure 9).

Three distinct sets of crack orientations, vertical, horizontal, and oblique, dominate these teeth (fig. 4). The vertical cracks are frequently open on the surface, and in some broken teeth the vertical cracks could be seen to continue for a short distance into the dentin. Few of these cracks run continuously from the base of the enamel to the tip of the crown. They are most abundant around the base of the crown. When viewed under high magnification the vertical cracks in the enamel often have edges polished by chewing wear (figs. 5, 6). A transverse scratch in the lower part of figure 5 and another near the top have caused slight notching of the margins of the vertical cracks, indicating that the cracks occurred first. In figure 6 the three smaller cracks with zigzag margins are less worn than the wider crack at the right side of the micrograph. Narrow cracks should be less worn than wide cracks because the edges of narrower cracks are less exposed to wear, provided that the width of the wide cracks was attained before abrasion ceased. Horizontal striae in figure 6 more frequently continue past the smaller cracks than past the larger crack, indicating that at least some of the striae occurred after the larger crack had attained large size. Often it is not clear whether the narrow cracks existed during life, but the evidence indicates that the broader, heavily abraded cracks did.

Horizontal cracks are seldom exposed as visible cracks on the surface of the enamel and therefore could not exhibit abraded edges. However, near the occlusal surface of older teeth that had been worn down to a dentinal platform, ledges representing faces of horizontal cracks can be found (fig. 7). The horizontal ledges formed at the upper occlusal margin of the enamel in figure 7 are aligned with horizontal cracks that extend around the tooth. The horizontal crack continuous with the lower "step" can be seen to the right as a line resembling a faint scratch. Another faint horizontal crack is visible to the right of the notch just under the upper step. Horizontal cracks were seen in these positions through the translucent enamel before the specimen was coated for SEM examination, otherwise it would have been impossible to verify that these faint lines represent cracks and not scratches. The edges of all of the cracks near the occlusal surface in the specimen of figure 7, vertical and horizontal, as well as the exposed crack walls, show the effects of food polishing and were therefore present during life.

The oblique cracks appear to be horizontal cracks that are more steeply inclined near the tip of the crown (figs. 8-10). The planes of these cracks in the occlusal one-third of the crown are usually aligned at an angle higher than a plane perpendicular to the surface of the enamel, whereas in the more basal part of the crown the cracks fall in a plane approximately perpendicular to the surface (that is, the right or left margin of the tooth, as seen in these figures). Near the tip of the crown, the cracks may form angles of 45° with the axis of the tooth (figs. 8, 10). Viewed anteriorly, the cracks of the labial and lingual sides of the tooth dip downward but in opposite directions (fig. 8). The two sets do not intersect, however.

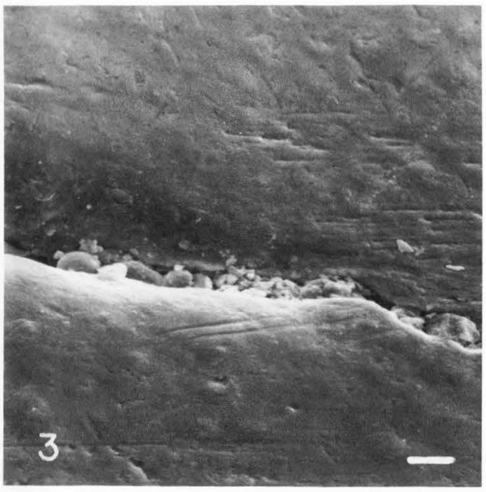


Figure 3. *Lepisosteus* scale, same specimen as in fig. 2. Micrograph of same crack, but in more heavily worn area (surface papillae almost obliterated by wear). Bar = 10 µm.

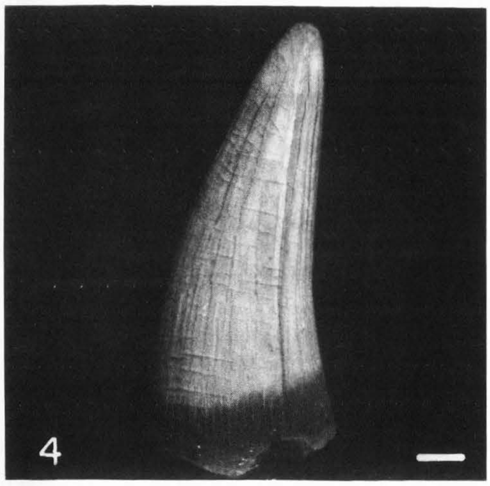


Figure 4. Crocodilian tooth, UWBM 59406, anterior view; early Paleocene (Puercan), Nacimiento Fm., New Mexico. Vertical, horizontal, 45° systems of cracks. Bar = 1 mm.

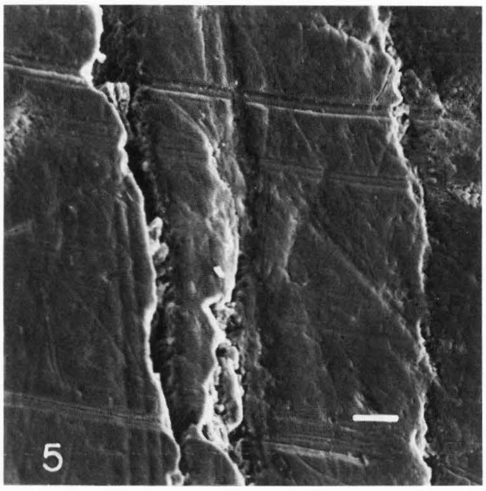


Figure 5. Crocodilian tooth, UWBM 52313-2, late Cretaceous, Hell Creek Fm., Montana. Micrograph of enamel surface well down from tip (tip toward top). Vertical cracks with worn margins. Two horizontal striae superimposed on left, center, and right vertical cracks. Bar = 10 µm.

Between the two is a third set of cracks that crosses the midline horizontally and overlaps with the labial and lingual sets.

The lingual cracks of the tooth of figure 8 continue across the posterior carina, but not the anterior carina (fig. 9). This suggests that the changes in shape of the tooth near the carinae were not major factors controlling the propagation of these cracks.

The horizontal cracks not infrequently terminate abruptly at vertical cracks, whereas vertical cracks rarely terminate at horizontal cracks, except near the tip of the tooth. This indicates that the two types of cracks have different timing and probably different causes, which is discussed in a later section.

Theropod teeth.

Small carnivorous dinosaurs have teeth that are similar in profile to crocodilian teeth but are flattened, forming a strongly lenticular cross-section. Vertical cracks are well developed in these teeth, but horizontal cracks are rarer than in crocodilians (fig. 11). As in crocodilians, the vertical cracks are most abundant at the base of the crown, most do not run the complete distance from the base to the tip of the crown, and many arise at varying positions in the middle of the crown and then fade away.

The vertical cracks near the margins of the tooth in figure 11 are parallel to the adjacent margin everywhere but at one point on the posterior edge (right side of figure). There they deviate and form short arcs that intersect the edge. At that point four of the denticles forming the serrated edge are broken away. Clearly the arcuate cracks in that area were caused by the trauma that broke the denticles. Cracks above and below the traumatized spot are parallel to the adjacent edge in the usual alignment.

The vertical cracks are often associated with thin dark marks extending from the inner margin of the crack a short distance into the dentin. Peyer (1968, pl. 57b) shows the same feature in a ground section of a theropod tooth from the Rhaetic (late Triassic). Occasionally the same apparent penetration of the enamel crack into the dentin for a short distance occurs in crocodilian teeth. Although enamel is more than four times harder than dentin, its tensile strength may be somewhat less than that of dentin (Waters, 1980). This may be the reason why most cracks observed in enamel do not penetrate the dentin.

Hadrosaur teeth.

These hypsodont cheek teeth have crack patterns that are quite different from those of the crocodilians and theropods. Horizontal cracks are fewer and less regular in alignment than in the crocodilians but are more prominent (fig. 12). The vertical cracks, unlike those of crocodilians, are less parallel and frequently are terminated by horizontal cracks (fig. 12).

The crack pattern near the occlusal surface is distinct from that in the middle and lower part of the crown. Near the occlusal surface are some arcuate horizontal cracks that dip more steeply than those farther down. Beneath the right margin of the occlusal surface is another set of closely spaced parallel cracks that intersect the surface at 60°. Where cracks near the occlusal surface intersect one another, the angle is 20° to 60°. The cracks lower in the crown are more widely spaced, less parallel, and intersect one another at angles close to 90°. The horizontal cracks near the occlusal surface of the median rib (near the left side of the tooth as illustrated) are more closely spaced than those lower on the crown. The crown shape in this specimen is quite prismatic but is narrower near the tip than at the base. This was the only available hadrosaur tooth in which a substantial amount of the crown remained.

Mammalian teeth.

Many of the brachyodont ungulates examined, including condylarths and equids, have numerous vertical cracks. These are most abundant near the base of the crown and are therefore suggestive of the vertical cracks in crocodilian and theropod teeth (fig. 13). Vertical cracks of this type are not commonly present in the *Ursus* (bear) canines examined. However, one specimen was seen that has numerous vertical cracks on the posterior side at the base of the crown and these cracks had been present during life because their edges are worn by chewing abrasion. Unlike the condition in the archosaurs, vertical cracks are much less common in the upper part of the crown in mammals. The enamel thickens in the upper part of the crown in mammals, which may account for this difference. However, occasionally vertical cracks do occur near the occlusal surface. An example is the long central crack of figure 13. The upper part of this crack has edges rounded by food abrasion, as may be seen under light microscopy (fig. 14). Figure 15 is a micrograph of a similar but finer vertical crack in the early Eocene horse, *Hyracotherium.*

Although some of the vertical cracks at the

Figure 6. Crocodilian tooth, UWBM 52313-3, late Cretaceous, Hell Creek Fm., Montana. Micrograph of enamel on side of tooth. Tip toward top. Four vertical cracks; sets of horizontal and vertical striae. Bar = 100 μm.

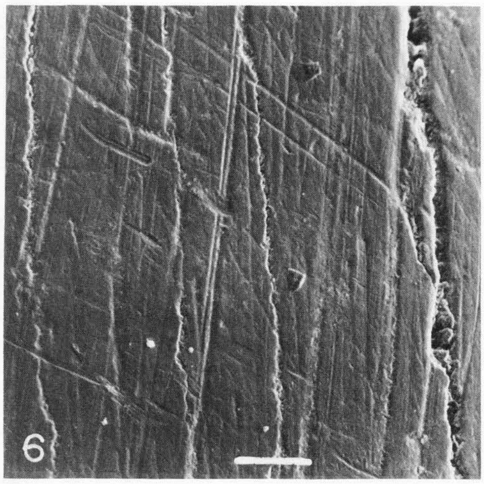
Figure 7. Crocodilian tooth, UWBM 52313-4, late Cretaceous, Hell Creek Fm., Montana. Micrograph of EDJ at margin of naturally worn dentinal platform (upper left corner). Tip toward top. Prominent vertical cracks worn by food abrasion, heavily where exposed at occlusal margin. Faint traces of horizontal cracks (arrows) identifiable as extensions of worn surfaces on horizontal enamel edges. Bar = 100 μm.

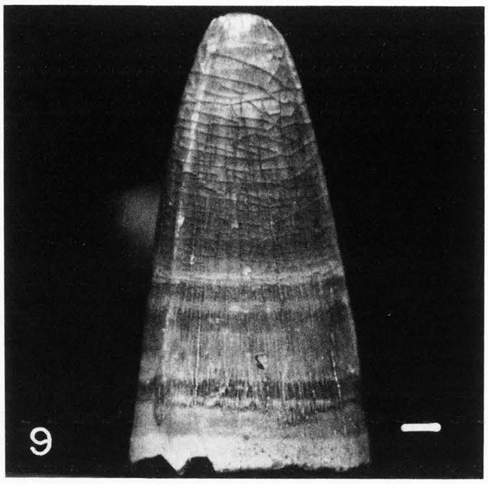
Figure 8. Crocodilian tooth, UWBM 52313, anterior view; late Cretaceous, Hell Creek Fm., Montana. Photograph showing horizontal cracks in middle region of tooth, oblique cracks in two high angle planes near tip of crown. Anterior carina of tooth showing as light vertical streak. Labial on right, lingual on left. Bar = 1 mm.

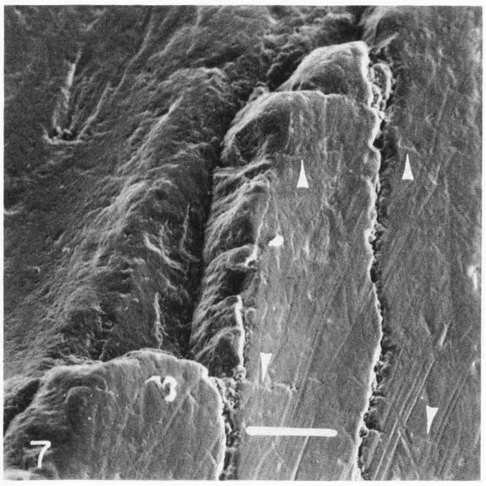
Figure 9. Specimen of fig. 8, lingual view. Vertical cracks dominant near the base of the crown. Bar = 1 mm.

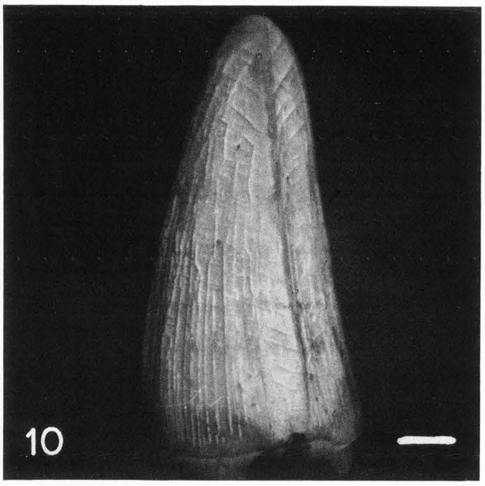
Figure 10. Crocodilian tooth, UWBM 59703, anterior view; early Paleocene (Puercan), Nacimiento Fm., New Mexico. High angle sets of cracks near tip of tooth as in fig. 8. Vertical cracks increasingly dominant toward base of crown. Bar = 1 mm.

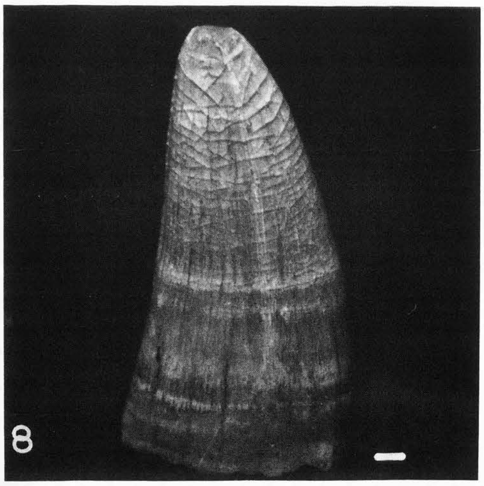
Figure 11. Theropod (saurischian dinosaur) tooth, UWBM 52285, lingual view; late Cretaceous, Hell Creek Fm.. Montana. Vertical cracks abundant; no horizontal cracks visible. Note Hertzian cracks converging on area of broken denticles (arrow). Bar = 1 mm.

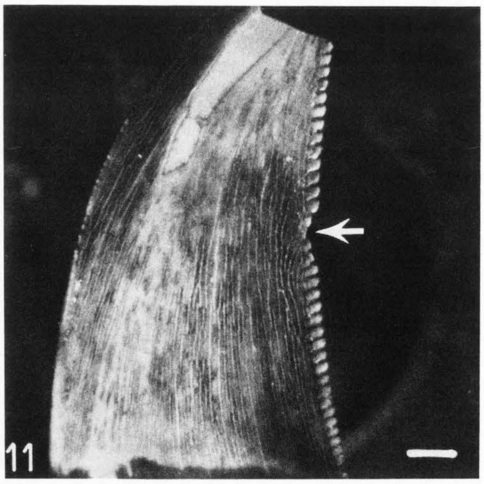

6


9


7


10


8


11

occlusal edge may run to the base of the crown (figure 14), others are confined to an area near the occlusal surface (fig. 16). At the position where the edge of enamel is notched, left of center in figure 16, a flake of enamel had been lost and the broken edge subsequently rounded by abrasion. This area is closely underlain by several arcuate horizontal cracks and several vertical cracks. Both the horizontal and vertical cracks are related to the event that caused the damage to the edge, which occurred during the life of the individual. Similar horizontal, shallowly arcuate cracks are present near the edge of the enamel to the left of the vertical crack in the specimen of figures 13 and 14. The edge of the enamel had been similarly chipped and subsequently rounded in other places in this specimen.

An unexpected condition was found in the Oligocene horse *Mesohippus*. Vertical cracks with worn edges are frequently present low on the lingual sides of cheek teeth, yet vertical cracks occurring on the labial sides of the cheek teeth of the same specimens were found to be largely unworn. Close inspection of the labial and lingual surfaces showed that the papillae that characterize the unworn enamel surface are present on the labial sides but missing on the lingual sides. Furthermore, the lingual cracks in these specimens are unworn close to the base of the enamel, the exact distance being approximately the same for a single tooth, but varying from 1 to 3 mm between teeth and individuals. The wear on the lingual surface must have been caused by action of the tongue in moving abrasive food against the side of the tooth. The horizontal boundary between the worn and unworn segments of the cracks must mark the margin of the gum. Vertical cracks occur on the sides of *Ursus* cheek teeth, and wear to crack edges is especially conspicuous on the lingual side.

The anterior teeth in mammals, especially the canine, are simpler in their architecture and more closely resemble the elongate conical form of crocodilian teeth than do the cheek teeth. Like crocodilian teeth, the canine of carnivorans functions as a grasping, holding, and pulling device.

The upper and lower canines of Recent *Felis concolor* (cougar) and *Ursus americanus* (black bear) tend to have numerous horizontal cracks on both the anterior and posterior surfaces. These are difficult to see unless the cracks are stained. In the specimens of *Felis* examined, the cracks were rarely stained and could only be seen when specular light reflected from the surface. All the horizontal cracks seen in *Felis* have rounded edges and were produced by chewing abrasion, which is extensive on these specimens.

In some of the Recent *Ursus* canines the cracks are stained reddish brown (fig. 17), the same stain that

Figure 12. Hadrosaurid (ornithischian dinosaur) tooth, UWBM 52314, lingual view; late Cretaceous, Hell Creek Fm., Montana. Worn occlusal surface at top. Note numerous vertical cracks concentrated just beneath occlusal edge. Bar = 1 mm.

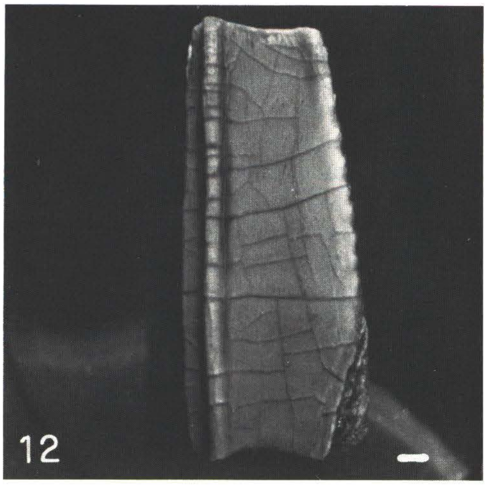
Figure 13. *Conacodon* (periptychid condylarth, a mammalian herbivore) upper premolar, UWBM 59581; early Paleocene (Puercan), Nacimiento Fm., New Mexico. Numerous vertical cracks ringing base of enamel crown, a few reaching occlusal surface. Bar = 1 mm.

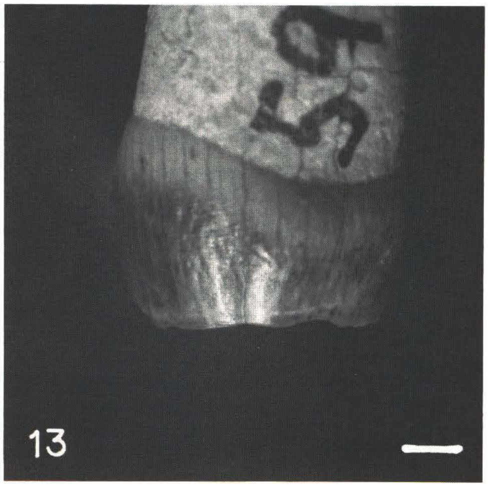
Figure 14. Specimen of fig. 13, enlarged, showing shallow lateral cracks (vertical arrow) to left of long vertical median crack (horizontal arrow). Dip in occlusal edge at large crack resulted from breaking away of similarly fractured shards of enamel and subsequent smoothing by food abrasion. Bar = 1 mm.

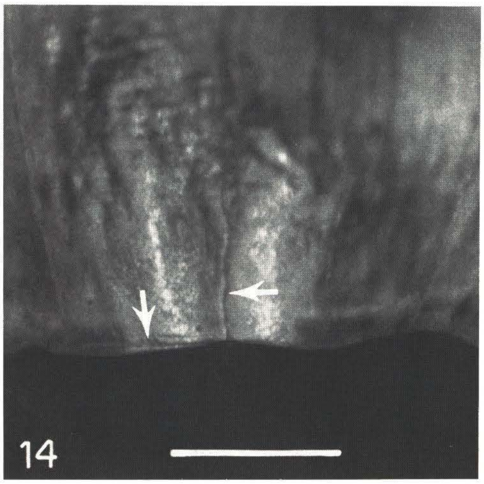
Figure 15. *Hyracotherium*, early equid (horse), lower molar, UWBM 71061, occlusal view of faceted enamel of entoconid; early Eocene, Wasatch Fm., Wyoming. Vertical crack worn by abrasion where near occlusal surface. Bar = 10 µm.

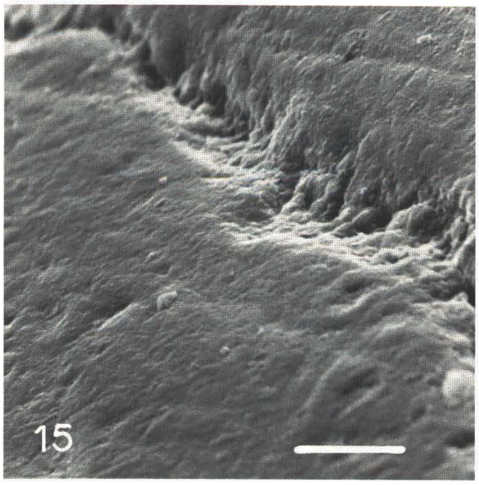
Figure 16. *Conacodon*, upper premolar, UWBM 59581, posterior view; early Paleocene (Puercan), Nacimiento Fm., New Mexico. Light oval area is worn dentinal platform. Concentration of shallow lateral and vertical median cracks (arrows) near occlusal edge of enamel. Dips in occlusal edge resulted from breaking away of similarly fractured shards. Bar = 1 mm.

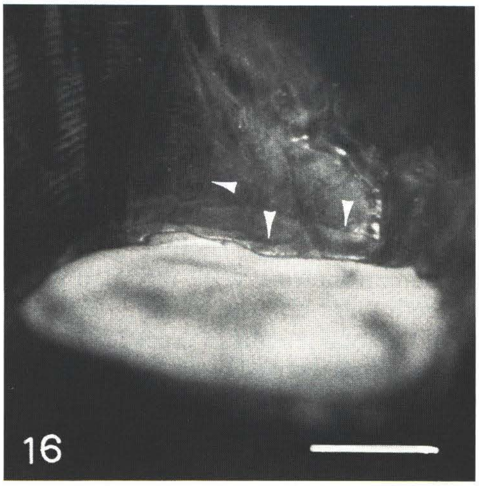
Figure 17. *Ursus*, left lower canine, lingual view; Recent. Stained horizontal cracks incurred during life of individual. Single unstained vertical crack, visible near left margin of tooth, runs completely through tooth to anterior side and occurred after death. Bar = 1 mm.

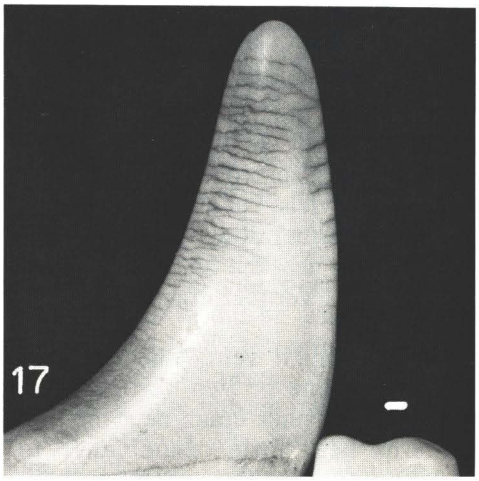

12


13


14


15


16


17

occurs in recessed areas of the cheek teeth. The stained cracks contrast prominently with a few open but unstained vertical cracks (for example, the crack running from the base to the tip near the posterior margin of the tooth in figure 17), indicating that the stained cracks formed during life and were stained by food, and the unstained cracks formed after death. This is further confirmed by the slightly rounded edges of the stained cracks and sharp edges of the unstained cracks.

The unstained cracks on the canines are almost always vertical, whereas the stained cracks are roughly horizontal except near the tip, where a few may be inclined up to 45°, as in the crocodilians. The cracks on the anterior and posterior surfaces of *Ursus* canines form distinct sets which are not continuous with one another but interfinger where they come together (fig. 17), resembling the condition in the crocodilians. The most abundant, closely spaced horizontal cracks occur on the posterior side of the tooth and disappear midway around the tooth.

Similarly stained horizontal cracks were observed in the incisors of several of the bears, and these are distinguishable from unstained cracks, usually vertical, that occurred after death.

Effects of drying.

Crack patterns in the enamel of a set of six extracted human incisors were recorded before and after the teeth were allowed to dry. Between 50% and 75% of the total lengths of cracks in the dry teeth were present in the undried teeth. Although much of the new crack length occurred in the form of new cracks, there was typically little change in the overall directional patterns (fig. 18). The drying cracks in the cementum of the roots are quite different, however, having the perpendicular intersections typical of shrinkage cracks in mud.

Experimental cracks in models.

Vertical compressive loads applied to glass-covered epoxy models produced vertical cracks that run the height of the crown. Vertical compressive loads also produced vertical cracks in the resin-coated models, but attempts to induce these cracks to extend farther down the crown resulted in shattering the resin near the tip. Under considerably increased pressure, vertical cracks appeared at the base of the crown.

Glass models which were embedded in sand and compressed bore one or two vertical cracks and occasionally a transverse crack near the tip. These crack patterns bear little resemblance to those observed in fossil teeth. The hydrostatic behavior of sand tends to produce equally distributed stresses on all sides of the crown and therefore does not seem to be a strong crack producer. It seems doubtful that compression of fossil teeth in sediment under typical circumstances causes many cracks. Where lithified rocks have undergone faulting, however, tooth crowns may be sheared apart or crushed. This latter source of cracking can usually be recognized by the severity of the damage.

When resin-coated tooth models were subjected to repeated lateral loads concentrated near the tip, multiple horizontal cracks appeared on the tensed side, the side against which the stress was applied (fig. 19). When a model was subjected to stress alternately on opposite sides, sets of interfingering discontinuous cracks appeared on the anterior and posterior sides (fig. 19). These sets are similar to those occurring on mammalian carnivoran canines and crocodilian teeth in their attitudes, interfingering relationships, and angular differences. When a resin-covered model of a conical tooth was subjected to an oblique load near the tip, steeply dipping cracks occurred near the tip on the side receiving the stress, similar to the high angle cracks in that area in conical teeth (fig. 19).

Discussion

The principal objective of this study is to determine the feasibility of distinguishing cracks in fossil enamel that occurred during the life of the individual from postmortem cracks. The two methods investigated, the recognition of wear superimposed on the edges of cracks and the recognition of crack patterns that are expected to result from stresses occurring during the life of an individual, each proved useful in identifying cracks that occurred during life.

Each method has certain restrictions in its applicability. Many cracks which are seen within the translucent fossil enamel under light microscopy were not seen on the surface under these low magnifications, so there was no possibility of observing abrasion. Further investigation using SEM might reveal some of these cracks, however. Abrasion due to chewing (in the case of teeth) or locomotion (in the case of scales) is identifiable. Identifying these sources of abrasion is not difficult because of their restriction to certain surface areas and absence in others. For example, the discovery of abrasion due to tongue activity was unexpected, but was identifiable because of the particular discontinuity in its distribution. The effects of biting activity in crocodilians are more widely distributed down the sides of the crown than is food abrasion in mammalian herbivores, but abrasion intensity progressively increases toward the tip. The presence of sharp edges on some scratches also helps verify that slight stream polishing has not occurred. Stream

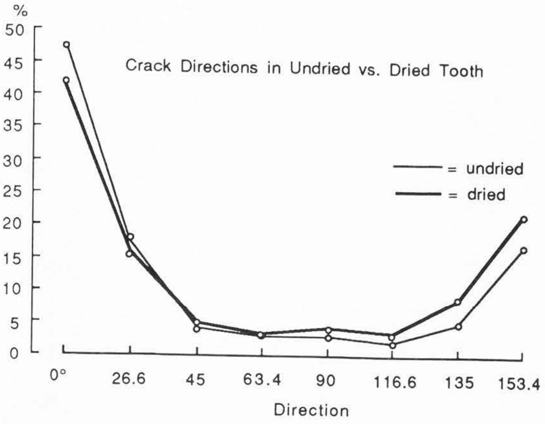


Figure 18. Percentage frequency distribution of crack directions in human incisor before and after drying. Total crack length in undried tooth = 45.6 mm; total in dry tooth = 71.0 mm. 0° = vertical direction; 90° = horizontal. Slightly uneven class widths result from computation from a digital image (Rensberger, et al, 1984).

abrasion uniformly smooths all striae.

It is not difficult to identify chewing and locomotor abrasion on specimens subjected to SEM, but many cases can be identified with light microscopy. Light microscopy is advantageous because the distribution of wear can be determined rapidly. To identify abrasion to crack edges, one needs to manipulate the specimen until the light reflects off the surface of the enamel near a crack. If the crack edge is worn, at some angle of manipulation the edge itself will show up as a line of specular reflection (fig. 14). An absolutely sharp edge does not reflect light. Of course slight wear may be present but escape notice under the low magnification of light microscopy.

When cracks are not visible on the surface, recognition of a pattern expected from locomotion or chewing activities may identify the source. Certain distinctive patterns were observed that are particularly indicative of premortem stresses.

The transverse cracks in the ganoine at the anterior end of gar scales are producible by a load exerted on the broad central and posterior surface when the anterior end was still attached to the fish (fig. 20). It is difficult to imagine these cracks having been produced by other than the scale bending toward the body against the resistance of the anchoring point. This suggests formation before the scales detached from the skin after death. Stress of this kind at some level of magnitude will occur in the impacted scales each time the fish bumps against an external object. An origin for these cracks during life is additionally indicated by the effects of locomotor abrasion to the edges of the cracks.

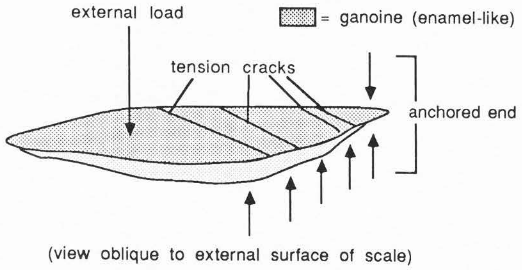


Figure 19. Relationship of parallel cracks in *Lepisosteus* scales to postulated external load and resistance of anchoring area.

The cracks in the posterior halves of the scales are more varied and their causes less certain. Cracks similar to the several cracks parallel to the two sides of the posterior half of the scale in figure 1 were observed in a number of scales. These could have been produced by loading at the margins of the scale. The transverse cracks near the posterior tip of some scales could have been produced by a load at the posterior end.

The horizontal orientation of the cracks in mammalian canines and incisors and crocodilian teeth indicates that they resulted from vertical tension. Cracks like these were produced in models subjected to lateral loads that caused bending (fig. 19). The cracks in the models subjected to cooling contraction and those occurring in human incisors as a result of drying bear no resemblance to these horizontal cracks. Cracks similar to the higher angle cracks observed near the tip of the cusp in conical teeth were produced in the models when nearly vertical, oblique loads were applied near the tip. The higher angle cracks were not produced in the models when the load was not applied near the tip, and did not occur in the middle or base of the crown. That crocodilian teeth had been loaded from different directions is verified by the multiple directions of striae marked on the enamel surfaces (figs. 5-7). The dominance of horizontal cracks on the posterior surfaces of carnivoran canines would be produced by frequent anteriorly directed loads when the teeth are used to pull back on grasped objects. Numerous horizontal and oblique striae are present on carnivoran canines. In the ursid having the greatest abundance of horizontal cracks (fig. 17), there is clearly a greater abundance of horizontal and oblique striae on the posterior than the anterior sides of the canines and incisors.

Certain patterns of cracks occurring near the

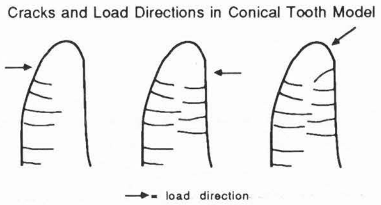


Figure 20. Experimental cracks produced in conical tooth model constructed of epoxy cast of crocodilian tooth covered with natural resin. Left, load from left near tip; center, cracks added by reversed loading; right, high angle load adds oblique crack.

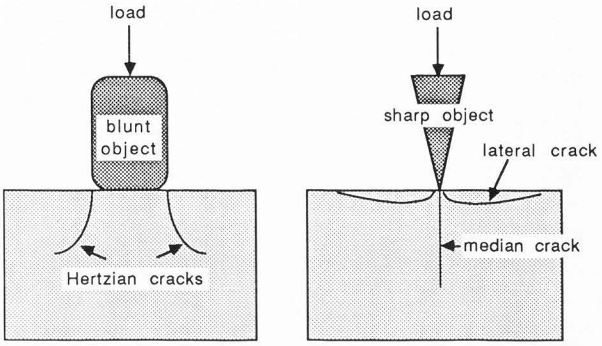


Figure 21. Cracks produced by blunt and sharp objects.

worn occlusal edges of enamel can be unambiguously attributed to vertical loads. Two types of point contact on the surface of a brittle material produce distinct crack patterns. A blunt object contacting a surface tends to produce Hertzian cracks that descend steeply and curve away from the impact area (fig. 21). A sharp object tends to produce shallow, arcuate lateral cracks and a vertical median crack (fig. 21). Hertzian cracks are visible descending from the occlusal surface in the hadrosaur tooth of figure 12 and from the notched margin of the theropod tooth of figure 11. Shallow lateral cracks are visible bordering a vertical median crack in the periptychid tooth of figure 14.

The patterns of multiple vertical cracks in crocodilian, theropod, and mammalian teeth are more difficult to attribute to a specific source of stress. Many of these cracks occurred during the life of the individual as indicated by chewing abrasion on their edges. Tooth models that were subjected to a vertical load at the tip of the crown acquired vertical crack patterns. On glass-covered epoxy models, each of the vertical cracks extended from the base to the tip of the crown unless it turned into another crack. In resin-covered epoxy models subjected to gradually increasing loads at the tip, cracks first appeared at the tip and later, under higher loads, appeared at the base. However, vertical cracks in both crocodilians and mammals are most abundant at the base of the crown and are progressively less numerous toward the apex (figs. 10,13). Many of the cracks present at the base appear to fade away and never reach the tip of the tooth or encounter another crack. It appears therefore that loads *concentrated* at the tips of conical teeth may not have produced the pattern of vertical cracks observed in the middle and lower parts of the crown in crocodilians, theropods and mammals.

Pfretzschner (in press), based on a shell-theory used in engineering and architecture (Flügge, 1981), found that a distributed vertical "snow" load as well as a distributed lateral "wind" load on an elliptical shell produce maximum horizontal tension in the shell near the base of the crown. In each case the horizontal tension decreases toward the tip. This stress state is consistent with the observed dominance of vertical cracks near the bases of teeth. To test this theory, glass-covered epoxy cones were subjected to wind loads. Cracks frequently originated at the base on the side receiving the load and these propagated upward to near the middle of the cone, where they turned laterally (fig. 22). According to Pfretzschner (in press), under a wind load, although horizontal tension diminishes toward the tip, the vertical tension actually increases toward the tip but does not exceed the horizontal tension. The point at which the observed vertical cracks in the glass models turn and become horizontal is clearly a transition level above which the horizontal stress becomes less than the vertical stress. Pfretzschner's shell model for the tooth is an ellipse rather than a cone and is broader relative to height than the glass cones which were tested, which may account for the vertical tension exceeding the horizontal tension midway up the height of the latter. It is possible, therefore, that the vertical cracks concentrated at the base of the crowns in the crocodilian and mammalian teeth are caused by chewing loads that are somewhat *distributed* on the tooth surface rather than concentrated at the tip.

There is evidence that a change in diameter of the tooth or the enamel shell has occurred in some cases. The evidence for a change in dimensions is the presence of a gap between the edges of some of the vertical cracks that bear evidence of chewing abrasion on their edges (fig. 6). It is possible that an enlargement occurred postmortem due to diagenetic changes, perhaps crystal growth, within some of the teeth. The only other explanations would seem to be developmental changes in crown dimensions or shrinkage of enamel due to loss of water from the

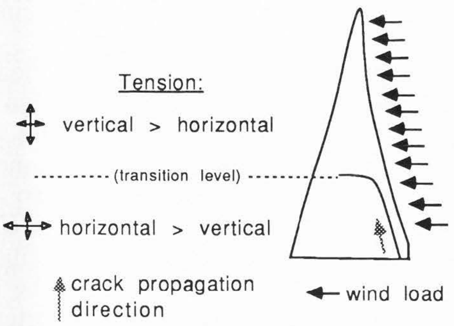


Figure 22. Experimental crack produced by asymmetric wind load on glass-covered epoxy cone. Dominantly horizontal tension at base of cone changes at higher level to dominantly vertical tension, causing vertical crack that began at base to stop or become horizontal.

hydroxyapatite molecules or free water within the enamel.

To examine the patterns of cracks resulting from shrinkage of the enamel shell, tooth models made of glass-covered epoxy were heated and then cooled rapidly to cause contraction. Although this resulted in dominantly vertical cracks, a number of oblique cracks were generated that were terminated by intersecting cracks, as in mud cracks and other shrinkage cracks. Although the vertical cracks in crocodilian teeth cross the horizontal cracks perpendicularly, the vertical cracks seldom terminate at horizontal cracks.

Postmortem drying produces a significant number of cracks in teeth. In dry skulls from museum collections and field carcasses there are often one or two vertical cracks that run through the entire incisiform, caniniform, or premolariform tooth. From 25% to 50% of the total crack length in the drying experiment with human incisors were produced by drying. However, the orientation of the cracks resulting from drying was little different from that present in the undried teeth.

In conclusion, it seems clear that numerous cracks in fossil enamel were living features and can be identified as such. However, drying of the tooth after death also introduces at least enough cracks to make it necessary to distinguish the living cracks from the postmortem cracks if one is concerned with the effect of cracking on natural selection. Under SEM and often under light microscopy, it is possible to differentiate cracks acquired during life when the crack edges are exposed on the surface and occur in areas of the tooth that were subjected to chewing abrasion. The specific causes of some cracks may be identified by the distinctive crack pattern. Cracks occurring near the occlusal surface can be particularly distinctive. Horizontal cracks occurring on slender caniniform teeth and incisors of mammals and possibly those on conical archosaur teeth seem to have resulted from lateral bending stresses involving food capturing and tearing activities. Many of the vertical cracks concentrated especially in the middle parts and bases of the crowns may be the result of distributed chewing loads, both vertical and lateral, as Pfretzschner (in press) postulates. However, drying of teeth after death also produces vertical cracks, although these do not seem to be associated with any particular part of the crown.

Acknowledgments

I am grateful to R. C. Bradt, Department of Materials Science and Engineering, University of Washington and H. U. Pfretzschner of the Zoological Institute, University of Kaiserslautern, West Germany, for discussions on fracture of brittle materials. D. W. Krause (Stony Brook, State University of New York), M. Fortelius (University of Helsinki, Finland), H. Krentz (Department of Anthropology, University of Washington), S. J. Jones (University College, London), and K. Lester (Parramata Hospital, Westmead NSW, Australia) also provided helpful comments on the manuscript. B. Olson kindly supplied human incisors for the study.

References

Boyde A. (1976). Enamel structure and cavity margins. Operative Dentistry 1:13-28.

Flügge W. (1981). Statik und Dynamik der Schalen. Springer Verlag, Berlin.

Fortelius M. (1985). Ungulate cheek teeth: developmental, functional, and evolutionary interrelations. Acta Zool. Fenn. 180:1-76.

Hassan R, Caputo AA, Bunshah RF. (1981). Fracture toughness of human enamel. J. Dental Res. 60:820-827.

Kay RF. (1978). Molar structure and diet in extant Cercopithecidae. In: Development, Function and Evolution of Teeth; Butler, PM, Joysey, KA, (eds). Academic Press, p. 309-339.

v Koenigswald W. (1980). Schmelzstruktur und Morphologie in den Molaren der Arvicolidae (Rodentia). Abh. Senckenberg. Naturforsch. Ges. Frankfurt a. M. 539: 1-129.

Peyer B. (1968). Comparative Odontology. Zangerl R, (ed). Univ. of Chicago Press, Chicago. 347 p.

Pfretzschner HU. (1987) Structure

reinforcement and crack propagation in enamel. Proc. VIIth Intern. Symp. on Dental Morphology. Mém. Mus. Nat. Hist. Paris. In press.

Powers JM, Craig RG, Ludema KC. (1973). Frictional behavior and surface failure of human enamel. J. Dental Res. 52:1327-1331.

Rasmussen ST, Patchin RE, Scott DB, Heuer AH. (1976). Fracture properties of human enamel and dentin. J. Dental Res. 55:154-164.

Rensberger JM. (1973). An occlusion model for mastication and dental wear in herbivorous mammals. J. Paleont. 47:515-528.

Rensberger JM. (1975). Function in the cheek tooth evolution of some hypsodont geomyoid rodents. J. Paleont. 49:10-22.

Rensberger JM. (1983). Effects of enamel structure on wear. (Abs.) Amer. J. Phys. Anthrop., Annual Meeting Issue, 60:243-244.

Rensberger JM, Forsten A, Fortelius M. (1984). Functional evolution of the cheek tooth pattern and chewing direction in Tertiary horses. Paleobiology, 10:439-452.

Rensberger JM, v Koenigswald W. (1980). Functional and phylogenetic interpretation of enamel microstructure in rhinoceroses. Paleobiology, 6:477-495.

Waters NE. (1980). Some mechanical and physical properties of teeth. In: Symposia of the Society for Experimental Biology XXXIV, The Mechanical Properties of Biologic Materials. Cambridge University Press. P. 99-135.

Discussion with Reviewers

D. Krause: Do the fossils from the Hell Creek Formation come from the Bug Creek Anthills locality? This is a high energy stream channel deposit. Even if they don't, most of the fossil localities in the Hell Creek Formation represent stream channel deposits. Therefore, I have no confidence that the striae on the teeth from that formation were formed before death.

Author: None of the specimens cited from the Hell Creek Formation came from the Bug Creek Anthills or the other stream channel deposits of that area. Although its channels have produced rich concentrations of small fossil teeth, the Hell Creek Formation consists of, in addition to interbedded sandstones, thick sequences of claystone and siltstone which at one place or another are fossiliferous and yield teeth that have not been stream abraded. In my experience, striae are rare in sediment abraded teeth and bones. The effect of stream action seems to be to subdue any striae by superimposing a coarse polish.

S. J. Jones: Have you examined equivalent fresh, wet material to compare with the fossil specimens, before, during and in repeated SEM?

Author: Wet *Aplodontia* (mountain beaver) incisors were examined in addition to the human teeth and compared to other dry *Aplodontia* teeth. The enamel of the wet rodent incisors bears numerous horizontal cracks (perpendicular to the incisal-cervical axis) like those described for *Ursus* canines and conical crocodilian teeth. Dry museum specimens of *Aplodontia* have cracks of the same orientation which were identified as premortem by the wear to their edges. The dry specimens additionally have vertical cracks with unworn edges that must have arisen from postmortem drying, as in *Ursus*.

D. Krause: A major disappointment is the lack of quantification. There are many qualitative statements concerning orientation and abundance of fractures; both these parameters would lend themselves well to quantification.

Author: The quantification of crack directions presents a problem when the surface is strongly curved. I digitized the crack patterns in crocodilian teeth, where the different directions are most interesting, and produced frequency distributions of the directions and lengths as projected in the viewing plane. However, I was disappointed by the information loss compared to the information one obtains when viewing a photograph or the actual specimen, and for that reason have included photographs in place of those data. Cracks may be entirely vertical, but only the crack or part of a crack lying directly between the view point and the axis of the tooth is captured as vertical, owing to the curvature of the surface. Only fully three dimensional digitization would accurately quantify the crack orientations on these teeth, and this is difficult to accomplish. The quantitative data on crack direction and lengths presented for human incisors were reasonably accurate because those crowns have relatively flat labial and lingual surfaces.

K. Lester: No real account is taken of any likely underlying histology or ultrastructure of the enamel.

Author: That is certainly integral to understanding the relationship between enamel structure and natural stresses. That is the next step, but it is a major one. Before seeking possible correlations between enamel microstructure and stresses that are inferred from cracks produced by chewing stresses, one needs to be able to distinguish premortem from postmortem cracks.

D. Krause: It is unclear why you chose to perform this study on fossil materials. Clearly, it has implications for the study of fossil enamels and for inferences concerning the biology of fossil animals, but the number of variables that one has to interpret in the study of fractures in enamel are greatly increased with fossil specimens.
Author: The number of variables that might have an effect is increased. You are thinking in part about the question of stream abrasion, which is answered above. However, the study includes *both* fossils and Recent specimens. If significant differences exist between crack patterns in fossils and Recent specimens, that would be informative in itself. The patterns in the two cases seem, up to this point, to be similar and to be dominated by the effects of premortem stresses and postmortem drying.

S.J. Jones: Is there any evidence for crown expansion during growth causing splitting of enamel in living species?
M. Fortelius: How would such growth actually happen?
Author: I know of no evidence from extant species. It seems more likely that "snow" or "wind" loading causes tension near the base of the crown, producing vertical cracks. Perhaps some nonelastic response to such repeated loading leaves some dimensional changes.