

CONTRIBUTIONS FROM THE MUSEUM OF PALEONTOLOGY

THE UNIVERSITY OF MICHIGAN

VOL. 25, No. 13, p. 259-275 (4 text-figs.)

December 31, 1981

**TAPHONOMIC INTERPRETATION OF ENAMEL-LESS TEETH IN
THE SHOTGUN LOCAL FAUNA (PALEOCENE, WYOMING)**

BY

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TAPHONOMIC INTERPRETATION OF ENAMEL-LESS TEETH IN THE SHOTGUN LOCAL FAUNA (PALEOCENE, WYOMING)

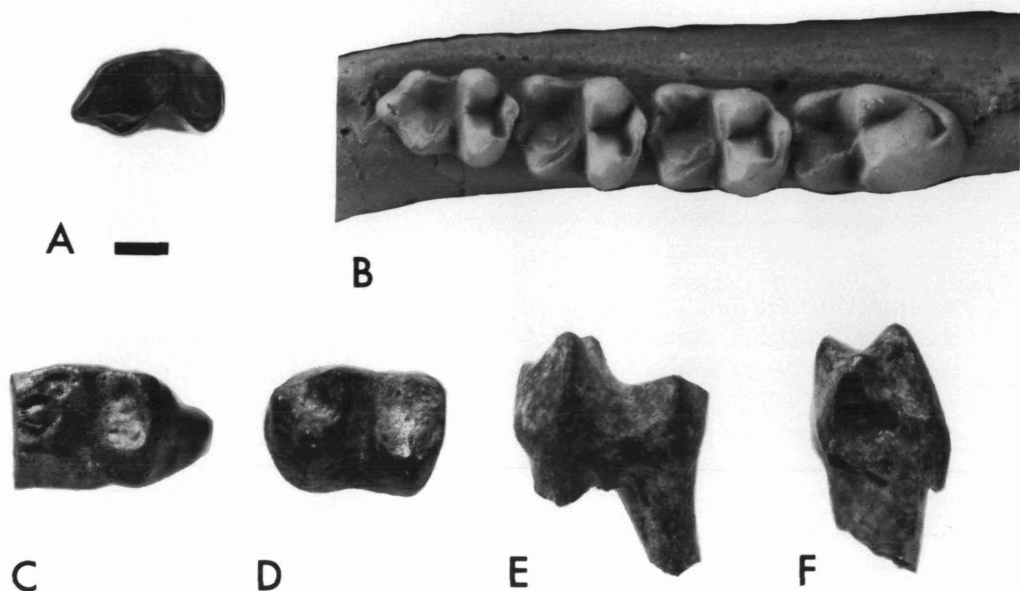
By

Daniel C. Fisher

Abstract.—A rare form of tooth preservation, in which most or all enamel has been removed from teeth, without loss of dentine or cementum, has been recognized in the Paleocene Shotgun local fauna. These teeth closely resemble teeth digested and defecated by extant crocodylians, suggesting that Shotgun enamel-less teeth may also be the remains of crocodylian prey. Since crocodylian digestion decalcifies tooth tissues, leaving only the organic matrix of dentine and cementum in the feces, preservation of such teeth as fossils requires a mechanism for remineralizing them. The proposed mechanism involves remineralization by amorphous hydroxyapatite within a reducing microenvironment. Analysis of the identity and conformation of tooth tissues preserved on enamel-less teeth, modifications of the histologic structure of their dentine and cementum, pyrite present in their pulp cavities, and the crystallinity and composition of their dentine confirms the interpretation that Shotgun enamel-less teeth were digested by crocodylians and then remineralized before complete decomposition could occur. Other mechanisms of enamel loss, such as digestion by non-crocodylian vertebrates, abrasion, enamel spalling, diagenetic dissolution, or dissolution by plant acids, do not satisfactorily account for the observed attributes of enamel-less teeth.

INTRODUCTION

Taphonomic studies of the Shotgun local fauna, a microvertebrate concentration from the Paleocene of Wyoming, have drawn attention to a rare and intriguing form of tooth preservation (Fisher, 1981a, 1981b). These teeth, all of which were derived from relatively small mammals, are distinctive in that they retain little or no enamel, though they often appear to retain all of their dentine and cementum (Text-fig. 1). Like other teeth in the Shotgun local fauna, enamel-less teeth occur isolated from the mandibular or maxillary elements that once held them. If enamel is present, it is restricted to small patches near the cervical margin of the original enamel distribution, at places where adjacent teeth in the tooth row came into contact prior to isolation. Those enamel-less teeth that are identifiable are derived from individuals of species that are ordinarily represented by teeth with enamel of normal thickness. All indications are that this enamel loss is an exclusively *post mortem* phenomenon. In the collections of the Shotgun local fauna at the Museum of Comparative Zoology, Harvard University, I have seen only about thirty examples of enamel-less teeth. I estimate this to represent a frequency of considerably less than one percent of the teeth examined. Since teeth of strikingly similar appearance have been recovered, during feeding experiments, from the feces of living crocodylians (Fisher, 1981a), I



TEXT-FIG. 1 — Enamel-less teeth from the Shotgun local fauna (except B); from Fisher (1981a, Fig. 4). A. Completely enamel-less right M_3 of *Aphronorus cf. fraudator*; occlusal aspect, anterior to right. B. Partial right dentary of *A. fraudator*, showing well preserved (enamel present) P_4 — M_3 (whitened cast of AMNH 35636); occlusal aspect, anterior to right; middle Paleocene, Gidley Quarry, Lebo Formation, Montana. C. Completely enamel-less left P_4 of *A. orieli*; occlusal aspect, anterior to left; portion of crown and one root removed for sectioning and x-ray diffraction. D. 'Enamel-less' left M_1 (one, small, interdental patch of enamel remaining) of *A. orieli*; occlusal aspect, anterior to left. E. Labial aspect of D. F. Anterior aspect of D, showing residual interdental patch of enamel (shiny, dark region on trigonid). Scale: all specimens 7x; bar in A equals 1 mm.

have hypothesized that the enamel-less teeth of the Shotgun local fauna were also digested and defecated by crocodylians. A similar hypothesis, not based on feeding experiments, was proposed by McGrew (1963), but it differed from the present one in that it concerned teeth that were much more common in the Shotgun fauna and that appeared to have lost some of their *dentine*. These cases have been reinterpreted as representing instances of death prior to completion of tooth formation and instances of *in vivo* tooth resorption associated with tooth replacement (Fisher, 1981b). Although McGrew's (1963) conclusion that the bulk of the Shotgun assemblage represents a concentration of crocodylian fecal residues must therefore be rejected in its original form, it may be valid when restricted to enamel-less teeth. The present paper offers additional description of the Shotgun enamel-less teeth, a consideration of alternative interpretations of their taphonomic history, and several tests of the interpretation that they are the remains of crocodylian prey.

The potential applicability of the results of this investigation has been broadened recently by the recognition of a number of other occurrences of enamel-less teeth (Fisher, 1981a). In some cases, as in the Shotgun local fauna, they are preserved as isolated teeth, while in others, they are retained within their alveoli. They may be associated either with microvertebrate concentrations or with other modes of fossil occurrence. They have received previous attention only in the form of passing comments (e.g. Clemens, 1973). However, the ease with which I have been able to accumulate reports of their existence and the broad geographic and temporal spread of those occurrences suggest that enamel-less teeth may be quite common in the fossil record as a whole, even though they are rare at any one locality.

MATERIALS AND METHODS

This study is based on collections of the Shotgun local fauna in the Museum of Comparative Zoology. Much of the examination of material has been done under a stereoscopic microscope, but many important features of tooth preservation are only evident in thin section. I have therefore studied 111 serial sections of 29 enameled teeth and 4 enamel-less teeth, chosen to give multiple representation of the major preservational variants within each of these categories. The thin sections allow a qualitative assessment of types of preservation, but do not provide a direct, quantitative reflection of the frequency of occurrence of different types of preservation. Three enamel-less teeth (one of which was also sectioned) were examined with a scanning electron microscope. Mineralogical analyses of both enameled and enamel-less teeth were done by Debye-Scherrer powder x-ray diffraction methods, in order to minimize the amount of sample used and the consequent destruction of the rare, enamel-less teeth. The radiation used was Fe $K\alpha$, with a Mn filter. Most of the enamel-less teeth that were sectioned or analyzed by x-ray diffraction were identifiable at least to the generic level, but, in order to avoid destruction of material useful for other paleontological studies, most of the enameled teeth used in this work were indeterminate at that level.

CROCODILIANS IN THE SHOTGUN LOCAL FAUNA

Crocodylians comprise a numerically significant portion of the Shotgun local fauna. On the basis of frequency of occurrence of teeth, *Allognathosuchus* is the most common crocodylian, though *Leidyosuchus* is also present. Functional morphological analyses do not suggest particularly unusual feeding habits for any of the Shotgun crocodylians. The broad, rounded teeth of *Allognathosuchus* have been cited as adaptations for feeding on turtles (Abel, 1928) or molluscs (Case, 1925), but even this degree of specialization has been disputed (Simpson, 1930). Both *Allognathosuchus* and *Leidyosuchus* can be reasonably interpreted as having had a varied diet of vertebrate prey, including at least some mammals (Erickson, 1976; W. S. Bartels, pers. comm.). Estimates of body size based on the size of some of the larger crocodylian teeth and bony scutes in the Shotgun fauna suggest a total body length within the range of 1.5–2.0 m. This is certainly large enough to have preyed upon the small mammals (such as the pentacodontid *Aphronorus*) represented by enamel-less teeth. The present taphonomic interpretation thus appears to be plausible in these respects.

MODEL FOR THE PRESERVATION OF ENAMEL-LESS TEETH

Teeth defecated by living crocodylians have lost their enamel as a result of being decalcified within the acidic environment of the fundic region of the stomach (Fisher, 1981a). Because enamel has very little organic matrix, decalcification destroys it, while dentine, cementum, and bone, with approximately thirty weight percent organic matrix, leave a decalcified matrix behind. Decalcification of bones and teeth usually results in the isolation of teeth, but in some cases, particularly when roots are divergent, teeth are not readily susceptible to isolation. Prevention or delay of isolation, relative to the interval during which ingested teeth reside in the fundic stomach, is presumably the cause of the retention of interdental patches of enamel. I

suspect that this is because the close apposition of neighboring teeth restricts the circulation of acidic fluids over the surface of a tooth. Even though the enamel of adjacent teeth may not be in contact over any great area, this may be enough to reduce the rate of diffusion of solutes and salts, which would consequently buffer the reaction and reduce the rate of enamel destruction. The effectiveness of this process would be enhanced if enamel decalcification proceeds preferentially in a direction parallel to enamel prisms. This, in turn, could result from differential permeability produced by the organization of hydroxyapatite crystallites within enamel. Although this interpretation is at present speculative, it seems preferable to postulating distinct solubility properties for interdental enamel.

In my feeding experiments, the only cases of incomplete decalcification other than those involving retention of interdental enamel were ones in which a particularly massive element retained an undecalcified core. These also can be interpreted as functions of permeability and diffusion.

Despite the occasional occurrence of incomplete decalcification, most of the remains of calcified tissues in the feces of crocodylians are completely decalcified. When deposited within an aerobic environment, they are extremely susceptible to bacterial decomposition, often disappearing completely within two days. This poses a double problem for the interpretation of fossil enamel-less teeth as crocodylian digestive residues. In the first place, it seems that the decalcified matrices of calcified tissues would decompose much more frequently than they would be preserved. Could they even be preserved at all? Secondly, mineralogical tests discussed below demonstrate that the dentine and cementum of enamel-less teeth are presently composed of hydroxyapatite. How could this be consistent with a history of complete decalcification? The following scenario, though admittedly speculative, attempts to suggest how this form of preservation could have developed.

By burying crocodylian feces within a local artificial anaerobic microenvironment, I have been able to delay the decomposition of included decalcified organic matrices for at least one month (Fisher, 1981a). Under the proper reducing conditions, produced in part by the fecal material itself, it may be possible to further extend this period. If the enamel-less teeth of the Shotgun local fauna are indeed the remains of crocodylian prey, digested in a similar fashion to that observed for living crocodylians, their organic matrices must have been remineralized with hydroxyapatite. Most of the calcium phosphate removed from calcified tissues is present in crocodylian feces in an amorphous, and probably readily mobilizable form (Coulson and Hernandez, 1964). If remineralization occurs, it would probably happen before disaggregation of the feces could separate decalcified tissues from this source of calcium phosphate, and would have to occur before these tissues were degraded by other processes. The probability of remineralization would be greatest in an environment in which decomposition of organic material was retarded, or remobilization of calcium phosphate was accelerated, or both. Whittemore (1976) has shown that hydroxyapatite is the stable phase of iron and calcium phosphates under most soil and sediment conditions, and that hydroxyapatite (especially in a finely divided, amorphous state) is subject to remobilization and precipitation under natural conditions. In addition, McKelvey et al. (1953) suggest that apatite remobilization is facilitated by high partial pressure of carbon dioxide, such as would be produced through the decay of organic material. Since enamel is destroyed during crocodylian digestion, it could not be reconstituted by remineralization. However, the remnant organic matrix of dentine, cementum, and bone might act as a substrate that would facilitate and control remineralization, within the reducing microenvironment of the feces. Subsequent to remineralization, feces could have been reworked enough to dissociate their enclosed, 'reconstituted' teeth and bones from any preservable coprolite and associate them with other teeth and bone fragments that had not necessarily shared a similar history.

Teeth preserved according to this model would have a number of more or less predictable attributes. In addition to showing the enamel-less condition (except for some residual interdental patches of enamel), they should often, if not always, show some signs of incipient bacterial decomposition and might also be expected to be associated with reducing conditions. Most important of all, they should show some evidence of having been demineralized and remineralized at some point in their history.

DIGESTIVE RESIDUES OF OTHER CARNIVOROUS VERTEBRATES

One set of alternative interpretations of enamel-less teeth involves simply transposing the present hypothesis to some other group of carnivorous vertebrates. Can the digestive residues of other groups be satisfactorily distinguished from calcified tissues modified by crocodilian digestion?

With the possible exception of Shotgun sharks preying on each other or scavenging floating carcasses of Shotgun mammals, it is unlikely that any carnivorous fish would have had access to most other elements of the Shotgun local fauna. Nevertheless, for the sake of interpreting other occurrences of enamel-less teeth, the digestive capabilities of fish should be considered. Fish digestion of bones and teeth ranges from defecation without appreciable alteration to complete digestion (e.g. Barrington, 1942; Phillips, 1969). Amphibians appear to be similar to fish in this respect (Barrington, 1942). For neither of these have I found an account of anything similar to what I have described for crocodilians. Non-crocodilian reptiles generally defecate undigested hair, claws, insect cuticle, etc., and completely digest bones and teeth (Benedict, 1932; Dandrifosse, 1974; Skoczylas, 1978). This pattern has been especially well documented for snakes (e.g. Pope, 1961; Dmi'el and Zilber, 1971). Regurgitation usually occurs only as a means of complete rejection of an ingested item, although the regurgitation of eggshell by the egg-eating snakes *Dasypeltis* and *Elachistodon* (Skoczylas, 1978) and the regurgitation of feather balls by some pythons (Petzold, 1967) are exceptions to this. Snakes decalcify bones and teeth within the stomach (Blain and Campbell, 1942; Skoczylas, 1970), but the organic matrix has never been observed to persist in the feces. The few cases in which bone or tooth fragments have been observed in snake feces (grass snakes, Skoczylas, 1970; and rattlesnakes, Fitch and Twining, 1946) have resulted from incomplete decalcification. These same patterns hold for lizards and chelonians (Petzold, 1967; Skoczylas, 1978). To my knowledge, there have been no published descriptions of the feces of *Sphenodon punctatum*.

Predatory birds offer a relatively great range of fates to vertebrate calcified tissues, but in no cases have any remains of bones or teeth been noted in their feces (Farner, 1960). In general, keratinous tissues are not digested (Mangold, 1931), but are formed into pellets and regurgitated. Any bones or teeth that survive digestion are incorporated into these pellets. In some birds, digestion of bones and teeth is essentially complete (e.g. eagles, sparrow hawks, herons, egrets, or bitterns; Sumner, 1933; Chitty, 1938; Glue, 1970). In most, however, it is only partial. Estimates of the retrieval rate of bones and teeth ingested by owls range from nearly 100 percent (Mayhew, 1977) to approximately 50 percent (Dodson and Wexlar, 1979). Bones show variable amounts of breakage, but, with a few exceptions (e.g. Raczynski and Ruprecht, 1974), neither bones nor teeth show macroscopic evidence of digestive corrosion. Tooth enamel and dentine are still in unmodified condition and teeth usually remain within their alveoli (Mayhew, 1977). In contrast, falconiformes such as kestrels and buzzards digest a considerable fraction of ingested bone, and typically regurgitate residual splinters of bone and partially digested teeth (Mayhew, 1977). These teeth may have much (usually not all) of their enamel removed, but

dentine is destroyed as well, with no preservation of its organic matrix. Teeth are thus rounded or truncated in a characteristic fashion. Such digestive residues can be distinguished from those produced by crocodylians (even considering cases of incomplete decalcification) because digestion tends to erode deeply into the dentine of one part of the tooth, while still preserving non-decalcified enamel and dentine elsewhere—not necessarily at sites of contact of adjacent teeth. A strikingly different pattern is shown by at least one other falconiform (P. Shipman, pers. comm.). Unpublished work by Shipman indicates that red-tailed hawks remove enamel from teeth *without* decalcifying the dentine. The mechanism by which this differential destruction occurs is not clear. Enamel loss may be incomplete, but residual patches of enamel appear to have no predictable distribution. If enamel loss were complete, or nearly complete, these teeth would strongly resemble the enamel-less teeth of the Shotgun local fauna. However, evidence of dentine (or cementum) decalcification would effectively reject a falconiform interpretation of the preservation of the Shotgun teeth.

For mammalian carnivores, there is also considerable diversity in the mode of digestion of vertebrate prey. A few mammalian carnivores regurgitate undigested fur, teeth, and bones, and many seem to completely digest weakly ossified prey, such as fish. In general though, mammalian predators tend to defecate teeth and bones (along with keratinous tissues) without obvious chemical alteration (though they are often isolated, disarticulated, or broken). For this reason, mammalian carnivores have figured prominently in scatological hypotheses for the origin of microvertebrate concentrations such as the Shotgun local fauna (Mellett, 1974). The treatment of calcified tissues by canids has been well studied. Foxes may digest at least half of the teeth and bones they ingest (based on the rate of occurrence in scat), but those remains which appear in their scat are in good condition (Lockie, 1959; Burrows, 1968; Goszczynski, 1974; pers. obs., *Vulpes vulpes* scat, Lincoln, Mass.). Work on coyotes (*Canis latrans*) has produced very similar results (Murie, 1946; pers. obs., Mendocino Co., Calif.), but Johnson and Hansen (1979) have disputed the interpretation that bone is digested at all. Through careful separation techniques they have retrieved microscopic fragments of bone from coyote scat which, together with macroscopically identifiable elements, account for essentially all of the ingested weight of skeletal material. Bones and teeth are rarely found in wolf (*Canis lupus*) scat (Floyd et al., 1978), but it is not clear to what extent selective ingestion, mastication, and digestion are each responsible for this. The record for mustelids and procyonids is similar to that for canids, with teeth and bone fragments being common and chemically unaltered in martens (*Martes martes*; Lockie, 1961) and raccoons (*Procyon lotor*; Greenwood, 1979), though more rare and highly fragmented in stoats (*Mustela erminea*) and weasels (*M. nivalis*; Day, 1966). Felids are also consistent with this pattern. I have fed mice to several domestic cats, and in each case, hair and claws were defecated without any obvious alteration. Claws frequently still contained their terminal phalanges—something that was never observed in crocodylians. Small compact bones were often defecated intact, but otherwise, bone breakage was extensive. Long bones were generally represented by fragments of their distal and proximal ends (occasionally showing tooth punctures) and by spirally fractured splinters of their diaphysis. Most bone destruction is probably produced mechanically, during mastication. If there was subsequent digestion of some fragments, it left no intact organic matrices. Teeth showed little indication, on gross examination, of chemical or mechanical degradation. They were usually isolated but occasionally were still loosely held within their alveoli. Examination of mountain lion (*Felis concolor*) kills and scat, from Mendocino Co., California, suggests a very similar picture, except that ingestion of bones and teeth is less frequent (probably because of the larger absolute size of their prey— young deer), resulting in a much lower rate of occurrence in scat. These results are similar to those reported for lynx (*Lynx canadensis*; Saunders, 1963), leopards (*Panthera pardus*; Grobler and Wilson, 1972), and African lions (Schaller, 1972). Even marsupial carnivores (e.g.

Sarcophilus harrisi and *Dasyurus maculatus*) show this pattern of treatment of bones and teeth (Douglas et al., 1966; Lundelius, 1966).

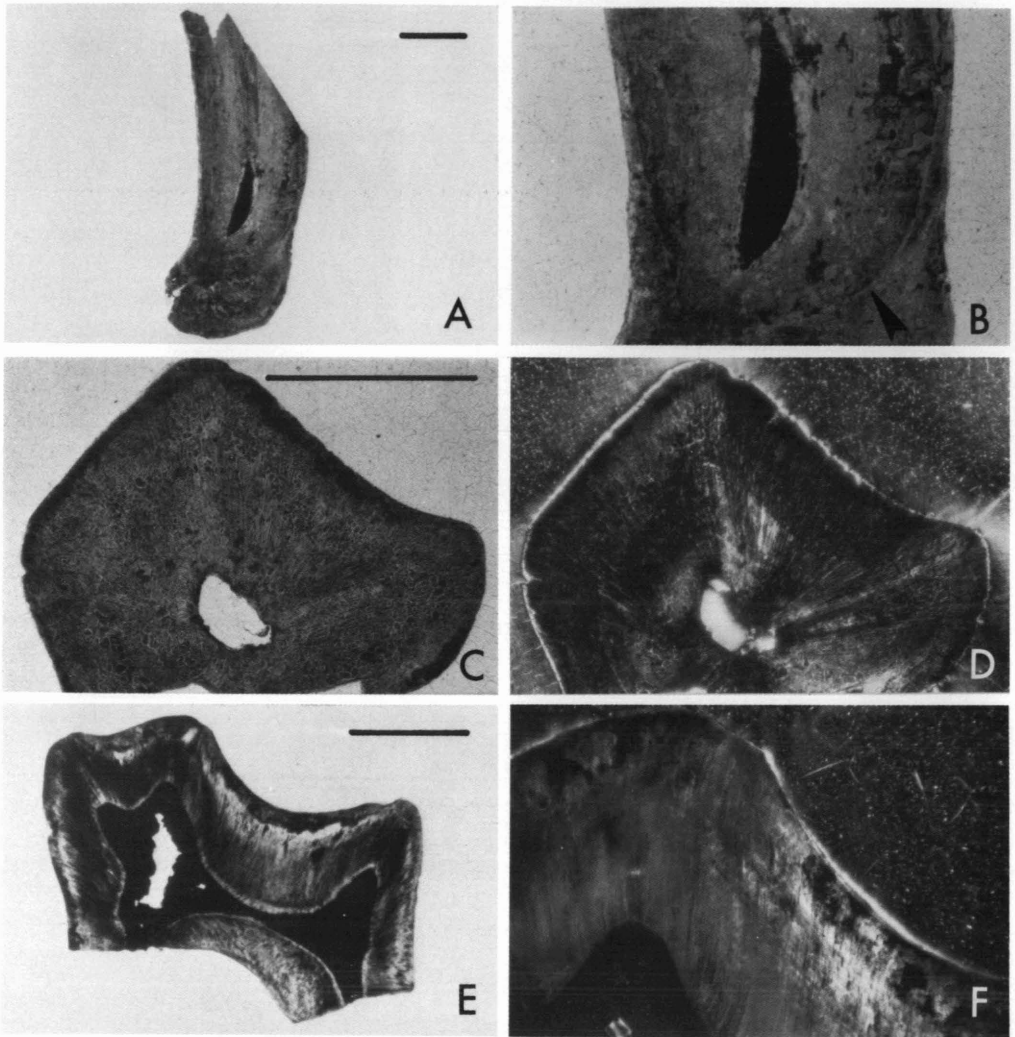
The most conspicuous exception to the pattern shown by other mammals is hyaenids. Although they ingest great quantities of bone, the only trace of it that usually appears in the feces is isolated crystallites of hydroxyapatite (Zapfe, 1939; Mohr, 1964; Kruuk, 1972). There is no indication, in published accounts, as to whether these are liberated directly through the breakdown of the organic matrix, or reprecipitated after dissolution from the bone itself. Occasionally, larger fragments of bone are defecated or regurgitated by hyenas (Sutcliffe, 1970), and these "have a characteristic polished and 'dissolved' appearance, often with sharply pointed ends" (Behrensmeyer, 1978, p. 14). However, there is no preservation of the organic matrix of digested bone. Hyaenids, and other mammalian carnivores as well, avoid ingesting the teeth of large prey (Kruuk, 1972).

This review indicates that the digestive residues of most vertebrates, particularly mammals, would not be easily confused with those of crocodylians. The digestive residues that most nearly resemble the remains of crocodylian prey are produced by certain falconiformes. In some cases, though not in this one, prey body size might help to distinguish which (if either) of these predators had produced a given enamel-less tooth. However, the most important criterion is evidence of dentine decalcification.

OTHER MECHANISMS OF ENAMEL LOSS

Enamel can also be removed from a tooth by a variety of physical and biological processes other than digestion. One of these is abrasion by sedimentary transport. In teeth subjected to abrasion, I would expect removal of material to occur most rapidly from initially prominent topographic features of the tooth, such as the tips of roots and cusps. I would therefore expect these features to be modified *before* the completion of removal of enamel from negative topographic features of the crown (e.g. the talonid basin). However, the Shotgun enamel-less teeth differ from this predicted appearance. Text-fig. 2A and B show the root of a completely enamel-less tooth. The amount and distribution of cementum (dentine-cementum boundary indicated in Text-fig. 2B) is normal for a fully formed root (Peyer, 1968) and suggests that little abrasion has occurred. Histologic features of the crowns of enamel-less teeth also indicate that little, if any, dentine has been removed, other than by normal processes of occlusal attrition. Incremental lamination within the dentine is almost concordant with the present outer surface of the crown (Text-fig. 2F), showing the same gradually onlapping relationship to it as to the enamel-dentine interface (originally the basement membrane separating ameloblasts and odontoblasts) of an intact tooth. In addition, dentinal tubules show increased branching near the present surface of an enamel-less crown, just as they do toward the enamel-dentine interface of a normal tooth. Although it is possible that some enamel-less teeth have experienced slight abrasion, I conclude that this cannot have been sufficient to account for their enamel-less condition.

Another process that should be considered is enamel spalling. As discussed in Fisher (1981b), this often develops through subaerial weathering and desiccation of teeth, but it occurs only rarely on small teeth. More important, the fracture which detaches fragments of enamel usually passes slightly internal to the interface between enamel and dentine, with no particular tendency for patches of enamel to be retained interdentially. In most cases, enamel spalling does not simply 'peel off' the enamel layer of a tooth, exposing the enamel-dentine interface. Enamel spalling is evident on some Shotgun teeth (particularly those of larger mammals), but it is only extensively



TEXT-FIG. 2 — Thin sections of enamel-less mammal teeth from the Shotgun local fauna. A. Anterior root of an enamel-less left P₄ of *Aphronorus orieli* (removed from the crown in Text-fig. 1C), showing preservation of both dentine and cementum; longitudinal section; anterior to right; 9x. B. Detail of A; note irregular regions of dentine decomposition; 28x. C. Enamel-less right lower molar (roots broken) of *A. orieli*; note irregular regions of dentine decomposition scattered throughout tooth; dark rim on crown probably consists of Mn and Fe oxides, and is unrelated to dentine decomposition; labiolingual, longitudinal section through talonid; 28x. D. same as C, viewed with crossed nicols; regions of dentine decomposition show extinction throughout the tooth; 28x. E. Enamel-less right lower molar (roots broken) of *A. orieli*; note rind of dentine decomposition and pyrite in pulp cavity; longitudinal section; anterior to left; 16x. F. Detail of E, showing well preserved dentinal tubules and incremental laminations within undecomposed portion of dentine; 48x. Scale bars in A, C, and E equal 1 mm.

developed (i.e. as much as half of the enamel removed) on individual teeth where it is associated with an extreme degree of fungal decalcification of dentine. This, in turn, is recognizable in thin sections as a dense network of meandering voids, about 2–4 μ in diameter, dissolved into the dentine by fungal hyphae (Marchiafava et al., 1974). The characteristic traces of fungal hyphae were present on one of the four enamel-less teeth that I sectioned (Text-fig. 2C and D), but they

were not nearly as abundant there as on enameled teeth showing partial enamel loss which I interpret as spalling. Furthermore, most enamel-less teeth show no evidence of fungal destruction of dentine. In other words, there is a clear discrimination of two modes in the extent of enamel loss on Shotgun teeth. One of these groups consists of teeth whose condition ranges from no enamel loss to moderate enamel loss; the other consists of teeth showing only interdental patches remaining, or complete enamel loss. The distinctness of these groups is confirmed by differences in the topography of the outer dentine surface and the extent of fungal modification. It therefore seems unlikely that the same process—either enamel spalling or crocodilian digestion—could be responsible for the condition of *both* groups of teeth.

Deminerlization during diagenesis could account for some tooth destruction, but it is not apparent how this could selectively destroy enamel, leaving dentine and cementum. In addition, such a process would not be expected to completely remove enamel from some teeth and leave enamel in perfect condition on others, when both types of teeth occur within centimeters of one another, in the same lithofacies, as they do in the case of the Shotgun local fauna. If diagenetic enamel loss is to be postulated for these teeth, it must have happened in an environment of temporary burial, from which enamel-less teeth have been reworked.

Decalcification by acids produced through the metabolic activities of plants can occur either during the initial early-burial weathering of teeth on or within a soil, or during the exhumation and weathering of fossil teeth. However, it typically affects dentine and cementum as well as enamel. It also produces a characteristic surface topography of shallow, vermiform grooves and irregular pitting (Bonnichsen, 1979; Morlan, 1980). Although I have seen such features on enameled Shotgun teeth, I have never seen them on enamel-less teeth.

All four of the alternative mechanisms of enamel removal discussed above (abrasion, spalling, diagenetic dissolution, and dissolution by plant acids) assume that the remaining dentine and cementum have never been thoroughly decalcified. None of them would be considered sufficient explanations of the condition of enamel-less teeth if it could be shown that enamel-less teeth *had* been decalcified. Here again, as in the case of distinguishing crocodilian digestive residues from those of certain falconiformes, evidence of decalcification assumes an important role.

TESTS OF THE DEMINERALIZATION—REMINERALIZATION HYPOTHESIS

If enamel-less teeth experienced a strongly reducing microenvironment such as I have suggested would be appropriate for remineralization, we might anticipate (if not predict) some record of this. In contrast, teeth which have undergone desiccation or decay in a subaerial environment, or transport within the relatively aerobic environment of a stream channel of moderate current energy, would in general not be expected to have encountered reducing environments. *All* of the enameled teeth whose pulp cavities I have examined, either by sectioning or by natural break, have had their pulp cavity either empty or sediment-filled (Fisher, 1981b). Of the eleven enamel-less teeth whose pulp cavities I have examined, three were empty (Text-fig. 2C,D), two were filled with sediment, and six were filled with pyrite (Text-fig. 2E,F). Only one tooth (not counted above) is at all problematic. Until its morphology is properly understood, it is thoroughly enigmatic, at once resembling a tooth crown, and yet clearly differing from that familiar shape. This unusual structure is a pyrite cast of a pulp cavity from which most of the rest of the tooth has been broken away. Only a few fragments of dentine still adhere to its outer surface. Although I am unable to verify that *no* enamel was present just prior to fracture of the dentine, the dentine that remains is identical in its preservation to the dentine of some of the confirmed enamel-less teeth. It almost certainly represents a twelfth enamel-less tooth, the seventh with a pyrite pulp filling. This exclusive association of pyrite with enamel-less

teeth suggests that many enamel-less teeth have been subjected to more strongly reducing environments than most enameled teeth. This corroborates the remineralization scenario proposed here and confirms the rejection of abrasion or spalling as sufficient mechanisms of enamel loss for these teeth.

The enamel-less teeth of the Shotgun local fauna preserve a considerable degree of histologic detail, making possible a structural approach to the question of whether or not demineralization has occurred. If enamel-less teeth were never demineralized at all (i.e. if enamel loss occurred through abrasion or spalling), I would expect their dentine to be histologically similar to that of enameled teeth. If enamel loss occurred through differential demineralization of enamel and dentine, as in red-tailed hawk digestion or any of the other selective dissolution processes discussed, it is more difficult to anticipate the exact outcome, since these processes are not well understood. However, if dentine is indeed left intact at a gross morphological level, I would anticipate that it would not be seriously altered histologically (at least to any great depth). The basis for this expectation is that teeth that are incompletely decalcified, either artificially or during crocodilian digestion, show normal dentine histology in the undecalcified core (Fisher, 1981a). In contrast to these predictions, if enamel-less teeth were demineralized and remineralized, I would expect them frequently to show a type of dentinal alteration not seen in enameled teeth. Remineralization would have had to occur before bacterial decomposition was complete, but there is still a range of time over which it might have happened. The best preservation would develop if matrices were remineralized before any decomposition, but, given their vulnerability to decay, this would probably happen rarely. The more common condition would probably involve remineralization subsequent to at least the initial stages of decay. The condition of partially decomposed matrices recovered from crocodilian feeding experiments (Fisher, 1981a) suggests that the process of decomposition causes the tooth to develop a "spongy" texture, proceeding from the outer surface of a tooth inward (for a tooth with patent apical foramina on its roots, the "outer" and pulpal surfaces of the tooth could be equivalent in this respect). A decalcified tooth 'caught' by remineralization during the initial stages of decomposition should thus have a centrifugal distribution of decomposed regions.

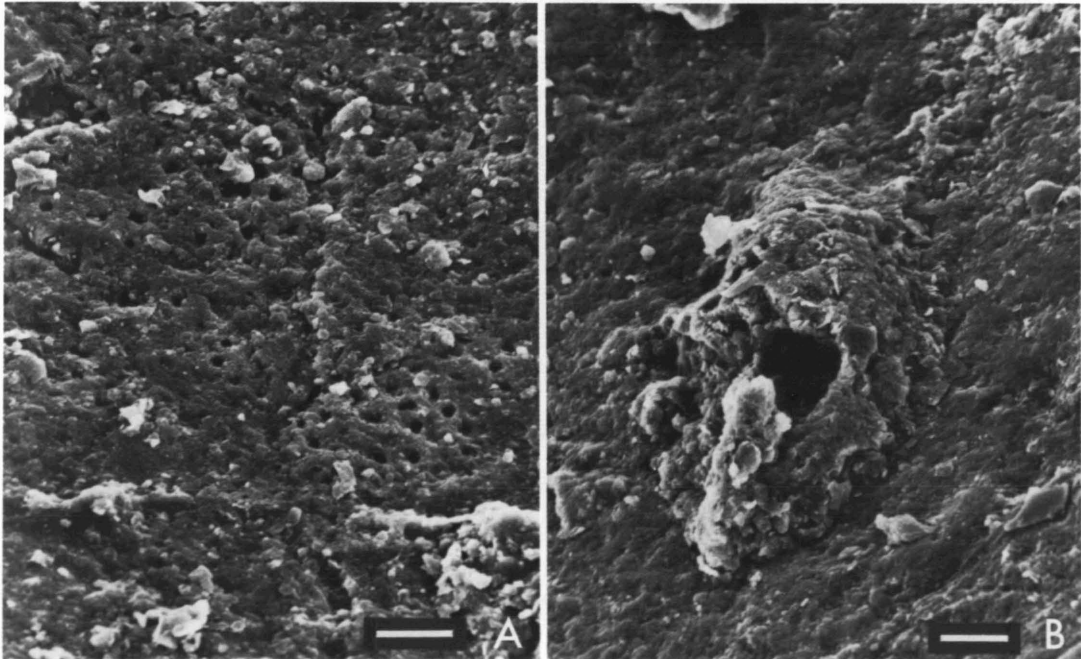
Thin sections of Shotgun teeth show that most enameled teeth have extremely well preserved dentine (Fisher, 1981b). However, the dentine of enamel-less teeth has a characteristic type of structure that is superimposed upon normal dentine histology. Although I have observed this in detail only in the enamel-less teeth I have sectioned or examined with the SEM, it is also apparent on broken surfaces of most other enamel-less teeth. None of the enameled teeth show a similar condition. This pattern of preservation consists of irregularly globular regions about 50μ in diameter (a different shape and more than an order of magnitude larger than the fungal excavations). Thin sections of these regions show greater opacity to transmitted light, a lighter color in reflected light, and isotropic behavior when viewed between crossed nicols. The hydroxyapatite in these regions may be more nearly amorphous, or composed of smaller, more randomly oriented crystallites. Dentinal tubules and incremental laminations do not extend through these regions. In some enamel-less teeth, such regions are scattered more or less throughout the dentine and cementum (Text-fig. 2A-D), though there is usually a considerable amount of well preserved structure remaining. If these regions do not extend throughout the tooth, they are restricted to a zone (of constant thickness on any one tooth) around the *outside* of the tooth. Such a 'rind' is shown in Text-fig. 2E,F.

These regions of dentine opacity apparently represent areas of bacterial decomposition of the organic matrix, developed following decalcification, but prior to remineralization. Although undecomposed tracts of matrix were able to control remineralization to the extent that some histologic structure could be preserved, the decomposed regions appear to have been remineralized in a less organized fashion. Their globular shape, the "spongy" texture which they

produce, and their apparent initiation at the surface of the tooth help to confirm this interpretation. These observations clearly differ from expectations based on other mechanisms of enamel loss.

The distinctive structure of enamel-less teeth is also evident under SEM examination. The preservation of some histologic structure is illustrated by the presence of dentinal tubules, outcropping on some areas of the present crown surface of enamel-less teeth (Text-fig. 3A). However, most of the dentine appears to be more 'disorganized', or 'poorly structured', than the dentine of enameled teeth. The material presently occupying the globular regions interpreted as the product of bacterial decomposition can be seen to be even more chaotic in its organization (Text-fig. 3B), an observation that is fully compatible with its appearance in thin section. Additional SEM work on both enamel-less and enameled teeth would contribute greatly to taphonomic interpretations, but even these preliminary results are sufficient to show that the alteration that has affected enamel-less teeth extends beyond the loss of enamel.

A further observation concerns the relationship between the distribution of regions of 'decomposed dentine' and the condition of the pulp cavity. Because the rate of decomposition would be retarded in a strongly reducing environment, when there is variation in the extent of decomposition, it should have proceeded less far in teeth whose pulp cavities are filled with pyrite, leading to the "centrifugal distribution" predicted above. Of the four sectioned enamel-less teeth, two had pulp cavities that were empty, and two were filled with pyrite. The two with empty pulp cavities and one with a pyrite filling had patches of decomposed dentine scattered throughout (Text-fig. 2A-D). The rind of decomposed dentine noted above appeared in the other sectioned, enamel-less tooth with a pyrite pulp filling (Text-fig. 2E,F). Examination of



TEXT-FIG. 3 — SEM photographs of the unground, unetched surface of a Shotgun enamel-less tooth (shown also in Text-figs. 1C and 2A). A. Dentinal tubules outcropping on the present surface of the dentine. B. Globular region of dentine decomposition. Scale bars in A and B equal 10 μ .

broken surfaces of other enamel-less teeth tentatively confirms this association. Combining this information with that from thin sections, the distribution of decomposed dentine can be seen in four of the five enamel-less teeth whose pulp cavities are either empty or sediment-filled, and in each of these, it is scattered throughout. Rinds of decomposed dentine occur exclusively on enamel-less teeth with pyrite pulp fillings, and on five of the six teeth in this class. I have counted, as one of these five, the only enamel-less tooth on which I have seen no indication of dentine decomposition; it could be said to have the thinnest rind of all.

As a further test of this demineralization-remineralization hypothesis I have considered types of alteration that either should be, or could be, associated with remineralization. The hydroxyapatite of normal teeth is moderately crystalline. If enamel-less teeth have in fact been demineralized and then remineralized as suggested above, their hydroxyapatite should be less coarsely crystalline (Whittemore, 1976). Though the results of this test are strongest if they are positive (i.e. if a clear difference in crystallinity parallels the presence or absence of enamel), negative results could argue, even if less persuasively, for falsification of the hypothesis.

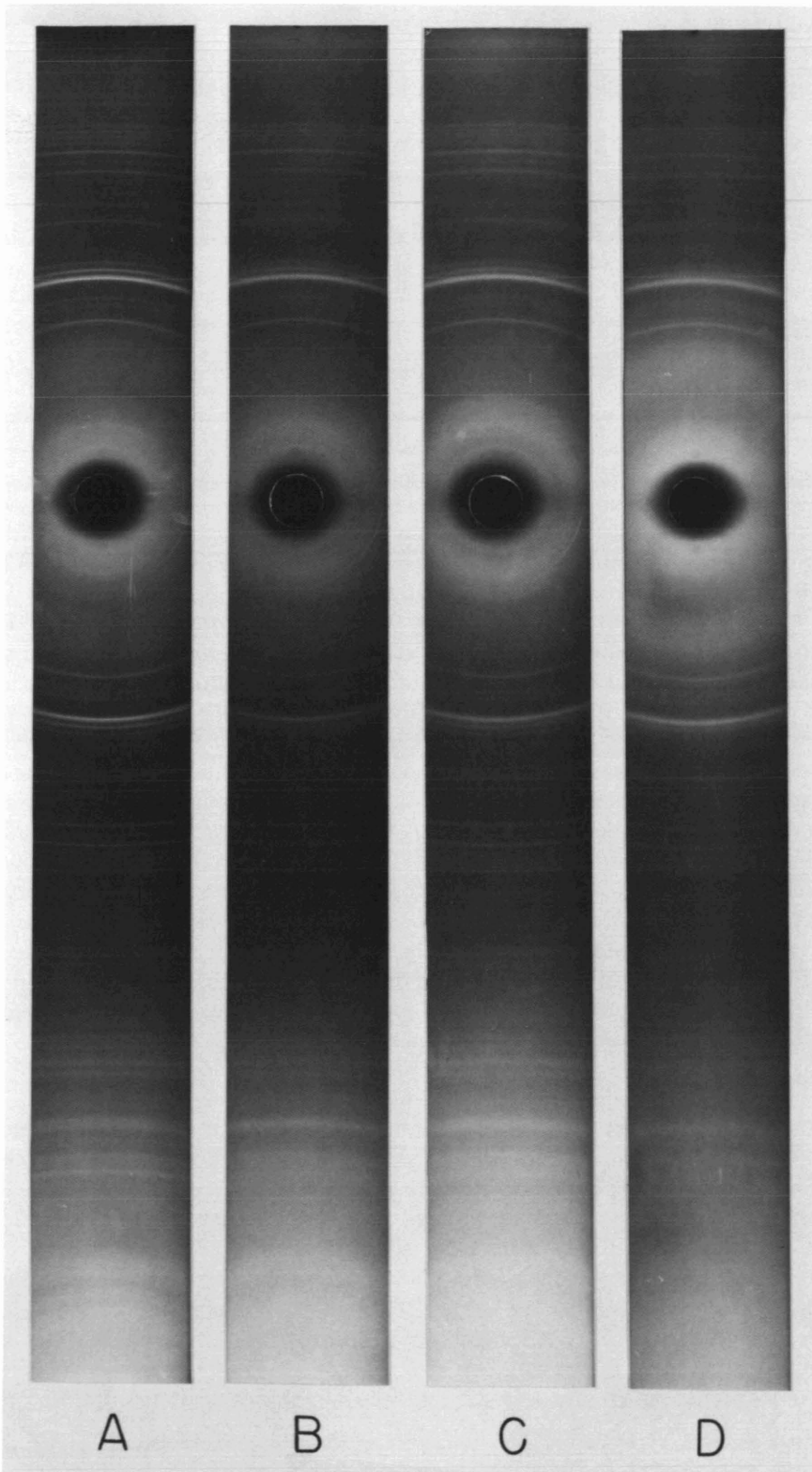
Another potential type of alteration involves composition. If demineralization occurred, and if skeletal-derived hydroxyapatite were not in equilibrium with the microenvironment of the feces and their immediate surroundings, there would have been an opportunity for compositional alteration of the hydroxyapatite. Remineralization would then produce a tooth that differed compositionally from its previous condition and, presumably, from undemineralized teeth. Since reequilibration would probably occur more rapidly while the hydroxyapatite was in an amorphous form, in the feces, than either before demineralization or after remineralization, it is possible that this process would produce a chemical alteration that would not be erased by subsequent diagenesis. Although further research (e.g. on the reaction kinetics of hydroxyapatite alteration) would be required to enable the *absence* of compositional differences to falsify the demineralization-remineralization hypothesis, the *presence* of such differences would demand some unique event in the taphonomic history of enamel-less teeth.

I have investigated the possibility of mineralogical differences between enamel-less teeth and other elements of the Shotgun local fauna by making Debye-Scherrer powder photographs of the x-ray diffraction patterns of a number of samples. Sample 1 is Pleistocene in age, locality unknown; sample 2 is from the Cretaceous, Bug Creek Anthills, Montana; and all other samples are from the Shotgun local fauna.

- (1) Enamel from a well preserved mastodon tooth;
- (2) Bone fragment from an amiid fish;
- (3) Weathered fragment of a turtle carapace;
- (4) Unweathered fragment of a turtle carapace;
- (5) Fragment of a well preserved shark tooth (ca. equal amounts of vitrodentine and trabecular dentine included); Text-fig. 4A;
- (6) Fragment of a well preserved multituberculate tooth (ca. equal amounts of enamel and dentine included);
- (7) Root fragment (dentine only) of an unidentified well preserved, placental mammal tooth (enamel present on this tooth but not included in this sample); Text-fig. 4B;
- (8) Enamel and dentine (ca. equal amounts) from the crown of tooth sample 7;
- (9) Root fragment (dentine only) of an unidentified, well preserved placental mammal tooth (different from sample 7; enamel present on this tooth but not included in this sample);

(Opposite page)

TEXT-FIG. 4 — Debye-Scherrer x-ray diffraction films of four teeth from the Shotgun local fauna. A. Shark tooth (both vitrodentine and trabecular dentine); sample 5. B. Root fragment (dentine only) of enameled mammal tooth; sample 7. C. Crown fragment (enamel and dentine) of enameled mammal tooth; sample 10. D. Root fragment (dentine only) of enamel-less right M_3 of *A. cf. fraudator*.



- (10) Enamel and dentine (ca. equal amounts) from the crown of tooth sample 9; Text-fig. 4C;
- (11) Root fragment (dentine only) of an unidentified, well preserved, placental mammal tooth (different from samples 7 and 9; enamel present on this tooth but not included in this sample);
- (12) Enamel and dentine (ca. equal amounts) from the crown of tooth sample 11;
- (13) Root fragment (dentine only) of an 'enamel-less' (one small interdental patch of enamel remaining) right lower molar of *Aphronorus orieli*; Text-fig. 2C,D;
- (14) Root fragment (dentine only) of a completely enamel-less left lower fourth premolar of *A. orieli*; Text-figs. 1C and 2A,B;
- (15) Dentine from the root and crown of an 'enamel-less' (one small interdental patch of enamel remaining) right lower first or second molar of a small arctocyoid;
- (16) Root fragment (dentine only) of a completely enamel-less right lower third molar of *A. fraudator*; Text-figs. 1A and 4D.

The first six of these samples were run primarily to determine the amount of variability that could be expected to result, either directly or indirectly, from differences in systematic affinities, age, and preservation. Ideally, samples 7–16 (among which the most relevant comparisons are to be made) would have been under better control taxonomically. However, 'enameled versions' of the enamel-less teeth 13–16 were not available for analysis.

With respect to the first mineralogical problem—that of crystallinity—samples 1–12 produced sharp, well-defined diffraction lines (e.g. Text-fig. 4A–C). However, samples 13–16 consistently produced more diffuse diffraction patterns (e.g. Text-fig. 4D). Since the sample preparation and exposure procedures were carefully standardized (and checked by separate runs of samples 9 and 10) to provide equal amounts of sample powder and accurate centering of the sample in the x-ray beam, this difference seems best explained as indicative of less well developed crystallinity for the enamel-less teeth. It cannot be interpreted as a trivial result of the absence of enamel from enamel-less teeth, since samples 7, 9, and 11 contain no enamel either, but have the pattern characteristic of enameled teeth. Moreover, this observation is not simply redundant to the observation of isotropic regions of dentine decomposition in the enamel-less teeth. The sample pattern illustrated in Text-fig. 4D (sample 16) is from the one enamel-less tooth which showed *no* globular regions of dentine decomposition. The less well developed crystallinity therefore seems to be on a different level of organization from that which was observed in thin section. It may, however, be associated with the relatively 'disorganized' appearance of dentine, observed by SEM (Text-fig. 3B) in areas *surrounding* the regions of dentine decomposition.

On the question of composition, the greatest difference in line position is between sample 1 and all others. Sample 1 is almost certainly much less permineralized than the others. However, the lines on patterns 1–12 correspond well with each other and with standard reference *d* values for hydroxyapatites. Although other constituents (e.g. iron and manganese oxides) are certainly present in samples 2–12, they must occur in amounts that are small enough not to add new lines to the pattern. Comparisons with reference *d* values suggest that most of the differences in line position for all of these samples are due to differences in the amount of fluorine and/or chlorine included in the hydroxyapatite. It is well known that fossil bone can become enriched in fluorine relative to Recent bone (Brophy and Nash, 1968; Parker et al., 1974). This may explain the differences between sample 1 and the others, and most of the differences among samples 2–16.

Preliminary analysis of samples 3–6 suggests that both details of preservation and higher-level taxonomic affinities may have an effect on hydroxyapatite composition. This argues for restriction of further attention to samples 7–16. Samples 7–12 have very similar patterns, both within and between teeth. Samples 13–16 also have very similar patterns, but they differ from 7–12. Qualitatively, the patterns from enamel-less teeth have one extra line, not present in 7–12, at a 2θ value of 33.67° . Quantitatively, many of their diffraction lines are shifted slightly relative

to those of enameled teeth 7-12. Since the number of samples is very small and the differences relatively slight (though larger than measurement error), the statistical significance of these results could be questioned. Further work, with more refined analytical techniques, is planned to deal with this problem, but these preliminary observations suggest that enamel-less teeth are indeed compositionally distinct from enameled teeth. Once again, consideration of samples 7, 9, 11, and 16 argues that this cannot be a trivial consequence of the absence of enamel or the presence of dentine decomposition. These results indicate that enamel-less teeth have had some unique history, probably involving demineralization and remineralization, prior to their final burial.

DISCUSSION

The hypothesis that the enamel-less condition of some teeth in the Shotgun local fauna was produced by crocodilian digestion was proposed because of the gross morphological resemblance between these enamel-less teeth and decalcified tooth matrices recovered from crocodilian feces. Although the details of how such matrices might be preserved require additional analysis, remineralization by hydroxyapatite, within the reducing microenvironment of the feces, appears to be the most probable mechanism. The condition of the pulp cavity of enamel-less teeth, the histologic structure of their dentine and cementum, and their mineralogy are consistent with this interpretation of their taphonomic history. In these same respects, the Shotgun enamel-less teeth differ from what would be expected if enamel loss had occurred through other processes, including: digestion by non-crocodilian predators or scavengers; abrasion; enamel spalling; diagenetic alteration; or dissolution by plant acids. It thus seems most reasonable to attribute the condition of enamel-less teeth to digestion by crocodilians. Additional work on both ultrastructure and mineralogy should provide further tests of this interpretation.

Preservation of bone fragments in the Shotgun local fauna may be characterized by a dichotomy parallel to that between enameled and enamel-less teeth. However, since digestion by crocodilians produces less dramatic gross morphological alteration of bone fragments than of teeth, the two classes of bone fragments will be more difficult to distinguish by unaided visual inspection. It may therefore be very difficult to recognize fossil bone digested by crocodilians, except when it is associated with enamel-less teeth.

The other occurrences of enamel-less teeth discussed in Fisher (1981a) were identified solely on the basis of their gross morphological appearance. Although it seems likely that some or all of these were eaten, digested, and defecated by crocodilians, the full evaluation of alternative taphonomic hypotheses will require more detailed investigation.

ACKNOWLEDGMENTS

F. A. Jenkins, Jr. generously provided access to the MCZ collections of the Shotgun local fauna, including material suitable for sectioning and x-ray diffraction work. C. B. Wood, in addition to introducing me to the Shotgun local fauna, assisted greatly by helping to search for enamel-less teeth in the course of his research on the paleoecology of the fauna. Versions of this manuscript have been read and commented on by P. D. Gingerich, J. A. Hopson, B. Patterson, K. D. Rose, E. E. Williams, and anonymous reviewers. In addition, I have appreciated

discussions of this material with R. T. Bakker, W. S. Bartels, J. G. Fleagle, D. W. Krause, M. C. McKenna, and D. R. Peacor. S. J. Carlson took the SEM photographs used here; J. A. Sharry, W. Stein, and J. D. McKean provided additional technical and photographic assistance; and D. Robins typed the manuscript.

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