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**MODE OF PRESERVATION OF THE SHOTGUN LOCAL FAUNA  
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TAPHONOMY OF A MICROVERTEBRATE CONCENTRATION**

BY

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# MODE OF PRESERVATION OF THE SHOTGUN LOCAL FAUNA (PALEOCENE, WYOMING) AND ITS IMPLICATION FOR THE TAPHONOMY OF A MICROVERTEBRATE CONCENTRATION

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Daniel C. Fisher

*Abstract.*—Previous analysis of the Shotgun local fauna by McGrew (1963) cited breakage, abrasion, and corrosion of bones and teeth as evidence that this fossil assemblage was formed as a concentration of crocodylian fecal residues. However, qualitative analysis of the depositional context of this concentration, the weathering features developed on bone fragments, and fungal decalcification of dentine on some teeth show that a variety of processes has been involved in the preservation of this assemblage. These observations may be consistent with, but certainly do not require, a scatological mechanism of concentration. The feature that previously seemed to be the most persuasive indication of digestive residues—absence (interpreted as corrosion) of dentine from some teeth—actually represents one of two situations: 1) death prior to completion of dentine formation; and 2) death during the period of dentine resorption, just prior to tooth replacement. There is thus no basis for interpreting the Shotgun local fauna as an assemblage of crocodylian prey. This result complements conclusions drawn from experiments on the scatology of living crocodylians. The most readily apparent indicator of crocodylian digestion of vertebrate prey is the discovery of teeth in an enamel-less condition.

## INTRODUCTION

The analysis of taphonomic history has come to be considered an important component of any biological interpretation of assemblages of fossil organisms. However, the need for taphonomic analysis is particularly evident when distinctive preservational characteristics seem to implicate some unusual set of conditions for accumulation and preservation. In this regard the Shotgun local fauna, from the Paleocene Fort Union Formation, Wyoming, deserves particular attention. It is a vertebrate assemblage composed predominantly of isolated teeth and small fragments of bone. Its overall character and certain details of its preservation led McGrew (1963) to suggest that much of the fauna represents a crocodylian fecal concentrate—i.e. that it is composed of incompletely digested material, sorted and concentrated from disaggregated crocodylian feces. In this paper I discuss observations on the mode of preservation of the Shotgun local fauna, as a means of evaluating McGrew's interpretation of its taphonomic history. This study also serves as background for a more direct test of the crocodylian fecal concentrate hypothesis, based on feeding experiments with living crocodylians (Fisher, 1981a).

The importance of carefully evaluating McGrew's suggestion goes beyond whatever degree of interest may accrue to this problem simply by virtue of its unusual character or its implications for the trophic relationships of Paleocene crocodylians and their prey. The Shotgun local fauna is one of the most diverse Paleocene vertebrate faunas in North America. A clearer understanding

of its taphonomic history should help to determine whether its diversity reflects unusually great species richness within a single original 'community,' mixing of relatively allochthonous with relatively autochthonous material (thus representing two or more contemporaneous 'communities'), unusually complete sampling of the original fauna, or some combination of these or other possibilities. To complicate matters further, there has been some question as to whether this fauna is even a temporally homogeneous sample or, alternatively, a composite of reworked older elements (probably Torrejonian in age) and material of Tiffanian age (Gazin, 1961, 1971). In any case, a better understanding of this fauna could contribute greatly to our perception of the composition and organization of terrestrial vertebrate communities around the time of the major diversification of mammals.

On another level, evaluation of McGrew's (1963) interpretation is important because the preservation of the Shotgun local fauna is representative of other concentrations of small, disarticulated and broken bones and isolated teeth. These are generally known as microvertebrate concentrations (Mellett, 1974). They are a relatively common type of fossil vertebrate occurrence and are often the only context from which species of small body size are known. Although McGrew's (1963) analysis considers only the Shotgun local fauna, it clearly has much greater potential generality. Indeed, similar suggestions had been made previously (though they were not developed in as great detail) by workers dealing with other occurrences (e.g. Weigelt, 1927; Simpson, 1937). Alternatives to the hypothesis that microvertebrate concentrations represent crocodylian fecal concentrates include suggestions that they are derived, in a similar way, from predators other than crocodylians (Mellett, 1974; Mayhew, 1977) and that their origin is more exclusively the result of weathering and hydraulic processes (Dodson, 1971; Wolff, 1973; Korth, 1979). Although there is no *a priori* reason to expect that all microvertebrate concentrations need be traced to the same origin, genetic criteria developed for one occurrence should be applicable to others. From this standpoint, analysis of the Shotgun local fauna is significant for understanding the origin and information content of other microvertebrate concentrations as well.

#### GEOLOGICAL CONTEXT OF THE SHOTGUN LOCAL FAUNA

The Shotgun local fauna occurs in the lower part of the Shotgun Member of the Fort Union Formation (Paleocene), in the Wind River Basin, Wyoming. The Shotgun Member is composed of grey-brown, evenly bedded claystone, siltstone, carbonaceous shale and sandstone, 2,830 feet thick at the type section in the northern Wind River Basin (Keefer, 1961). It interfingers to the east with the Waltman Shale Member, a homogeneous, thick sequence of brown to black, silty, micaceous shale and claystone. These two members comprise the upper part of the Fort Union Formation. The lower part of the Fort Union Formation is formed by the lowermost Waltman Shale Member in the east, and by an unnamed member, underlying the Shotgun Member, in the west. The general paleogeographic picture reconstructed by Keefer, and corroborated by others (Love et al., 1963; Keefer and Troyer, 1964; Keefer, 1965), is "that an extensive body of water [Waltman Lake] occupied approximately the northeast quarter of the Wind River Basin during middle and late Paleocene time" (Keefer, 1961, p. 1319). Although typical marine faunas of the contemporary epicontinental seaway are absent from the Fort Union Formation, the proximity of the Cannonball Sea (across the Casper Arch), the presence of hystrichosphaerids and glauconite in the Waltman Shale Member, the presence of sharks in the Shotgun local fauna, and the rarity of *Lepisosteus* (McGrew, 1963), indicate that Waltman Lake may well have been at least brackish. Keefer interprets the Waltman Shale Member as having been deposited in

offshore areas of Waltman Lake, and the Shotgun Member as representing the contemporaneous development of a fluvial facies near the lake margin, during the period of its maximum expansion and uneven regression. Relief in the surrounding area was probably very low, and stream channels may have been flooded occasionally by brackish waters.

The Shotgun local fauna is preserved in medium- to fine-grained channel sands in the lower portion of the Shotgun Member, near Twin Buttes, Wyoming. The concentration of fossil material seems to vary greatly within this sand. However, within a large (approximately 180 kg) block of Shotgun matrix collected from a relatively fossiliferous outcrop of the sand (as part of a paleoecological investigation initiated by C. B. Wood) vertebrate fossils account for less than a few percent of the rock volume. On a scale of tens of square centimeters of bedding plane or outcrop surface, teeth and bone fragments are disseminated more or less randomly. There are no conspicuously coprolitic concentrations. The channel sands are moderately to poorly sorted and in addition to the vertebrate fossil material contain bits of coalified plant material and clay intraclasts. The size of individual teeth or skeletal fragments approximates hydraulic equivalence with the surrounding sediment (Behrensmeier, 1975; Korth, 1979; Hanson, 1980). These observations suggest that, whatever the earlier history of specimens comprising the Shotgun local fauna, their immediately predepositional history involved slight to moderate transport as individual particles.

#### TAXONOMIC COMPOSITION AND PRESERVATION OF THE SHOTGUN LOCAL FAUNA

The taxonomic composition of the Shotgun local fauna has been discussed by a number of workers (e.g. Gazin in Keefer, 1961; McGrew and Patterson, 1962; Patterson and McGrew, 1962; Gazin, 1971). Among the more abundant components are chondrichthyans, crocodylians, multituberculates, marsupials, insectivores, primates, creodonts, condylarths, and pantodonts. Collections on which the present work was based are from the Museum of Comparative Zoology (Harvard University). This is a larger sample than was available to McGrew, but I assume that the frequency of occurrence of different modes of preservation in it does not differ greatly from previously collected material.

McGrew (1963, p. 41) suggested "that all of the specimens [preserved in the Shotgun local fauna] have passed through the alimentary tract of crocodiles, especially the smaller mammals and sharks." This was based on observations which he recorded as follows:

"The teeth of . . . small forms are almost invariably complete with abrasion or corrosion limited to the roots. In the larger mammals such as taeniolabids [sic], phenacodontids, peryptichids [sic], and pantodonts, the teeth are rarely complete, and consist only of fragments. Except for a few phalanges, skeletal elements are broken, abraded or corroded, and consist mostly of fragments of bone shafts. The roots of most of the shark teeth show similar corrosion or abrasion" (McGrew, 1963, p. 41).

The most important set of assumptions underlying this interpretation is that crocodylian digestive processes would be capable of producing the observed effects. This is examined in detail by Fisher (1981a). In addition to this, however, McGrew has implicitly rejected other, more conventional explanations for bone and tooth breakage, isolation of teeth, and loss of dentine. Can this decision be upheld? I will address this question by considering the preserva-

tional states of Shotgun material in greater detail. This will be done by discussing four broad categories of elements: non-dental skeletal material, shark teeth, teeth of larger mammals (mostly over 5 kg body weight), and teeth of smaller animals (mostly under 5 kg body weight). Descriptions of preservation are based on gross and stereomicroscopic examination of bones and teeth, and on study of 111 serial thin sections of 33 teeth chosen to represent a range of preservational states.

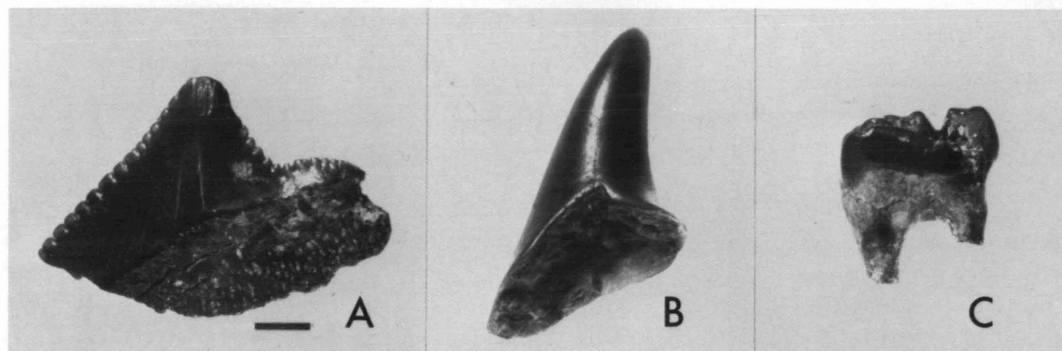
*Skeletal material.*—Reexamination of Shotgun non-dental skeletal material suggests some modifications of McGrew's observations. In addition to phalanges, complete bones include caudal vertebrae, carpal and tarsal elements, crocodylian scutes, and other elements. Most are small, compact bones, and their original surface textures are often well preserved. Nevertheless, as McGrew noted, most skeletal elements have been broken. Some of this breakage must have occurred during diagenesis, weathering associated with exhumation, or collection. This post-depositional origin is demonstrated by examination of specimens excavated *in situ* in the large block of Shotgun matrix mentioned above. A considerable amount of material in this block has been fractured, but its fragments remain in juxtaposition. By dissociation of these fragments (even ignoring the possibility of further breakage) most collecting techniques (e.g. washing and sorting of disaggregated sediment or anthill concentrations) would increase the apparent incidence of breakage well above its preburial level. Postdepositional breakage (particularly of recent origin) is usually distinguishable, even following collection, by the orientation of break surfaces (often normal to original bone surfaces) or by their 'fresh' appearance. It must be recognized and deleted from any consideration of the breakage that might be attributable to predation.

Much breakage of Shotgun skeletal material is, however, of prediagenetic origin. This can be determined most directly through *in situ* examination. After collection, prediagenetic breakage may still be indicated by "spiral breakage" of the shafts of long bones. This occurs prior to permineralization or even extensive loss of organic material (Kühne, 1956; Mellett, 1974). Spiral breaks are usually oblique to the original bone surface and to the long axis of the shaft. Predepositional fracture is also evident on the ends of long bones, or on elements such as carpals, tarsals, or vertebral centra, by the presence of compact sediment filling their cancellous interiors. Such sediment is a mixture of sand and clay not significantly different from that in which the bone fragments occur. On most bone fragments in the Shotgun local fauna the present topography of a fragment intersects the original surface of the bone at a well marked edge. For these fragments, the bone may be appropriately described as broken, or more rarely, as punctured or crushed. However, these cases grade into ones in which the damage was apparently produced when the bone was much more friable. Such break surfaces are not at all distinct, and in extreme cases, the difference between fracture and abrasion becomes insignificant operationally. In the sample I have examined there was little evidence of abrasion that was not associated with surface features indicating original friability. The rarity of smooth, solid, well rounded bone fragments indicates that most material was not transported long distances in a fresh, unweathered condition (Korth, 1979). Furthermore, only rarely does the surface of bone fragments show pitting or "corrosion." Surface textures of most bone fragments range from well preserved to the 'fibrous,' porous condition indicative of subaerial exposure and weathering prior to burial (Clark et al., 1967; Behrensmeyer, 1978; weathering stages 0-5 are recognizable). This range of preservational features and stages of weathering is consistent with the Shotgun local fauna being an attritional assemblage, in which individual skeletal elements have experienced considerable variation in *post mortem*, predepositional history. Although some transport is evident from the mixture of terrestrial and aquatic forms, it may well have been minimal.

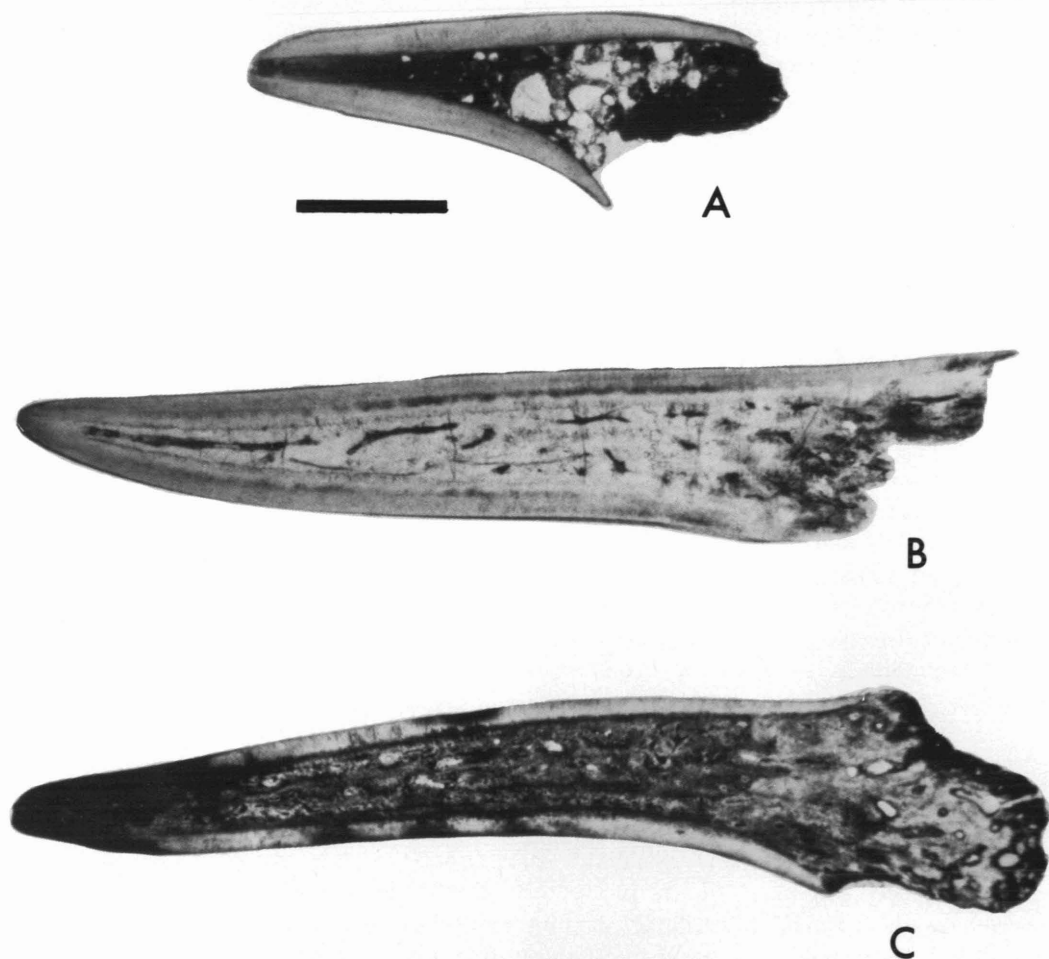
*Shark teeth.*—The shark teeth of the Shotgun local fauna usually have intact crowns (Text-fig. 1A,B), with no evidence of any destruction of the vitrodentine (the dense, shiny, enamel-like tissue forming their outer surface). As verified by thin sections (Text-fig. 2A-C), vitrodentine occurs in a layer of normal thickness over all of the crown that is present. There are teeth with bases completely intact, and also ones with slight breakage of the base (Text-fig. 1A). However, the teeth that correspond most clearly to McGrew's description, both in abundance and condition, are ones that consist only of a more or less 'hollowed out' crown (Text-fig. 1B). These teeth range from diminutive hollow cones to teeth that are essentially complete except for their bases. On a histologic level (Text-fig. 2A,B), the main differences among these teeth are in the amount of trabecular dentine. When present, trabecular dentine is always well preserved. While this range of conditions could be interpreted speculatively as the result of some process of 'dental corrosion,' no such process has ever been demonstrated. In contrast, precisely these conditions have been documented as stages in the *formation* of shark teeth (Peyer, 1968, Pl. 16a, 17b; Grady, 1970). The vitrodentine forms first, progressively thickening and extending abapically, and this hollow cone is subsequently filled in by the abapical deposition of trabecular dentine. No similar morphologic series is associated with tooth replacement in sharks; shedding of teeth does not involve appreciable resorption of the tooth base or interior (Peyer, 1968, p. 4). Therefore, until similar effects are shown to be produced by digestive corrosion, I believe it is preferable to interpret these 'hollow' shark teeth as teeth that were never completely formed. The presence of incompletely formed teeth in association with fully formed ones would in fact be expected if shark teeth accumulated through the death and disarticulation of sharks, rather than exclusively through the shedding of teeth during the normal replacement process in living individuals. Although the death of these sharks may or may not have been due to predation, and although their teeth may or may not have ever been ingested, it is clear that the incomplete teeth themselves need not be interpreted as evidence of digestion.

*Larger mammal teeth.*—The teeth of larger mammals, as mentioned above, are usually broken. As was the case with bones, it is important to distinguish pre- and postdepositional breakage. Predepositional breaks have occurred most frequently along roughly vertical planes, passing through, or near, the pulp cavity. In this respect they resemble the cracks that develop through desiccation of the organic matrix of dentine (Behrensmeier, 1978). Although further observations and experiments would be necessary to characterize this mechanism of tooth fragmentation adequately, it is possible that the condition of these teeth could be due simply to a period of *post mortem* subaerial exposure. In contrast, McGrew suggests (explicitly in Love et al., 1963; in more qualified fashion in McGrew, 1963) that this fragmentation was produced by crocodylians. However, the only potential tooth crushing mechanisms—forceful jaw adduction (e.g. in crocodylians such as the broad-toothed *Allognathosuchus*) and crushing between gastroliths—would operate, respectively, *before* and *during* the interval within which digestion itself would be effective. Therefore, if tooth breakage was produced by crocodylians, and if (as assumed by McGrew, 1963, though rejected by Fisher, 1981a) crocodylian digestion does preferentially destroy dentine, there should be a conspicuous recession of the dentine surface where a break truncates both enamel and dentine. Since no such recession is apparent, it seems that no process selectively removed dentine subsequent to tooth breakage.

Another conceivable agent for the production of tooth breakage is a mammalian predator. However, extant mammalian predators dealing with relatively large prey avoid mastication or ingestion of the teeth of their prey—presumably because of the risk of breakage to their own teeth (e.g. Schaller, 1972). This is true even for hyenas, which devour everything except teeth, horns, and hooves (Kruuk, 1972). For the same reason, I would anticipate a similar behavior pattern among Paleocene mammals.



TEXT-FIG. 1 — Teeth from the Shotgun local fauna. A. Shark tooth with complete base (except for minor fracture). B. Shark tooth with little trabecular dentine and a sediment in-filling of the crown. C. Well preserved multituberculate left  $M^2$ ; anterior aspect. Scale: all specimens 7x; bar in A equals 1 mm.

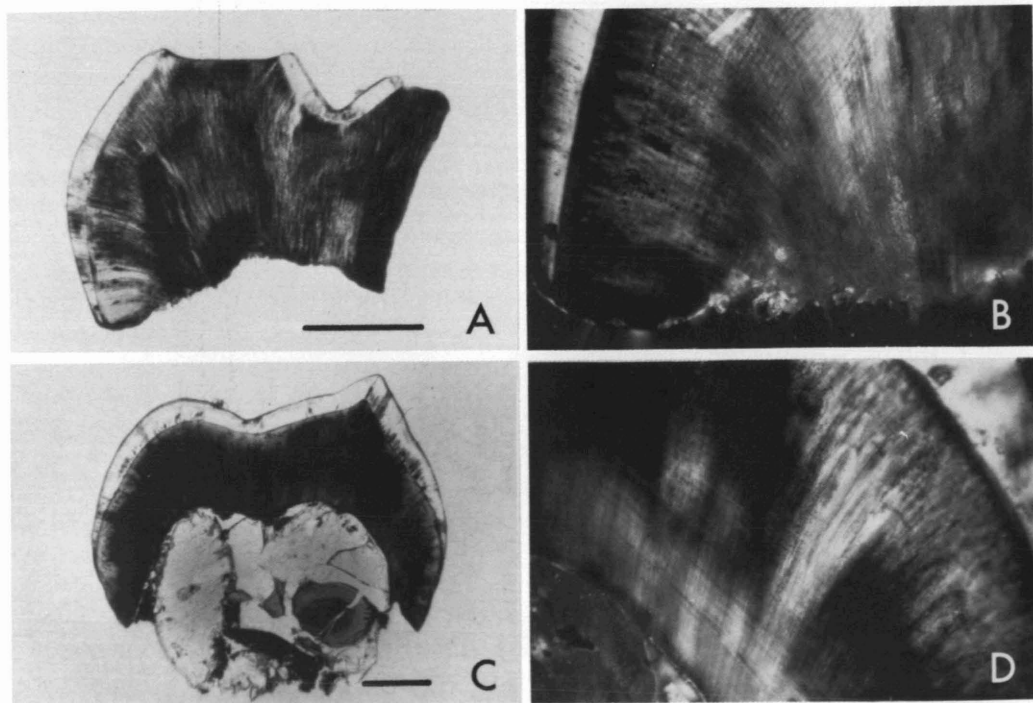


TEXT-FIG. 2 — Thin sections of shark teeth from the Shotgun local fauna. A. Shark tooth with only incipient development of trabecular dentine in core of crown; most of crown filled by sediment. B. Shark tooth with crown almost filled by trabecular dentine, but no base yet formed. C. Shark tooth with complete base. Scale: all sections 20x; scale bar in A equals 1 mm.



Enamel on the larger mammalian teeth is almost always well preserved. Clearly defined and frequently striated attrition facets on the occlusal surface of some teeth demonstrate that at least these surfaces have not been modified (at this level of analysis) by *post mortem* mechanical or chemical effects. Original, small scale topographic features, such as the enamel crinkling typical of many mammalian teeth, are frequently preserved. Occasionally, enamel is somewhat "crazed" (fractured normal to its surface, in a fairly regular, reticulate pattern), and in some instances, small patches of enamel have spalled off the dentine core. These conditions may be partly related to desiccation during subaerial exposure (through differential shrinkage of dentine and enamel), though in some extant mammals enamel crazing begins to develop even during the life of the animal. A cursory examination of patterns of enamel spalling on Recent and fossil teeth suggests that they vary with some taxonomic regularity, and that they may be related to the microanatomy of the enamel-dentine junction. In any case, we are dealing here with local loss of *fragments* of enamel, rather than a more diffuse attrition of the enamel surface. Furthermore, these fragments are frequently detached along an irregular surface lying slightly *internal* to the enamel-dentine junction. This type of enamel loss is recognizable as a mechanical, as opposed to a chemical, phenomenon.

The dentine of Shotgun mammal teeth is usually extremely well preserved (Fig. 3). However, in some cases it has been modified by the growth of fungi. There is a more or less complete range



TEXT-FIG. 3 — Thin sections of mammal teeth from the Shotgun local fauna. A. Fragment of a deciduous premolar of an unidentified placental mammal; pulp surface of dentine shows clear evidence of resorption: development of Howship's lacunae and discordant relationship between pulp surface and incremental lamination in dentine; note wear on cusp, and the normal recession of the exposed dentine surface below the enamel margin; 16x. B. Detail of A; enlargement of Howship's lacunae and incremental laminations; 48x. C. Incompletely formed tooth of an unidentified placental mammal; 9x. D. Detail of C; note concordance of pulp surface of dentine and incremental lamination within the dentine; 48x. Scale bar in A and C equals 1 mm.

of degrees of modification, but in the most extreme cases, the dentine looks almost 'chalky' in reflected light, and dentinal tubules and incremental laminations are obscured in plain transmitted light. Even in these teeth though normal dentine histology and patterns of extinction are seen when viewed between crossed nicols. Although the excavations of fungal hyphae may be extensive, they seem to have left the remaining dentine structurally unaltered. They are now represented by narrow, meandering voids with a diameter of about  $2-4\mu$  (c.f. Marchiafava et al., 1974), distributed with varying density throughout the dentine. As noted by Sognnaes (1963), fungal decalcification does not affect tooth enamel directly. However, examination of Shotgun teeth suggests that fungal modification may make enamel more prone to spalling.

The only remaining evidence that might be interpreted as indicating *post mortem* abrasion or corrosion of teeth (and particularly of dentine) involves certain cases in which roots are missing. This is discussed in the context of the teeth of small mammals.

*Small mammal teeth.*—Teeth of the smaller mammals are preserved similarly to those of larger mammals, except that breakage is much less frequent, and enamel damage is rare. This difference may be due largely to the less severe consequences of desiccation and shrinkage at smaller absolute size.

Because the crowns of small mammal teeth tend to be whole, they offer a clearer record of the fate of roots than do larger teeth. Four general preservational classes can be distinguished: 1) whole teeth with roots well preserved; 2) teeth with roots broken along a distinct fracture surface either before permineralization or after; 3) teeth with roots completely or partly absent (without topographic indication of fracture), and with significant portions of the dentine surface truncating incremental laminations within the dentine; and 4) teeth with roots completely or partly absent, pulp cavity open, and the dentine surface concordant with incremental laminations within the dentine (except for some fracture of the thin wall of dentine extending toward where the roots should be).

The teeth that correspond most closely to McGrew's description of the typical condition of Shotgun small mammal teeth are those of the third and fourth classes. In the third class, the discordant relationship between the surface of the dentine exposed at the base of the tooth and lamination within the dentine suggests that this is a destructive rather than a constructive surface (Text-fig. 3A,B). However, as an alternative to McGrew's hypothesis that dentine destruction occurred after the death of the animal, it could be interpreted as having occurred during the life of the animal—as resorption associated with the replacement of the deciduous dentition. If dentine destruction occurred after death, it should have affected dentine exposed on the occlusal surface (on attrition facets) in addition to that exposed on the roots. This would lead to recession of a dentine 'inlier' beyond what is normally encountered as a result of the differential resistance of enamel and dentine to masticatory attrition. I have not seen such a condition on any teeth (cf. Text-fig. 3A). On the other hand, if dentine destruction occurred as resorption, these teeth should show evidence of at least moderate occlusal wear and should have the crown morphology (and root morphology, where it is both diagnostic and at least partly preserved) of deciduous teeth. In all cases I have examined, these expectations are met. Finally, the interpretation that these teeth were being resorbed during the life of their producer is confirmed by thin sections (Text-fig. 3B) which show the characteristic topography of Howship's lucanae (occupied in life by individual osteoclasts; Sicher and Bhaskar, 1972; Scott and Symons, 1974) developed along the receding surface of the dentine.

Turning to the fourth preservational class, it seems unlikely that any chemical, mechanical, or biological process would neatly 'peel off' complete laminae. Thus, dentine surfaces that are perfectly concordant with incremental lamination are almost certainly *constructional* (Text-fig. 3C,D). The teeth in this class are most easily interpreted as incompletely formed. Predictably, they show at most only the beginnings of occlusal attrition, and they of course grade into the first and second classes.

There is one additional type of preservation that I have noted on Shotgun small mammal teeth, though it occurs on fewer than one percent of the specimens (approximately thirty examples in the MCZ collections). These teeth are usually complete and well preserved except that they have no enamel. They are thus almost the antithesis of the type of preservation that McGrew described as common in the Shotgun local fauna, and that he supposed had been produced by crocodylian digestion. It is thus ironic that they, of all the types of preservation represented here, most nearly resemble teeth retrieved from the feces of living crocodylians (Fisher, 1981a). Because of the complexity of problems involved in their interpretation, and the distinct difference between their mode of preservation and that of all other Shotgun material, they will be discussed in detail elsewhere (Fisher, 1981b).

The teeth of vertebrates other than sharks and mammals (e.g. those of crocodylians or osteichthyans) tend to be preserved in a manner similar to small mammal teeth. One qualification, however, is that as might be expected, I have seen no evidence of fungal destruction of osteichthyan dentine. In all teeth whose pulp cavities are filled by sediment (except for trivial cases in which the opening of the pulp cavity is too small to admit the full range of grain sizes), this sediment is identical to that which surrounds the teeth.

## DISCUSSION

The primary goal of this analysis has been to evaluate McGrew's (1963) interpretation that the Shotgun local fauna represents a concentration of crocodylian fecal residues. The original basis for this interpretation was observation of abrasion and corrosion of bone fragments, high incidence of breakage of bones and teeth (especially among large mammal teeth), and absence of some dentine from many teeth (especially those of sharks and small mammals). In contrast, my qualitative evaluation is that fresh to moderately weathered bone fragments are much more common than fragments showing well developed abrasion or corrosion. The incidence of breakage is undeniably high, but has at least as adequate an explanation in normal processes of weathering and transport. Dentine is indeed absent from some teeth, but in all cases I have observed, this may be confidently interpreted as the result of death prior to completion of dentine deposition, or of resorption associated with tooth replacement. The observations discussed here thus provide no basis for preferring the crocodylian fecal concentrate hypothesis over alternative interpretations.

This result is confirmed by analysis of feeding experiments reported by Fisher (1981a), in which crocodylians are shown to decalcify ingested calcified tissues, while often leaving their organic matrices intact. Dentine, cementum, and bone matrices may be preserved in some cases by remineralization, but decalcification completely destroys enamel and similar tissues. Teeth defecated by crocodylians and subsequently remineralized are therefore usually completely enamel-less. Most material in the Shotgun local fauna—and most material in other micro-vertebrate concentrations as well—thus differs strikingly from the expected appearance of crocodylian digestive residues. Only the rare enamel-less teeth in the Shotgun local fauna appear to have any relation to crocodylian digestion.

Other interpretations of the taphonomy of the Shotgun local fauna remain viable, but will require additional characterization and testing. As noted by Mellett (1974), many micro-vertebrate concentrations, including this one, show a certain resemblance to fecal residues of mammalian carnivores. However, additional description of such residues, preferably at both gross and microscopic scales, is desirable. In the case of the Shotgun local fauna, the variety of stages of weathering and fungal alteration indicates that even if most material was processed by mammalian carnivores, it also experienced, to a variable degree, a subsequent history of

weathering and decomposition during early burial. In fact, it is possible that microvertebrate concentrations such as this develop without significant intervention by predators. Relatively simple variations on the theme of death-exposure-transport-burial, such as a short period of temporary burial (which would allow decomposition of much organic material), followed by exhumation, moderate transport, and final burial, could produce much more bone breakage and isolation of teeth than would occur during transport and burial of fresh material. What is needed to distinguish between these and other possible mechanisms is quantitative, experimental work directed toward characterization of the suites of preservable material that they would produce. The qualitative nature of the present investigation, although adequate for evaluation of the crocodylian fecal concentrate hypothesis, allows only the most tentative conclusions as to the actual taphonomic history of the Shotgun local fauna. The preservation of material appears to be consistent with interpreting this fauna as a fluviually concentrated attritional assemblage derived from material that was either: 1) present in the local aqueous environment; 2) exposed subaerially; or 3) subjected to temporary burial and slight reworking. The observed relationships of fossil specimens and sediment matrix argue against reworking of material from significantly older, consolidated sediments as an explanation for the high diversity of the Shotgun local fauna.

#### ACKNOWLEDGMENTS

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