Crocodilian scatology, microvertebrate concentrations, and enamel-less teeth

Daniel C. Fisher

Abstract.—It has been suggested that certain fossil assemblages consisting of disarticulated and broken remains of small to medium-sized vertebrates ("microvertebrate concentrations") may be accumulations of incompletely digested material defecated by crocodilians. Experiments on crocodilian digestion show, however, that these reptiles demineralize calcified tissues, frequently leaving intact organic matrices of dentine, cementum, and bones in their feces. Such matrices, even if preserved as fossils, would not resemble most specimens in microvertebrate concentrations. Therefore, crocodilian digestion does not appear to have been an important factor in the formation of these fossil assemblages. Teeth similar to those defecated by crocodilians nevertheless do occur in the fossil record. Such teeth, lacking enamel but often complete in other respects, are interpreted here as having been digested by crocodilians, defecated as demineralized organic matrices, and subsequently remineralized. Enamel, with its extremely low organic content, does not yield a demineralized matrix susceptible to remineralization. A number of recently recognized occurrences of enamel-less teeth attest to the significance of crocodilian digestion as a factor in the taphonomic history of many Mesozoic and Cenozoic fossil vertebrate assemblages.

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Introduction

Microvertebrate concentrations are a distinctive mode of fossil occurrence consisting of accumulations of small, disarticulated or broken bones and isolated teeth (Mellett 1974). They are known from a variety of geographic locations, stratigraphic intervals, and depositional environments, especially those sampling a terrestrial biota. In many cases they are almost the only source of information on species having a body size less than about 5 kg—a category that includes many ecologically and phylogenetically significant taxa (particularly small mammals during the Cretaceous and Paleogene). For this reason, much speculation and analysis have focused on the taphonomic history of microvertebrate concentrations. Although non-biological processes (e.g. hydraulic concentration; Dodson 1971; Wolff 1973) have been considered as possible mechanisms of concentration, much recent attention has been given to suggestions that microvertebrate concentrations represent accumulations of incompletely digested remains of prey, defecated or regurgitated by predators (e.g. Mellett 1974; Mayhew 1977). One version of this hypothesis is that crocodilians were the predators responsible for such accumulations

(e.g. Weigelt 1927; Simpson 1937; McGrew 1963). Crocodilians are indeed known from many of the faunas represented by microvertebrate concentrations and are plausible concentrators of a wide variety of vertebrate remains in association with an aquatic (generally non-marine) depositional setting. If accepted, this hypothesis would have obvious implications for the trophic relationships and autecology of fossil crocodilians and their prey. In addition, whether accepted or rejected, it would affect analyses (e.g. of faunal composition or community structure) that depend on some understanding of the bias implicit in the faunal sample preserved in a microvertebrate concentration.

The hypothesis that microvertebrate concentrations consist of material sorted and concentrated from disaggregated crocodilian feces was defended in detail by McGrew (1963), in a description of the Paleocene Shotgun local fauna, a microvertebrate concentration from the Fort Union Formation in the Wind River Basin, Wyoming. McGrew's taphonomic interpretation was based partly on the fragmentary state of most material but primarily on his observation of apparent "corrosion" of many bone fragments and tooth roots, though the enamel of the

same teeth was usually in excellent condition. He described this type of preservation as particularly characteristic of the teeth of the small mammals and sharks in the fauna. McGrew evidently reasoned that since tooth enamel (or the vitrodentine of shark teeth) is more resistant to abrasion than is dentine (trabecular dentine of sharks), it would also be more resistant to dissolution and destruction during digestion. Thus, tooth crowns (except when fractured) would be relatively protected and would tend to survive digestion intact, while tooth roots and bone fragments would be subjected to the unmitigated effects of digestion. Given this, McGrew's taphonomic interpretation is by no means implausible. The diet of extant crocodilians commonly includes mammals but often includes other taxa as well. On the basis of both body size and inferred habits, it is conceivable that the Shotgun crocodilians could have fed on members of any other species in the fauna.

Acceptance of this interpretation of the fossil concentrations clearly depends on acceptance of the above assumption concerning the effects of crocodilian digestion on calcified tissues. The observations and experiments described in this paper were undertaken to evaluate this assumption directly and to determine whether potentially preservable material defecated by crocodilians bears an unambiguous signature of its history. If criteria can be developed for the recognition of crocodilian fecal residues, they will be useful both for testing one interpretation of the genesis of microvertebrate concentrations and for analyzing evidence for crocodilian predation elsewhere in the fossil record.

Food Processing in Crocodilians

Previously published accounts of crocodilian digestive processes all agree that bones and teeth are completely digested (Gadow 1901; McIlhenny 1935; Cott 1961; Neill 1971; Skoczylas 1978). It is stated or implied that no trace of mineralized tissues is left in the feces. However, this conclusion is apparently based on very little direct inspection. For instance, Cott's (1961) account is based primarily on observation of stomach contents. He found the stomachs of recently killed crocodiles in a series of states which were presumed to represent progressive stages of digestion: (1) partially full of fresh, nearly un-

digested prey; (2) soft tissues more or less liquified, and calcified tissues "in all states of digestion"; (3) only materials of keratinous or chitinous composition remaining; and (4) empty. Cott (and others) assumed that since bones and teeth disappear from the stomach and have not been evident on cursory inspection of feces, they must have been completely destroyed. This unanimity is almost as complete concerning the fate of keratinous or chitinous tissues, which are supposedly defecated without alteration of composition or condition. This view is based both on analysis of stomach contents and on the discovery of compacted masses of hair, claws, insect cuticle, etc. in association with crocodilians (e.g. Cott 1961; Neill 1971).

These views were also substantiated by individuals experienced in maintaining crocodilians (see Acknowledgments). The only contradictory observations were offered by F. W. King, who had noticed teeth and bones in crocodilian feces (only in about five percent of all defecations; pers. comm. 1970), and by R. A. Coulson, who had observed that rat teeth were often found in the tanks used to house alligators fed on rats (pers. comm. 1970). These teeth had presumably been defecated, but no distinctive features were noted on them.

If the generally accepted characterization of crocodilian digestion is correct, there is little reason to expect any fossil record of calcified tissues ingested by crocodilians. However, experimental testing of this conclusion is desirable.

Procedure.—In order to determine more precisely the fate of material ingested by crocodilians, I conducted a series of feeding experiments with four individuals of each of two species, *Alligator mississippiensis* (total body length: 45 cm, 75 cm, 1 m, and 1.6 m) and *Caiman crocodilus* (total body length: 45 cm, 70 cm, 70 cm, and 1 m). The experiments involved recording information on all material ingested by each animal, and all material either regurgitated or defecated. The duration of feeding experiments on a given individual varied from two months to about one year, with defecation and regurgitation occuring at approximately one week intervals in the alligators, and 2–3 week intervals in the caimans. The diet of these animals consisted of laboratory mice or rats (depending on the size
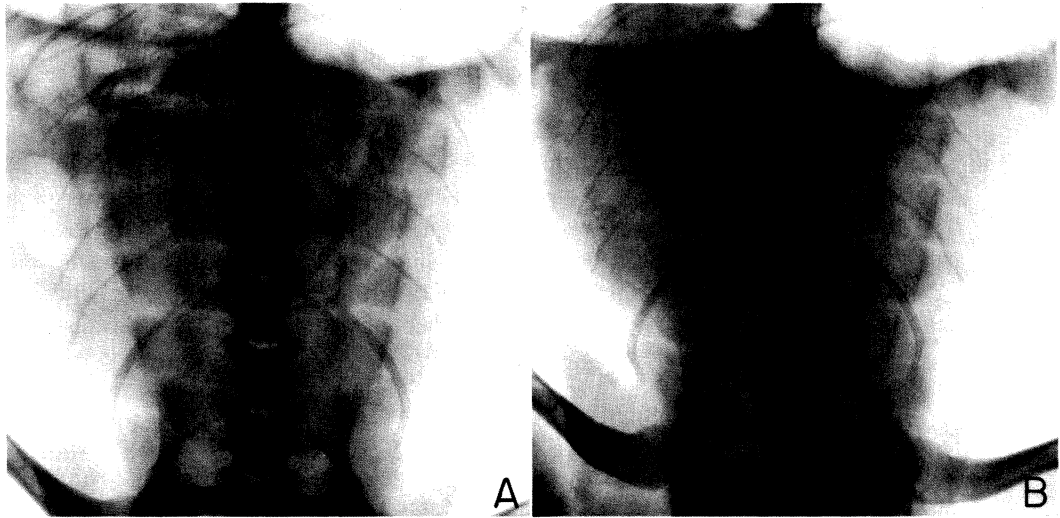
FIGURE 1. X-rays of *Caiman crocodilus* bracketing decalcification of an ingested mouse; caiman was undisturbed (at 25°C) between time of feeding and first x-ray, and between first and second x-rays; dorsoventral aspect. A. Abdominal region of *C. crocodilus* (anterior toward top) showing ingested mouse within fundic portion of stomach; mouse skull is directly under the vertebral column; 4 hr after feeding. B. Mouse has been completely decalcified; 24 hr after feeding.

of the crocodilian) old enough to have well ossified bones and a fully erupted dentition. I have assumed that the bones of mice and rats would be comparable to those of most small mammals. However, mouse and rat teeth do not represent as broad a spectrum of sizes and morphologies as would be useful to examine. Nor do mouse and rat 'parts' cover the full range of composition and structure represented within other potential prey. Therefore, I occasionally inserted extraneous items (no more than two at a time) into the visceral cavity of a recently killed 'prey' before offering it to the intended 'predator.' These 'dietary supplements' included isolated teeth of muskrat (*Ondatra zibethicus*), vole (*Microtus* sp.), cat (*Felis domesticus*), raccoon (*Procyon lotor*), rhesus monkey (*Macaca mulatta*), and an unidentified shark. In addition, a crushed muskrat skull, a complete vole mandible, a partial rhesus monkey mandible, and gar scales (*Lepisosteus* sp.; both isolated and in articulated series) were included. Shed alligator epidermal scales, feathers, insect cuticle, gastropod opercula, gastropod shell fragments, eggshell fragments, and pieces of wood fiber comprised the non-osteological inclusions.

Additional information and documentation was provided by high resolution x-ray plates of the abdominal region of one of the experimental animals, taken at regular intervals during its digestive cycle (Figs. 1, 2). In order to supplement these observations, and extend them to other crocodilians, I have dissected the alimentary tracts of a number of preserved specimens: *Alligator mississippiensis* (2 individuals); *Caiman crocodilus* (3); *Caiman latirostris* (3); *Melanosuchus niger* (1); *Crocodylus acutus* (1); *C. johnstoni* (1); *C. novaeguineae* (1); *C. palustris* (1); *Osteolaemus tetraspis* (1).

Feeding.—The movements associated with prey capture and ingestion have been described previously (e.g. Neill 1971). Prior to swallowing, crocodilians systematically work their prey back and forth in their mouth, biting down on all parts of it. It is usually implied that the purpose of this is to crush the bones of the prey. If true, this would be consistent with McGrew's suggestion that crocodilians produced the extreme fragmentation of Shotgun skeletal material. However, jaw adduction during this phase of prey manipulation, at least under the conditions of my observations, was never forceful or complete. X-rays of recently ingested mice show very little bone breakage (Figs. 1A and 2A). Crocodilians may even be vulnerable to injury by bones broken prior to swallowing, and might therefore be expected to avoid extensive bone breakage. Coulson (pers. comm. 1970) reports

that captive alligators fed on chopped rabbit carcasses occasionally suffered fatal esophageal punctures from broken rabbit bones. This risk might indeed vary with the size and tooth morphology of the crocodilian and the size of the prey. In general, I would expect an increased incidence of bone breakage with increased bluntness of crocodilian teeth and increased relative size of the prey. Nevertheless, jaw adduction does not always produce extensive bone breakage. The 'mouthing' that prey items receive is partly related to inertial swallowing, but it is also possible that the epithelial punctures that it produces in the prey allow accelerated access of digestive fluids to internal tissues. A similar suggestion has been made for some snakes, by Pough (1977).
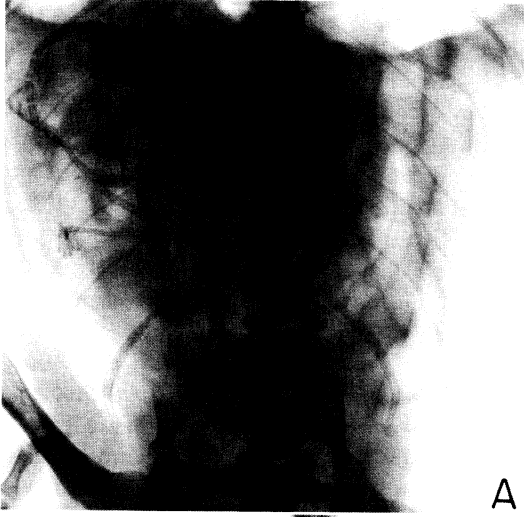
Digestive processes.—While observations on the residues of crocodilian digestion provide only indirect evidence on the nature of digestive processes, they do offer important insight into the fossilization potential of crocodilian prey. These digestive residues include both material that is regurgitated and material that is defecated. Regurgitated material consists almost entirely of tissues of keratinous or chitinophosphatic composition (hair, claws, feathers, insect cuticle, etc.). These retain their original color and texture and (except when brittle) have not even been mechanically altered. Prior to regurgitation, all of these materials are compacted into a large number of generally ellipsoidal hairballs. Although such masses of hair have been previously described, it has usually been assumed that they were defecated (e.g. Neill 1971, p. 302). The only published accounts of regurgitation of hairballs by crocodilians (Petzold 1959, 1967) have received little recognition. In addition to my own observations, however, at least one other person (C. O. daC. Diefenbach) has independently observed hairball regurgitation (C. Gans, pers. comm. 1972), though it was not regarded as normal behavior (Diefenbach 1975a). The mechanism of hairball formation will be discussed elsewhere (Fisher in prep.).

Crocodilian feces are composed predominantly of dark brown, very fine grained, homogeneous, organic material, compacted into fusiform masses. Occasionally, very small amounts of hair are included within the feces, but this usually accounts for less than one per-
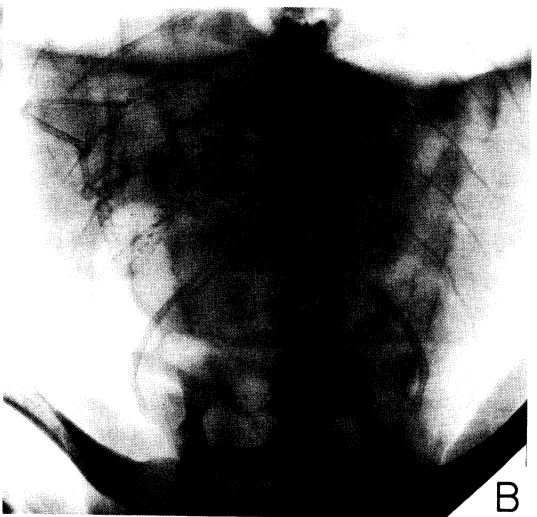
cent of the hair that has been ingested and that is eventually regurgitated as hairballs. If the feces are deposited within a relatively aerobic environment, and if they are not examined within about two days of their deposition, no other inclusions are usually evident. It is thus not surprising that most previous accounts record no trace of calcified tissues. However, if the feces are disaggregated promptly and examined closely, the remains of teeth and bones frequently can be recovered (Fig. 3). The most distinctive feature of these teeth and bones is that they have been decalcified. All that is usually left is the organic matrix of the original calcified tissue. In the case of teeth and bones that were recovered very soon after defecation, the organic matrix was often completely intact, with a firm, rubbery consistency. Other teeth and bones occurred in a range of conditions that I interpret as progressive stages of bacterial decomposition. In the earlier stages, a surface layer of the decalcified structure acquired a porous, spongy texture which could be easily deformed or torn away. Later, this texture spread to the entire structure. Further decomposition resulted in vague wisps of collagenous material and eventual total disappearance. If the feces were left within the pool of water in which defecation usually occurred, this complete transformation took place within about two days.

The defecated organic matrices of bones vary in completeness. Some of the denser or more robust skeletal elements (e.g. femora, humeri, mandibles, or astragali) are often complete and have only slightly subdued surface features. Less robust bones often occur in pieces (Fig. 3C). These rarely show discrete breaks such as would have developed before decalcification. Rather, they appear to have developed by tearing of the decalcified matrix while it was intact or just beginning to decompose. In some cases, decomposition seems to have begun even prior to defecation. Decalcification of bones is almost always complete; only a few (less than ten percent) of the mandibles show a residual, nondecalcified core of bone.
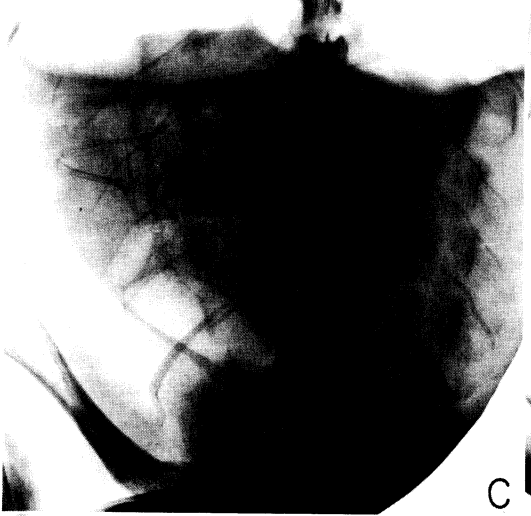
Teeth recovered from the feces are usually isolated, unless root morphologies prevent them from sliding out of their alveoli. In overall topography, teeth may almost seem unmodified. However, their external crown surface is ac-
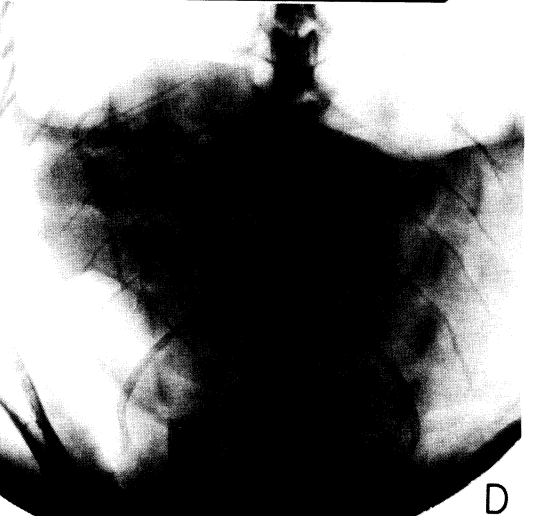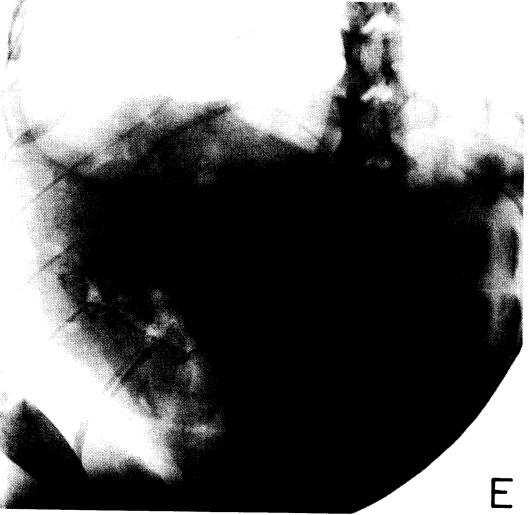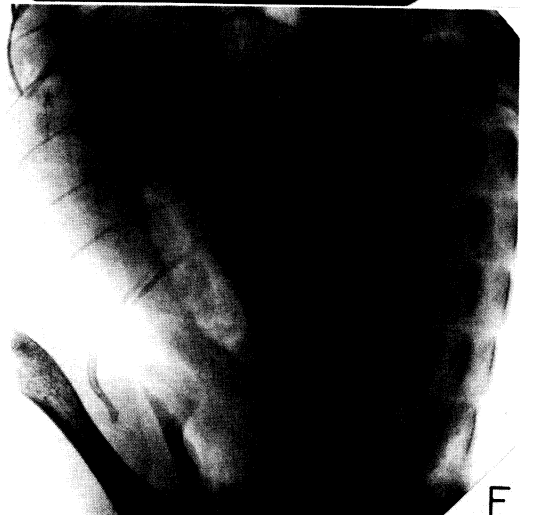
tually the enamel-dentine interface of the original tooth. Decalcification during digestion (just as during preparation of histologic sections) completely destroys the enamel (Fig. 3A, C, D). Since intact enamel has only 2–4% organic matrix, by weight, as opposed to about 28% for dentine, cementum, or bone (Sicher and Bhaskar 1972, p. 39), its decalcification leaves virtually no tissue behind. The vitrodentine of shark teeth and the ganoine layer on gar scales also have very little organic matrix and are similarly destroyed.

In those cases where teeth are retained in their alveoli, there is sometimes incomplete decalcification, especially where adjacent teeth contact each other, resulting in residual patches of enamel in these areas (Fig. 3F). Since it is unlikely that the enamel on this portion of the tooth is distinct chemically or structurally, this pattern of enamel retention may result from the reduced circulation of digestive acids and the reduced exposure of enamel surface at the point of contact of adjacent teeth. This pattern would be accentuated if enamel decalcification occurs preferentially in a direction parallel to enamel prisms.

As occasionally happens with bones, relatively robust teeth may retain a core of non-decalcified dentine. For a fully formed tooth, this is located within the crown, next to the pulp cavity. In the feeding experiments, a core was retained only in teeth that were derived from 'prey' that would have been too large, as whole animals, for the crocodilian to have swallowed

(e.g. the cat carnassial, Fig. 3E, fed to the 75 cm *A. mississippiensis*). Further observations would be necessary to determine the frequency of incomplete decalcification under natural conditions. However, present data indicate that most decalcification is complete.

Dissections of preserved specimens of the two crocodilian species used in these feeding experiments help to elucidate certain aspects of the processing of indigestible prey tissues. Crocodilians have a relatively simple alimentary tract (Reese 1913; Guibé 1970). The esophagus opens into a large, muscular, fundic portion of the stomach, which is followed by a much smaller, but still very muscular, pyloric portion. The fundic and pyloric portions are separated only by a sphincter-like closure, but the pyloric portion and the intestine are separated by a moderately complex, vestibular valve. Distal to this are the small intestine, large intestine, caecum, and cloaca. The individuals I dissected had been wild and were killed at different times (presumably by chance) relative to their last meal. As with the series of animals described by Cott (1961), they represented more or less stop-action views of the process of digestion. In almost all cases, the pyloric portion of the stomach was empty. Hairballs, dissociated hair, claws, and cuticle, any gastroliths that were present, and undigested and partly digested prey occurred within the fundic portion of the stomach. Dissection of the intestine, caecum, and cloaca failed to reveal any sign of hairballs. This supports the conclusion, derived from ob-

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FIGURE 2.   X-ray sequence showing *Caiman crocodilus* (kept at 25°C) decalcifying an ingested mouse; note movement of mouse within fundic portion of stomach and gradual decalcification of mouse bones; light region at top of photographs is lung; pelvis is at bottom of photographs; dorsoventral or oblique dorsoventral aspect. A. Abdominal region of *C. crocodilus*, with mouse (head beneath vertebral column; hindquarters and tail to left), taken 1 hr after ingestion; no evidence of decalcification; light tracts in this and other x-rays are gas accumulations within the intestine. B. 12.5 hr after ingestion (three sessions of handling and x-rays intervened between this and A); parts of the cranium and the anterior lumbar vertebrae are beginning to decalcify. C. 14.5 hr after ingestion (no intervening sessions); all four feet, the radii, and the ulnae are beginning to decalcify. D. 20.5 hr after ingestion (two intervening sessions); the tibiae-fibulae and some of the thoracic vertebrae and ribs are beginning to decalcify. E. 27 hr after ingestion (no intevening sessions); the distal humeri, distal femora, most caudal vertebrae, and most ribs have now been decalcified. F. 35.5 hr after ingestion (one intervening session); mouse body has separated into at least five regions, of which the remaining visible parts are: (1) mandibles, premaxillae, maxillae, teeth (beginning to decalcify), otic region, and several cervical vertebrae; (2) posterior cervical and anterior thoracic vertebrae, possibly still associated with one scapula and humerus (partly decalcified); (3) the other humerus (partly decalcified), probably still articulated with its scapula; (4) one half of pelvis (partly decalcified), femur (half decalcified), sacrum, and several lumbar vertebrae; and (5) other half of pelvis (partly decalcified) and femur (half decalcified). By the next sequence (8 hr later), no trace of this mouse was visible. The longer time required for complete decalcification in this instance, relative to the meal illustrated in Fig. 1, is probably due to the more frequent handling of the caiman.
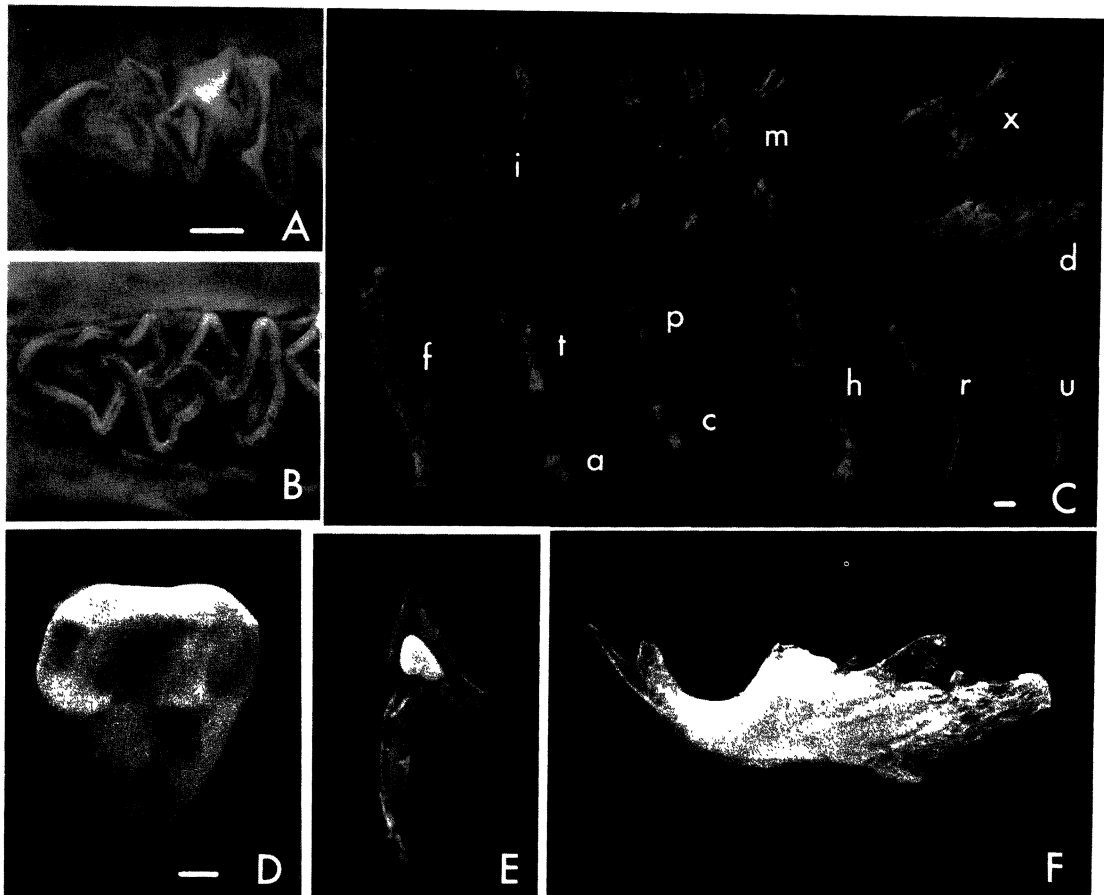
FIGURE 3. Digestive residues (except B) of *Alligator mississippiensis*. A. Right M^3 of muskrat (*Ondatra zibethicus*); all enamel destroyed, and dentine decalcified, by digestion; organic matrix preserved in alcohol; occlusal view, anterior to right; 7×. B. Undigested right M^3 of muskrat; compare with A, same orientation; 7×. C. Representative decalcified mouse bones and teeth (fixed in alcohol and dried; now partially transparent) removed from alligator feces; a, astragalus; c, caudal vertebra; d, mandible , f, femur; h, humerus; i, incisors; m, molars; p, metapodial; r, radius; t, tibia; u, ulna; x, maxilla and partial premaxilla; 2.5×. D. Right dP^4 of rhesus monkey (*Macaca mulatta*); all enamel destroyed, and dentine decalcified, by digestion; organic matrix preserved in alcohol; occlusal view, anterior to right; 5×. E. Right P^4 (broken, fixed in alcohol, and dried) of cat (*Felis domesticus*), incompletely decalcified by digestion; all enamel has been destroyed, and most dentine has been decalcified, but a core of undecalcified dentine remains; 5×. F. Left dentary of mouse, incompletely decalcified by digestion; although atypical (this is the least thoroughly decalcified dentary retrieved during the feeding experiments), this specimen demonstrates the preservation of some enamel on the proximal, alveolar portion of the incisor, and as patches surrounding areas of contact between the molars; dentine immediately underlying this enamel has been decalcified; 5×. Scale bars in A, C, and D equal 1 mm.

servation of the captive animals, that hairballs are almost always regurgitated rather than defecated. This implies the existence of some mechanism, acting within the general region of the stomach, which acts to segregate residual tissues by their composition (or other associated properties). Portions of the alimentary tract distal to the stomach were never observed to contain non-decalcified tissues. This and the fact

that calcified tissues were present in the fundic region in all stages of decalcification, suggests that decalcification occurs within the fundic region. This is not surprising since this region of the stomach is the site of hydrochloric acid secretion (Staley 1925; Skoczylas 1978) and has been observed to have a pH as low as 1.2 (Diefenbach 1975b). Decalcification within the fundic region was also confirmed by the x-ray

plates. Plates taken only a few seconds apart, from both dorsoventral and lateral aspects, at intervals throughout digestion, make it possible to map the movement of x-ray opaque objects within the viscera (Figs. 1, 2). After swallowing, prey skeletons reside in the fundic portion of the stomach. They tumble in association with stomach contractions, but no change is usually evident in skeletal tissues until eight to twelve hours after ingestion. At this point x-rays begin to show the first signs of decalcification. This proceeds according to the size and compactness of structures, with teeth, mandibles, maxillae, and the most robust limb elements being the last to become transparent to x-rays, still without leaving the fundic portion of the stomach. The entire process of decalcification usually required about one day (though this varied with the amount of disturbance to which the animal was subjected; cf. Figs. 1 and 2; Gans [1976] notes similar effects). Throughout this time, breakage of bones was not observed, confirming the suggestion of post-decalcification tearing noted above.

One unexpected result of the dissections was that no definitely identifiable decalcified organic matrices were found within the intestine, caecum, or cloaca. Although this would appear to confirm the traditional view that these tissues are completely digested, their defecation by live animals is indisputable. Since none of the dissected individuals showed evidence of having been carefully perfused or otherwise fixed immediately following death, it may be that enough time elapsed between death and the penetration of preservative to the intestinal contents, to allow the organic matrices to decompose. Such decomposition would probably be more rapid within the intestine (because of its relatively high bacterial content and its relatively low acidity; Skoczylas 1978) than within the stomach.

Retrieval probability of calcified tissues.—Although decalcified prey tissues frequently occur in crocodilian feces, the retrieval of ingested calcified tissues is never complete. It varies considerably from time to time, individual to individual, and particularly between the two species used in the feeding experiments. All of the caimans had much lower retrieval records

than the alligators. The probability of retrieval of different anatomical parts seems to vary according to their robustness (i.e. their resistance to breakage, tearing, and decomposition). For variation between meals, individuals, and species, three possible explanations are apparent. One involves incompleteness of compositional segregation of residual tissues. Just as some hair occasionally appears in the feces, some decalcified organic matrices may be incorporated into hairballs. If this happens, these matrices are eventually destroyed within the acidic environment of the stomach. I have disaggregated hundreds of regurgitated hairballs and have never found any clear trace of bones or teeth. A second possibility, related to the first, is that variation in retention time in the stomach may even affect the retrievability of matrices that are not incorporated into hairballs. A third possibility is based on the suggestion that bacterial decomposition may begin internally. If this is an important process, its consequences should become more pronounced with decreased gut passage rate. Either of the latter two explanations may apply to the interspecific differences observed here. Previous biochemical experiments have shown that caimans retain food in their stomach much longer than do alligators (Skoczylas 1978, p. 596). In addition, all four caimans used in the feeding experiments reported here had slower passage rates (measured as either elapsed time from ingestion to defecation of some distinctive inclusion, or time required for the first defecation, after the first meal, following a period of mild starvation) than did the alligators.

Extension of results.—Although my observations have concentrated on relatively small individuals, the results are identical across a size range that includes the 1.6 m alligator. This suggests that I am not just dealing with idiosyncrasies of juvenile physiology. This is corroborated by the published and verbal observations of other workers. If adult crocodilians did not decalcify bones and teeth, Cott (1961) would not have found them "in all states of digestion," and they should have been seen more often in the feces of zoo animals maintained on whole animal diets. On the other hand, if bones and teeth were always complete-

ly destroyed, King and Coulson could not have found them. Thus, present information suggests that both juvenile and adult crocodilians decalcify calcified tissues and at least occasionally defecate intact organic matrices.

My dissections of other species revealed no conspicuous interspecific variation in the anatomy of the alimentary tract, and offered no reason to expect physiological differences. The location and condition of food material within each individual was consistent with the present description. I would therefore tentatively extend these results to other extant species. Extrapolation to fossil crocodilians seems justifiable as a working hypothesis.

Fossilization Potential of Crocodilian Digestive Residues

Even though recognizable remains of bones and teeth are sometimes found in crocodilian feces, the potential for these to become part of the fossil record seems at first to be exceedingly slight. The cores of incompletely decalcified teeth and bones might be preserved relatively easily, but completely decalcified material, more characteristic of crocodilian digestive residues, would be apt to decay before it could be preserved. Prospects for preservation are better if the fresh feces are deposited in an anaerobic environment. I buried three samples of alligator feces (including decalcified bones and teeth) in large, closed jars containing fine, organic-rich, black mud, crudely simulating a naturally occurring reducing environment. Samples uncovered one week after burial and one month after burial still retained tooth and bone matrices. The third sample had apparently decomposed by the time its jar was opened three months after burial, but this is not necessarily an upper limit for the survival of decalcified organic matrices under natural conditions. A mechanism for more 'permanent' preservation of matrices is suggested by the fact that the feces contain much of the calcium phosphate that was originally removed from bones and teeth. This is present in an amorphous and readily mobilizable form. Under the appropriate local reducing conditions, it may be possible to remineralize matrices before they decompose. Depending on the amount of subsequent reworking, they may or may not be retained within a recognizable coprolitic mass. Additional details of this preservational model are given by Fisher (1981b).

It is possible to use the nature and decompositional fate of defecated teeth and bones to predict some of the attributes of fossil crocodilian digestive residues. First, because enamel is destroyed by decalcification, teeth (or tooth-like structures, such as gar scales) should be enamelless, with the possible exception of residual patches of enamel centered on areas of contact between adjacent teeth. Second, because decalcification does not alter bones in such an obvious way, they will be more difficult to recognize, but should generally show subdued surface features. Third, if preserved organic matrices retain their histologic structure, they might frequently show signs of at least incipient bacterial decomposition. Finally, I would expect at least the better preserved organic matrices to be associated with reducing conditions.

Digestive Residues of Other Carnivorous Vertebrates

Before claiming diagnostic significance for the details of crocodilian digestion discussed here, it must be shown that crocodilians are unique in their treatment of vertebrate calcified tissues. A review of digestion in extant vertebrate predators is given by Fisher (1981b). Although complete digestion and various forms of incomplete digestion are common, only crocodilians are known to decalcify calcified tissues, while leaving their organic matrices intact. The closest approach to crocodilian digestive residues occurs in certain falconiformes that regurgitate pellets containing teeth from which at least some enamel has been lost, without associated dentine decalcification (P. Shipman, pers. comm. 1980). Enamel-less teeth defecated by crocodilians could be distinguished from these by evidence of dentine decalcification.

Comparison with Microvertebrate Concentrations

Most of the material in microvertebrate concentrations shows no resemblance to the predicted appearance of fossil crocodilian digestive residues. Bones, even if broken, are generally in much better condition than those recovered from feces of living crocodilians. As noted by McGrew (1963) and Mellett (1974) enamel and
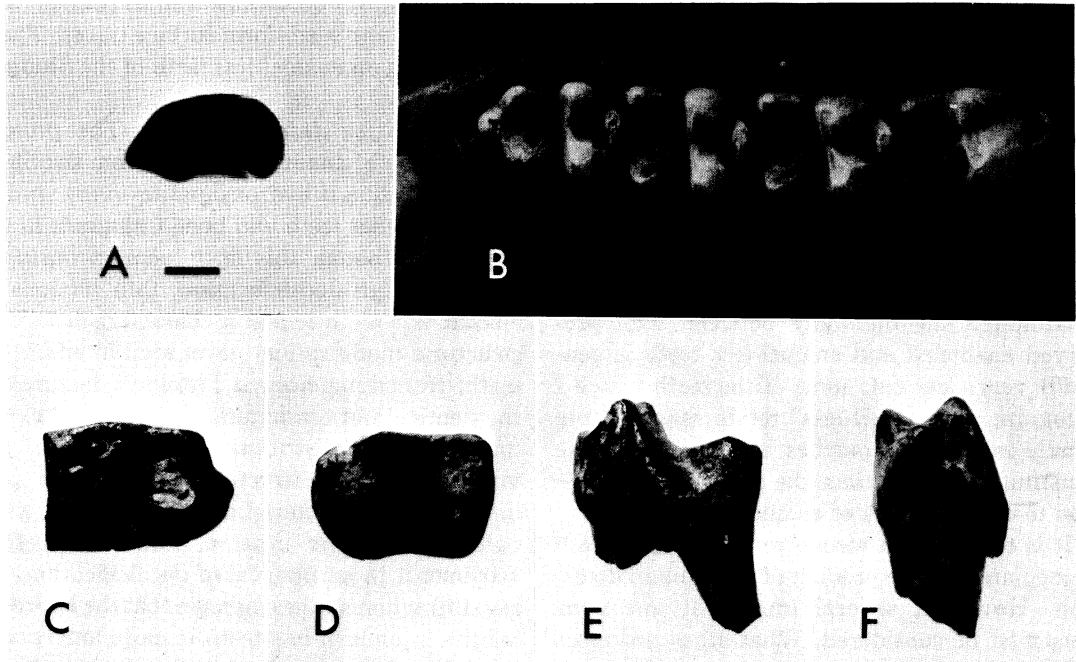
FIGURE 4. Enamel-less teeth from the Shotgun local fauna (except B). A. Completely enamel-less right M_3 of *Aphronorus* cf. *fraudator*; occlusal aspect, anterior to right. B. Partial right dentary of *A. fraudator*, showing well preserved (enamel present) P_4–M_3 (whitened cast of AMNH 35636); occlusal 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 7×; bar in A equals 1 mm.

enamel-like tissues in microvertebrate concentrations are usually well preserved. The aspects of tooth preservation interpreted by McGrew (1963) as digestive corrosion are just the opposite of what we would expect crocodilians to produce. Furthermore, thin sections of teeth from the Shotgun local fauna, conforming to McGrew's description, suggest that such teeth do not represent the effects of digestion at all (Fisher 1981a). On some of them root formation was simply incomplete; other examples are deciduous teeth whose roots were undergoing resorption at the time of death. These arguments do not, of course, reject hypotheses positing a non-crocodilian scatological origin for microvertebrate concentrations (Mellett 1974), but they do suggest that such assemblages should not be interpreted as crocodilian fecal concentrates. By way of qualification, it must be remembered that this result depends on the reasonable, but untested, assumption that crocodilians in the past dealt with calcified tissues in a fashion similar to that observed for living alligators and caimans.

Enamel-less Teeth in the Shotgun Local Fauna

Some teeth in the Shotgun local fauna do correspond closely to the predicted appearance of fossil crocodilian digestive residues. Because these teeth are extremely rare, they do not seem to compromise the idea of a non-crocodilian origin for this assemblage. I have seen approximately thirty examples of this type of preservation in the collections of the Shotgun local fauna at the Museum of Comparative Zoology, Harvard University. All of them represent small mammals. They account for less than one percent of the mammal teeth I have examined from this fauna. The teeth showing this unusual preservation are often complete (in the sense of retaining roots as well as crowns) and well preserved, except that they usually have no enamel (Fig. 4A, C). What now forms the outer surface

of the crown (based on its topography and its relation to dentinal tubules and incremental lamination, seen in thin section) is the enamel-dentine interface of the original tooth. The absence of enamel can make identification difficult, for incisors, canines, and some premolars preserved in this fashion leave little diagnostic topographic detail. Among the molars that are identifiable, the pentacodontid *Aphronorus* is most common.

Although the dichtomy between well preserved enameled and enamel-less teeth is generally very clear cut, some of the teeth which I recognize as "enamel-less" retain one or more small, interdental patches of enamel. These constitute no more than the anticipated exception to complete loss of enamel.

It is tempting to recognize enamel-less teeth immediately as the product of crocodilian digestion. However, several important questions must first be considered. What other processes might have been responsible for enamel loss? Is there evidence, independent of enamel loss, that these teeth were decalcified? Is there evidence of a reducing environment that might have retarded decomposition of their organic matrix? These questions are considered briefly below. Additional detail and documentation are given in Fisher (1981a and 1981b).

Mechanisms of enamel loss.—Perhaps the most obvious alternative explanation for enamel removal is abrasion during sedimentary transport. However, the ends of roots of enamel-less teeth and the dentine of tooth cusps are prominent, and usually unabraded, even when all enamel is removed from the crown. Subaerial weathering and desiccation may lead to enamel spalling, but this process is rare in small teeth. It also involves the detachment of fragments of enamel along an irregular surface lying slightly *internal* to the enamel-dentine junction. No diagenetic process is known to destroy enamel while leaving dentine and cementum intact. Even if some such process were postulated, it could not have operated subsequent to final burial of the Shotgun teeth, because enameled and enamel-less teeth occur together in the same deposits. Enamel loss through decalcification by plant acids is known to occur, even during recent exhumation and weathering of fossil teeth,

but this destroys dentine as well as enamel, and leaves pitted or vermiform surface traces. These are not seen on enamel-less teeth of the Shotgun deposits.

Evidence for decalcification.—The present composition of enamel-less teeth from the Shotgun local fauna is hydroxyapatite—very similar to that of other teeth and bone fragments in the deposit. Although this may seem inconsistent with thorough decalcification, thin sections of enamel-less teeth reveal a characteristic microstructural modification (never seen in enameled teeth) truncating normal histologic features of the dentine and cementum. This duplicates the nature, spatial distribution, and stages of development of the structural modification produced through bacterial decomposition of a decalcified organic matrix, and I therefore attribute it to an interval of decalcification. X-ray diffraction studies indicate that the hydroxyapatite in enamel-less teeth is more amorphous than that of enameled teeth and also that it differs in chemical composition. These differences further confirm the occurrence of decalcification, followed by remineralization.

Evidence of a reducing environment.—Most Shotgun enamel-less teeth, especially those which show the least modification by bacterial decomposition of their organic matrix, have pulp cavities filled with pyrite. Despite diligent search, I have never seen this in enameled teeth. This suggests that somewhere in their unique history, enamel-less teeth usually encountered a reducing environment that was not encountered by enameled teeth.

Taphonomic interpretation of enamel-less teeth.—It now seems most probable that enamel-less teeth lost their enamel through decalcification of the whole tooth. Some process affected Shotgun enamel-less teeth in the way that crocodilian digestion affects teeth today, and these results are not duplicated by any other known process. The identification of enamel-less teeth as the result of crocodilian digestive processes therefore seems appropriate. It is clearly most parsimonious to attribute to the Shotgun crocodilians a digestive physiology similar to that of their extant relatives. This in turn favors the *rejection* of crocodilian digestion as the effective agent for accumulation of

most of the material in the Shotgun local fauna, as well as other microvertebrate concentrations in the fossil record.

Other Occurrences of Crocodilian Digestive Residues

Most of what has been previously considered to be crocodilian fecal material is preserved as, or within, coprolites. Jepsen (1963), in a discussion of the early Eocene (Wasatchian) Golden Valley local fauna, ascribed most of the coprolites in this assemblage to crocodilians. The evidence for this was the occurrence of crocodilians in this fauna, and similarities of "shape, size, and surface texture" between feces of Recent alligators and the Golden Valley coprolites. Many of these coprolites contain gar scales, as well as fragmentary bones and occasional teeth. Although I have no information on the teeth, the enamel-like ganoine is still present on the gar scales (F. A. Jenkins, Jr., pers. comm. 1972). Thus, I would not attribute these coprolites to crocodilians. Although no large mammalian carnivores are known from the Golden Valley local fauna, this may be an artifact of small sample size and the low predator/prey ratio typical of mammalian communities (Bakker 1975). The Golden Valley coprolites may well have been produced by these as yet undiscovered members of the fauna.

A coprolite filled with gar scales from the Cretaceous Oldman Formation of Alberta has been reported by Waldman (1970) and tentatively assigned to a crocodilian. Waldman's evidence consists of a variety of reasons for eliminating other elements of the fauna from candidacy. Although he does not describe the gar scales in detail, he does refer to them as "enameled scales of *Lepisosteus*" (1970, p. 1011), and they appear in his photograph to have a normal ganoine layer. As before, this argues against their digestion by a crocodilian.

A different case has been described by Wetmore (1943), who reported the occurrence of fragments of bird feathers in a large coprolite from the Miocene of Maryland. Again, a crocodilian was judged potentially responsible for the specimen, though fish were also considered. Since feathers, like hair, are regurgitated by

crocodilians, I would interpret this "coprolite" as either not crocodilian or not fecal in origin.

Most other reports of presumed crocodilian coprolites or digestive residues (e.g. Robert 1832/1833; Young 1964; Carpenter and Lindsey 1980) cite inconclusive arguments similar to those of Jepsen, Waldman, or Wetmore. However, in the Eocene lignites at Geiseltal, Germany, coprolites are preserved within and in close association with crocodilian skeletons (Walther and Weigelt 1932; Nürnberger 1934) and thus appear from their context to be crocodilian. These coprolites contain bones and teeth of frogs, juvenile crocodilians, and fish. Insufficient detail is given in published accounts of this material to apply the criteria adduced in this paper, but comments by Voigt (1934), on the poor preservation of most skeletal material in the coprolites, are suggestive of demineralization. Further work on this occurrence might offer a critical test of the conclusions reached here.

Although most previous identifications of fossil crocodilian fecal material now seem ambiguous at best, there is growing evidence that the preservation of enamel-less teeth (sometimes, but not always, within microvertebrate concentrations) may be rather widespread. A brief literature survey and inquiries among colleagues reveal that several workers have recognized enamel-less teeth as rare and enigmatic components of a number of Mesozoic and Cenozoic faunas. Clemens (1973) gives a brief description of four isolated mammal teeth of unclear taxonomic affinity, from the Upper Cretaceous Lance Formation. Two of them are well preserved, with enamel, but on one of the others "the enamel is missing from several parts of the crown," and the fourth "completely lacks enamel" (Clemens 1973, p. 73). *Gypsonictops*, and perhaps other taxa, are occasionally represented by completely enamel-less teeth in the Late Cretaceous Bug Creek local fauna (J. A. Lillegraven, pers. comm. 1976). Enamel-less teeth of several species of Tiffanian mammals have been found in the Judson and Brisbane local faunas of the Tongue River Formation, Paleocene, North Dakota (R. C. Holtzman, pers. comm. 1977). Such teeth have also been noted from the Lower Eocene Willwood For-

mation, in several parts of the Bighorn Basin (Bown 1979; P. D. Gingerich, pers. comm. 1979). A particularly well known specimen which may belong in this category is the holotype of *Aeolopithecus chirobates,* an Oligocene primate from the Fayum, Egypt. This specimen is a complete mandible, the teeth of which have been described as lacking enamel (Simons 1968), though examination of casts made by P. D. Gingerich shows that restricted interdental patches remain. The loss of enamel has been presumed to result from "chemical corrosion during burial" (Simons 1968, p. 32), but the specimen occurs at Quarry I, along with many other specimens which retain their enamel; there is no independent evidence of a unique diagenetic history. The completeness of the specimen may seem to argue against interpreting it as resulting from crocodilian digestion. However, this degree of completeness may not be surprising for a moderately large crocodilian eating a small primate (with a fused symphysis and well formed roots). This interpretation would require that the mandible be remineralized along with the teeth. As a final example, P. D. Gingerich (pers. comm. 1979) has noted a number of fragmentary mandibles and maxillae of sub-fossil lemurs from Madagascar, on which the teeth are either completely enamelless or have only restricted interdental patches of enamel. In all of these cases, crocodilians are known from the respective faunas. As in the case of the Shotgun local fauna, further testing of these apparent instances of crocodilian digestive residues should include a search for evidence of dentine (and bone) decalcification in addition to enamel loss. Now that attention has been called to this form of preservation, more accounts of it will undoubtedly come to light.

Acknowledgments

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