ANALYSES OF COPROLITES PRODUCED BY CARNIVOROUS VERTEBRATES

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ABSTRACT—The fossil record contains far more coprolites produced by carnivorous animals than by herbivores. This inequity reflects the fact that feces generated by diets of flesh and bone (and other skeletal materials) contain chemical constituents that may precipitate out under certain conditions as permineralizing phosphates. Thus, although coprolites are usually less common than fossil bones, they provide a significant source of information about ancient patterns of predation. The identity of a coprolite producer often remains unresolved, but fossil feces can provide new perspectives on prey selection patterns, digestive efficiency, and the occurrence of previously unknown taxa in a paleoecosystem. Dietary residues are often embedded in the interior of coprolites, but much can be learned from analyses of intact specimens. When ample material is available, however, destructive analyses such as petrography or coprolite dissolution may be used to extract additional paleobiological information.

INTRODUCTION

WHEN PREDATOR-PREY interactions cannot be observed directly, fecal analysis provides the next best source of information about carnivore feeding activity because refractory dietary residues often reveal what an animal has eaten. This approach is very effective in studying extant wildlife, and it can also be used to glean clues about ancient trophic interactions. Yet, although fossilized carnivore feces are often present in fossiliferous sediments, their antiquity makes analysis more difficult. Diagenetic alteration of specimens obscures the original digestive residues, and it is often impossible to ascertain which animal produced the coprolite. Fossil feces also show significantly more variation in morphology and composition than skeletal fossils: animal diets are often highly variable, and soft fecal material can assume a range of shapes—especially after post-depositional deformation. In spite of such complexities, coprolites provide important information about ancient predator-prey interactions that is not available from body fossils. Coprolite analyses, however, require different approaches from those used to study most skeletal fossils. Furthermore, different types of coprolites may provide different types of information.

Diet and depositional environment largely determine which animal feces may be fossilized and the quality of preservation of a lithified specimen. Significant concentrations of calcium and phosphorus in bone and flesh often favor the preservation of carnivore feces by providing autochthonous sources of constituents that can form permineralizing calcium phosphates (Bradley, 1946). Thus, although herbivores outnumber carnivores in terrestrial ecosystems, carnivore feces are more likely to be preserved. Preservation is also facilitated by rapid burial, so coprolites from aquatic taxa usually far outnumber those from terrestrial animals. These taphonomic biases explain why coprolites are relatively rare in most terrestrial deposits, while fish coprolites can be quite common.

WHAT CARNIVORE COPROLITES TELL US ABOUT PREDATOR-PREY INTERACTIONS

The identity of the animal that produced a coprolite is very difficult, if not impossible, to pinpoint because our knowledge of ancient faunas is incomplete and because fecal material is so variable. Although we know that spiral coprolites (or intestinal casts; see Williams, 1972) were produced by one of the groups of fish with spiral intestinal valves (e.g., sharks, lungfish, or gars; Gilmore, 1992), morphology usually provides little information about the animal of origin because many animal droppings produced by different taxa are quite similar. Coprolite contents, composition, size, and stratigraphic placement can, however, constrain the number of likely perpetrators. Carnivore coprolites are usually easy to differentiate from herbivore coprolites because they are typically phosphatic and often contain skeletal inclusions. Coprolite size is also very informative, since fecal volumes generally scale with animal size. While fecal amounts are variable, it's clear that small animals cannot produce large individual fecal deposits. Field guides to modern scat provide analogs that can be used to roughly approximate the size range of animals that produce feces of a given mass. Thus, even when the taxa of fecal producers are unknown, carnivore coprolites provide evidence that predators of an approximate size range frequented a given habitat. This indicates a trophic niche that may be further defined by dietary residues that reveal prey selection patterns.

In many cases, inclusions within a coprolite provide more information about prey animals than about the coprolite producer itself. The integrity of included digestive residues depends on their composition and the extent of their exposure to digestive and diagenetic processes. Some coprolites contain no recognizable inclusions, but refractory skeletal constituents have been found in numerous carnivore coprolites (e.g., Hantzschel et al., 1968). When dietary residues are incompletely digested, the morphology of elements such as mollusk shells, ganoid scales, and small bones may allow identification of prey. Specific taxa of mollusks (e.g., Speden, 1969; Stewart and Carpenter, 1990), crustaceans (Bishop, 1977; Sohn and Chatterjee, 1979), fish (e.g., Zangerl and Richardson, 1963; Waldman, 1970; Coy, 1995), reptiles (e.g., Parris and Holman, 1978), and mammals (e.g., Martin, 1981; Meng et al., 1998) have been recognized in coprolites. Furthermore, fragments of larger bones may be ascribed to higher-level taxonomic groups on the basis of histological analysis (e.g., Chin et al., 1998).

Coprolites may also show signs of ingested soft tissues as organic residues or in the form of three-dimensional impressions. Some exceptional specimens have revealed evidence of feathers (Wetmore, 1943), fur (Meng and Wyss, 1997), insect exoskeletons (Northwood, 1997), and muscle tissues (Chin et al., 1999). Such remarkable preservation requires depositional conditions that minimize diagenetic recrystallization.

These studies show that coprolites may contain dietary residues that provide concrete evidence of ancient carnivory. It is clear, though, that the challenges of coprolite analysis stem from the difficulties involved in determining the animal of origin and in identifying residual dietary components. This analytical complexity reflects the fact that coprolites are relatively anonymous packages that represent varying diets, digestive processes, and diagenetic alteration. Such marked variability necessitates that care be exercised in drawing conclusions from a limited number of samples. Even so, coprolites provide cumulative clues that help flesh out our understanding of patterns of predation in ancient environments by identifying prey species within a given paleoecosystem, and by indicating general size and/or age classes of prey animals (e.g., Zidek, 1980; Martin, 1981). The composition and integrity of these inclusions may also provide information about the diet and digestive processes of the predator itself.

COPROLITE ANALYSIS

Documentation.—Both destructive and non-destructive techniques may be used to analyze coprolites, and the choice of analytical method depends on the questions addressed by the research project. Regardless of experimental approach, each study of coprolites must include careful documentation of provenance and of the physical characteristics of each specimen.

The collection of coprolites is similar to the collection of vertebrate fossils where documentation of locality and stratigraphic information is of critical importance. In many cases, coprolites have eroded out of their encasing sediments and are collected as float. Although such specimens contribute notable baseline information about a given formation, the informative value of coprolites is greatly enhanced when they are collected *in situ* and can be correctly placed within a detailed stratigraphic column. Mapping specimens in place will also indicate coprolite orientation and density. Such taphonomic information contributes important information about the environment of deposition.

Photographic documentation of specimens is as useful for coprolite analysis as it is for research on other fossils. Unfortunately, most coprolites are not as strikingly photogenic as many skeletal fossils! Nevertheless, images of seemingly amorphous coprolitic masses are quite useful because they document the range of coprolite size and morphology, and help create search images for paleontologists likely to encounter fossilized feces in the field (Fig. 1). Such records become even more important when destructive analyses alter the original form of a specimen. Photos should always include a scale.

If a coprolite specimen is very important or has an unusually distinctive morphology, standard paleontological molding and casting methods (see Goodwin and Chaney, 1994) can be used to replicate the external form. Care should be taken, however, if this technique is applied to fragile specimens; some coprolites are composed of soft materials that can be easily scratched or gouged (possibly obscuring paleobiologically informative impressions), or may absorb compounds applied as separators or mold release agents. This technique should not be used on highly fractured specimens.

Non-destructive Analyses.—Intact coprolite specimens can be characterized by morphology, size, and surface features. Although coprolites from many different taxa can have similar traits, documentation of the physical characteristics of coprolite specimens is important because recurring features may reveal distinct morphological categories. Such forms may be designated as coprolite morphotypes. One early classification scheme differentiated spiral coprolites into "heterpolar" or "amphipolar" types, depending on the spacing of coils along the long axis of the specimen (Neumayer, 1904). This system has been applied to other spiral coprolites, though there is debate as to whether these morphotypes have any taxonomic significance (e.g. Price, 1927; Zidek, 1980).

Linear dimensions of coprolites (e.g., diameter and length) provide rough approximations of fecal size, but volumetric measurements give much more informative assessments. Volume can be measured in several ways. The volume of small, dense specimens can be determined by measuring water displaced by submerged samples; porous specimens should be allowed to absorb water before displacement is measured. This approach can also be applied to large, fractured specimens by using water displacement to calculate the density of small fragments; volume can then be determined by extrapolation after weighing the entire specimen (e.g., Chin et al., 1998). In a few cases a coprolite may be so large and fractured that it remains in the plaster jacket in which it was collected (e.g., Fig. 1a), and cannot be accurately weighed. The volume of such specimens can be approximated by visualizing the mass as being composed of one or more geometric shapes whose volumes can be calculated.

When a large number of coprolites from a given locality represents an unbiased sample, recurring size classes and other physical characteristics may indicate specimens produced by a small number of taxa and/or age groups. Such groupings may be subtle, however. Edwards and Yatkola (1974) analyzed 106 coprolites from the White River Formation and found no distinct size classes within a continuum of coprolite diameters ranging from 15 to 36 mm. But when the data was re-analyzed using the mean diameter of *in situ* coprolites that occurred in small "clusters" (suggesting individual fecal deposits), they found three distinct size groups that may reflect the sizes of the carnivores that produced them. Correlating coprolite size with other physical attributes will refine interpretations, though some features (such as color and degree of flattening) probably provide

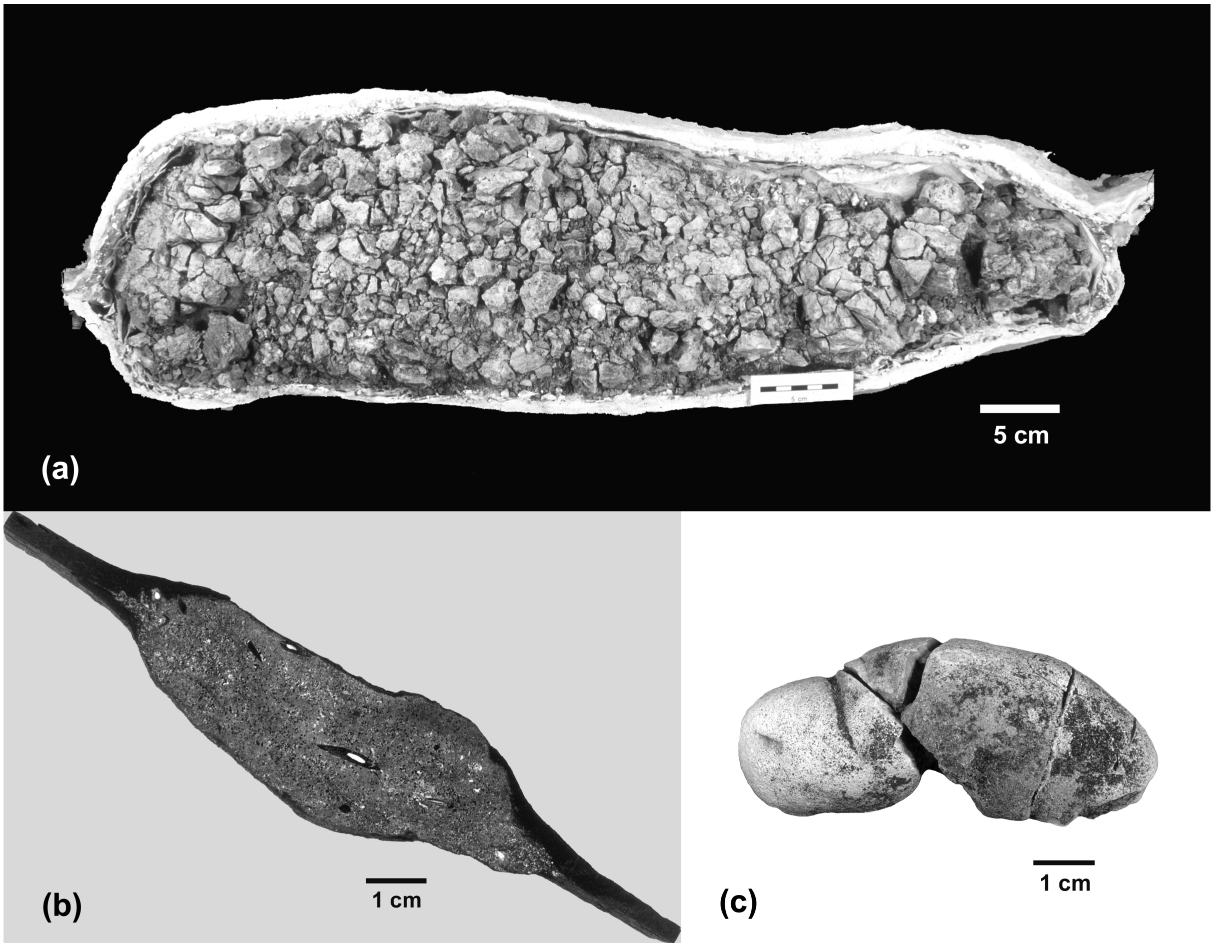

FIGURE 1—Coprolites can have many morphologies, from easily recognizable forms to nondescript masses. (a) Very large Cretaceous coprolite from Alberta (Royal Tyrrell Museum, TMP 98.102.7). This specimen was so fractured from weathering that it was removed in a plaster jacket. (b) Probable fish coprolite from the Pennsylvanian black shale of Indiana (Field Museum of Natural History; FMNH PF2210; see Zangerl and Richardson, 1963). Photograph shows lateral view of sliced specimen; the specimen originally appeared as a lump in the sediments, but was sliced through the center to reveal the coprolitic material sandwiched between the black shale. (c) Small coprolite with more typical, 'sausage' fecal shape (Royal Tyrrell Museum, TMP 80.16.1098).

little taxonomic information (Sawyer, 1981).

Non-destructive analyses of coprolites should also include careful examination of specimen surfaces for distinctive impressions or inclusions. These surfaces can be scanned with a stereo microscope; if warranted, higher magnifications can be obtained using scanning electron microscopy. Scrutiny of the outer surface of a coprolite may reveal dietary inclusions protruding from the coprolitic ground mass. Mineralized skeletal elements are commonly observed in carnivore coprolites, and inclusions on outer surfaces may be accentuated by weathering processes. Coprolite exteriors may also show three-dimensional impressions of the vegetation or detritus on which the feces were deposited. Such impressions are of interest, but should be distinguished from those that represent dietary components.

Broken coprolites allow scrutiny of fractured internal surfaces. In most cases, recognizable features evident in the interior of a specimen can be confidently attributed to diet. This includes three-dimensional impressions that may indicate undigested soft tissues.

Destructive Analyses.—As a general rule, damage of fossil specimens should be studiously avoided. At the present state of our technology, however, destructive analyses appear to provide some of the most effective means to extract paleobiological information from coprolites. Techniques such as petrographic analysis or acid dissolution may reveal dietary components that aren't evident on coprolite surfaces. Because such analyses destroy the morphological integrity of a specimen, several factors should be considered before a sample is altered. If numerous comparable coprolites are available or if a specimen is very large and/or fragmented, the information obtained from destructive tests is likely to compensate for the loss of some coprolitic material. But the decision of whether to perform destructive analyses becomes more difficult if the tests will damage a unique specimen. When destructive analyses are planned, they should be preceded by careful measurements, photo-documentation, and scrutiny of accessible surfaces (see above).

Thin sections of coprolites provide exceptionally informative views of specimen contents because they permit analysis with compound microscopes. Such analyses may reveal dietary inclusions with considerable histological detail. They also shed light on patterns of diagenetic mineralization. The jumbled nature of fecal contents makes thin section sampling rather unpredictable, however, because identification of dietary components depends on fortuitous slices through recognizable structures. Fortunately, some features diagnostic of certain taxonomic groups (such as patterns of bone vascularization) may be evident on small fragments.

Thin sections can be made from relatively small pieces of coprolite, and careful scrutiny of coprolite fragments or intact specimens will help identify optimal sampling sites. When possible, thin sections can be taken from the end of a specimen in order to preserve more of the original morphology. Although techniques for preparing coprolite thin sections are similar to those for preparing standard petrographic sections of rock, more efforts are made to minimize damage to and loss of coprolitic material (see Wilson, 1994 for a useful discussion of methods for preparing fossil thin sections).

Saws with diamond-embedded blades are used to reduce large samples to sizes that can be affixed to glass slides. A diamond saw is also necessary to shave off the thin sample slices that are mounted on slides (the sample can be sliced thin before or after it is mounted on the slide). The use of a precision saw with a thin diamond wafering blade will facilitate more accurate cuts and help reduce loss of coprolite material during the cutting operation. In a few cases, indurate coprolites can be cut with a precision saw without embedding, but fragile or fractured specimens should be embedded in or impregnated with an epoxy or polyester resin before being cut.

The cut surface of a specimen must be ground smooth before it is affixed to a microscope slide with a strong epoxy bonding agent. Standard petrographic slides are 27×46 mm, but specimens can also be mounted on larger slides (or glass plates) as well. Grinding/polishing machines or lapping wheels are used to grind and polish the sample to an appropriate thickness (around 30–40 µm, depending on the nature of the sample). Slides can then be cover-slipped for examination with a light microscope, or finely polished for chemical analyses with a microprobe or scanning electron microscope.

In a few studies, coprolites have been mechanically disaggregated in order to release dietary residues from the ground mass. This technique will be most effective when the prey have been poorly digested, and it may reveal the presence of small prey taxa that are not otherwise represented in a faunal assemblage. Acid dissolution may also facilitate chemical and morphological studies of amorphous organic residues (e.g., Hollocher et al., 2001). Some of the techniques used in the acid preparation of vertebrate fossils may be modified for use on coprolites (see Rutzky et al., 1994). In such procedures, the exposed portions of skeletal elements that are encased in well-lithified sediments are carefully coated with a hardener for protection before the specimens are immersed in weak acid solutions (usually phosphate-buffered acetic or formic acids). As this process is repeated, embedded skeletal elements are gradually released from the sediments.

Because the ground mass of most coprolites is phosphatic, acid solutions prepared for dissolving this material should not have a phosphate buffer (unless it is very weak). The acid dissolution procedure will be easier when the ground mass of a coprolite is more susceptible to acid than the dietary inclusions. The operation will be more challenging, however, when both included skeletal elements and the coprolitic ground mass show similar susceptibility to the acid solution. Because the phosphatic ground masses of different coprolites can have widely varying compositions, it is clear that experimentation will be necessary to identify the most effective methods for releasing inclusions from a given type of coprolite. Some authors (Sohn and Chatterjee, 1979) have used formic acid to release ostracods from coprolites. Others (Burmeister et al., 1999) report that using ultrasonication with weak acetic acid is effective in freeing inclusions from coprolites that have a significant carbonate component. Mechanical disaggregation alone may also be used on coprolites that have a softer ground mass (e.g., Parris and Holman, 1978).

CONCLUSIONS

Coprolite analysis is quite different from the study of fossil skeletal elements. Because morphology is usually not diagnostic, the chemical and physical composition of a coprolite assumes greater importance and may provide as much (or more) paleobiological information than size and shape. The ambiguity of coprolite morphology also makes it difficult to unequivocally associate a coprolite with the animal that produced it.

Despite these challenges, some carnivore coprolites provide unique perspectives on ancient predator-prey activities. Although they may not provide complete information about the carnivorous habits of specific animals, coprolites can supply important fossil evidence that reveals prey selection patterns, digestive efficiency, and the occurrence of smaller fauna in a given paleoenvironment.

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