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A fresh look at sideritic "coprolites"

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Abstract.—Sideritic ''coprolites'' from the late Miocene of southwest Washington, the Upper Cretaceous of Saskatchewan and Madagascar, and the Permian of China have often been claimed to be pseudofossils. They are here interpreted as intestinal casts (cololites) prefossilized by bacterial activity and later transformed into siderite with no traces of original food particles left. All occurrences are found within fluvial overbank deposits that carry no other vertebrate remains. Their absence could be due to aquifer roll-fronts that destroyed phosphatic bones and teeth but favored siderite precipitation.

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Introduction

When thinking about an adequate title for a chapter on vertebrate fossils, the senior author once came up with the triad ''Teeth, Bones, and Coprolites'': these are the remains most commonly found in Silurian and Triassic placer bonebeds, together with coarse sand grains and rolled rock fragments (Reif 1971). That teeth and bones have a relatively high durability is understandable—but why coprolites? Animal droppings, we would think, should disintegrate within days, particularly in subaqueous environments.

The reason for their preferred preservation is that excrements are a prime target for bacteria whose metabolism produces phosphates and iron sulfides as side products, which mineralize the originally soft material. As we know from the fossil record, this happens preferably in sediments (sapropels) deposited under low-oxygen conditions. From coprolites in the Devonian Hunsrueck-Shales, the Jurassic Posidonia Shales, and the Eocene lake deposits of Messel, it is also clear that bacterial mineralization happened very early in diagenesis: while carcasses, shells, and sometimes even bones became flattened during compaction of the sediment, coprolites retain their three-dimensional geometry. In the Messel lagerstätte, this preservational pathway appears to apply only to feces of carnivores, while associated droppings of herbivorous species are preserved as flat coaly films (Wuttke 1988).

Thus, ''prefossilization'' due to early bacterial mineralization may transform coprolites into resistant and heavy clasts that may survive reworking of the host shales and become concentrated in placer bonebeds, together with fragments of bones and teeth having undergone a similar preservational history (Reif 1971). Early mineralization is also the reason that phosphatized coprolites themselves may become a kind of conservation lagerstätten: they often preserve insect wings, small bones, and other food items much better than the host rock (Pollard 1990; Hunt et al. 1994). In contrast, the specimens here considered consist of siderite (Amstutz 1958), in which food particles can no longer be identified. Thus, their origin can only be inferred from external morphology.

The Washington Coprolites

Coprolite research has a long history and it is a particular delight to delve into the literature on this sociologically marginalized subject. The term ''coprolite'' was created by the Reverend William Buckland (1829), noted geologist and divine (Folk 1965; Pemberton and

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Frey 1991), with a focus on occurrences in the Lias of Lyme Regis that he attributed mainly to ichthyosaurs. In contrast, the Washington occurrence has been, with the exception of a few studies (Amstutz 1958; Spencer 1993; Danner 1994), very much a matter of amateurs. Most authors rejected the coprolite nature, (1) because the fossils consist of siderite rather than phosphate and contain no recognizable food particles, (2) because they occur by the thousands in the absence of other vertebrate remains, and (3) because there is a tremendous variation in size. As Don Major (1939) put it, ''some are perfect twisted specimens with the 'strings' no larger in diameter than the lead of a pencil. Others in twisted masses show individual 'ropes' as large as two inches in diameter. If these are of animal origin they must represent a great many different size animals, and Lewis County might have been the spot where Noah's Ark came to a rest.'' Major therefore interpreted these fossils as bryozoan colonies—as opposed to the stalactite theory of Dake. In a later paper defending his interpretation, Dake (1960) also reports that in the mid-Thirties the Ward's Establishment of Natural History supplied ''Washington coprolites,'' but called them in for refund after the coprolite origin was questioned. He continues: ''They were good specimens indeed for the several learned medical experts to identify them as the real article. Ward's did not knowingly perpetrate a fraud, they simple [sic] judged on specimen appearance alone, as many others have done since then . . . . It is most unfortunate that the Washington specimens are of a more prosaic genesis, otherwise this whole region would have become a Mecca for wide scientific research including that of paleontology, and perchance Bible scholars.'' Another study (Spencer 1993), based on in situ observations, clarified not only the stratigraphic relationships of the Washington ''coprolites'' (fluvial or lake deposits of the late Miocene Wilkes Formation). Spencer also provided an alternative interpretation: because the siderite bodies are closely associated with organic-rich clay and fossil wood, they might have formed when compaction injected sediment through knotholes into hollow tree stems. In the meantime, fossil dealers have tacitly returned to selling these fossils as coprolites. With the commercial interest renewed, present-day fossil hunters appear to be turning to excavation of the bedrock. Therefore ''Washington coprolites'' now offered are much better than the worn fragments from modern riverbeds, on which many earlier studies have been based.

Coprolites or Cololites?

The present study dealt primarily with the morphology of the Washington coprolites. It was initiated at a most unlikely place: a mineral fair in Stamford, Connecticut. The coprolites offered among other curio fossils (Fig. 1B,C) carried no stratigraphic information, but they reminded the senior author immediately of a much larger specimen, late Permian in age, that he had drawn and photographed years ago in China (Figs. 1A and 2). In both cases the regular and three-dimensional meanders were incompatible with even the most artistic mode of defecation. So were the pinched ends on either side, because observation of our dog tells us that droppings become pinched only at the rear end. Instead, these fossils resemble the shapes of intestines, in which meandering increases the digesting surface. Closer inspection and the veterinary experience of one of us (C. M.) confirmed this suspicion: the coprolites are usually meandering and pointed at both ends. They may also carry longitudinal grooves that appear to correspond to folds, or ridges, inside the intestinal wall, rather than to the shape of the anus. More-slender specimens from Washington (Fig. 3) show a third feature that is incompatible with excrements: some of them consist actually of several sections, whose closely apposed ends pinch in opposite directions. All these features—meanders, grooves, double-ended pinching and overlap—strongly suggest that we are dealing with intestinal casts (cololites) rather than coprolites. But which part of the guts is recorded?

In general, the digestive system of vertebrates can be subdivided into successive functional units. After having been chopped in the mouth, food passes through the pharynx to the stomach for further mechanical and biochemical processing. Absorption of nutritious

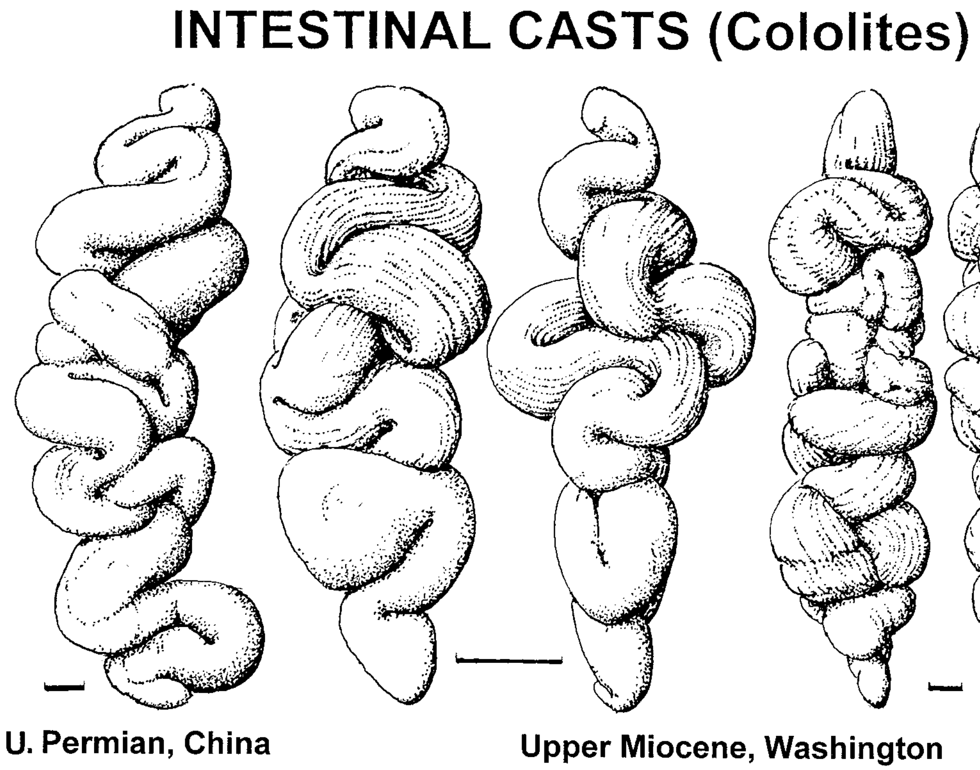

FIGURE 1. Cololites of different sizes and geologic ages differ from coprolites by three-dimensional meandering and by having pinchings at both ends. (A, Beijing University; B, GPIT 1860/1; C, GPIT 1860/2.) All scales, 1 cm.

FIGURE 2. Large "coprolite" from the Upper Permian of China (collections of Beijing University). The similarly shaped object in the back is a delicacy from a Chinese bakery.

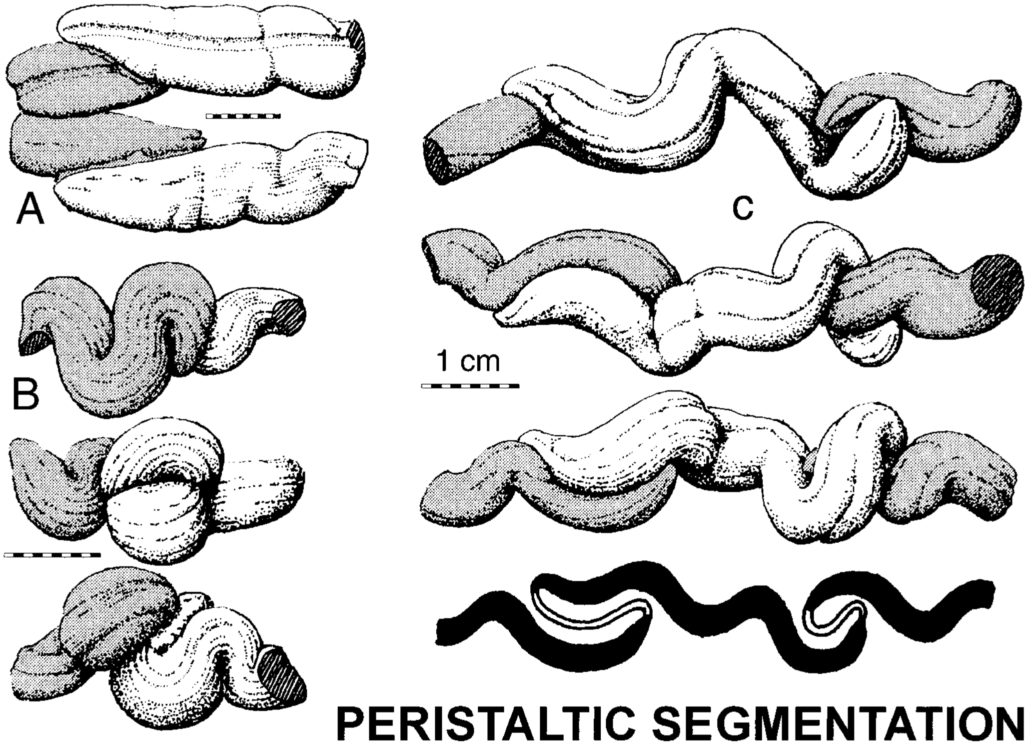

FIGURE 3. More-slender variants from the Washington occurrence consist of segments whose pinched ends are closely apposed. This is the result of peristaltic waves that transported the contents along the dynamically meandering gut. Since the contracted sections were empty, they are not represented in the intestinal cast. (A, GPIT 1860/3; B, GPIT 1860/4; C, GPIT 1860/5.)

substances then takes place in the small intestine, while water and electrolytes become recovered in the large intestine. Ultimately the waste leaves the body through the rectum and the anus. Throughout this process, digesta are mixed and transported along the bowels by muscles of the intestinal wall that are arranged in two layers (Stevens and Hume 1995). The muscles of the circular layer contract in periodic waves that squeeze the contents along by pinching down on the intestinal lumen. In the longitudinal layer, muscle fibers are often concentrated into bands of muscles, called *taeniae.* By contraction of these bands, the mesenterially suspended intestine is pulled together into accordion- or meander-like sections. These *haustra* continuously change shapes and positions as the contents are being propelled.

Three-dimensional cololites are most likely to form in the large intestine of the carcass, because at this station the contents had become consistent enough to maintain shapes until prefossilization occurred. The meanders of the cololites thus reflect the configuration of the haustra, and the pinchings the positions of contraction waves, at the moment of death, while longitudinal grooves in the cololites correspond to taenial muscle bands.

There is also a straight specimen (Fig. 4), which may be interpreted as the cast of a cecum. In animals that possess one, the cecum forms a blind sack at the junction of the most distal small intestine with the proximal large intestine. The present fossil strongly resembles the haustrated shape of a cecum, including impressions of longitudinal taenial bands on the upper and lower surface and the presence of a short, slightly looped segment interpreted as distal small intestine. Fittingly, the small-intestinal segment is attached near the unpinched end of the specimen.

Identification of these fossils as cololites (Hunt et al. 1994) implies a number of questions and possibilities. (1) Question: After coprolites have been defined as trace fossils

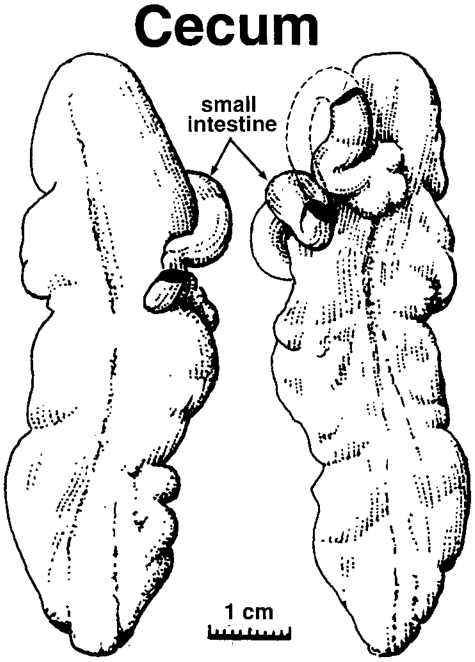

FIGURE 4. Straight specimen from Washington interpreted as the cast of a cecum, whose port was at the bottom. The narrow appendage near the upper end could correspond to the distal part of the small intestine. (YPM 56257.)

(Bertling 1999), should this definition also apply to intestinal casts, only because they are made of the same material? Intuitively one would tend to call them body fossils; but on the other hand cololites refer to a process shared by many tetrapods (and to a particular preservational situation), rather than a distinctive and static anatomical feature. (2) Possibilities: If intestinal contents can become prefossilized by bacterial activity within a carcass (a possibility that could potentially be tested in modern carcasses buried in a variety of sediments), this provides us with a durable replica of an otherwise unpreservable organ. Devoted scatologists may also describe, compare, and classify cololites in terms of parataxonomy—in the hope that the parataxa can eventually be tied to particular kinds of vertebrates. The available literature (Neumayer 1904; Häntzschel et al. 1968; Williams 1972; McAllister 1985; Pemberton and Frey 1991; Gilmore 1992; Hunt et al. 1994) provides an adequate basis.

Other Occurrences

Our morphological results are still in conflict with the evidence that led previous workers (Major 1939; Dake 1960; Danner 1994; Spencer 1993) to refute a coprolite origin: (1) The absence of vertebrate bones and teeth (and possibly of true coprolites) in the beds yielding the Washington coprolites and (2) their sideritic nature. These objections could be dismissed if we were dealing with a single occurrence; but they also apply to sideritic cololites in other formations. The oldest occurrence of sideritic cololites has been reported in Pennsylvanian shales of southern Texas (Danner 1994). The facies context of the Permian specimen from China (Fig. 2) is unknown to the writers, but presumably it also comes from fluvial deposits. In the Late Cretaceous Whitemud Formation of Saskatchewan (Broughton et al. 1977, 1978; Schmitz and Binda 1991) siderite nodules and "coprolites" are locally so abundant that they decrease the economic value of otherwise important ceramic clays. Some of the Whitemud nodules actually have already been interpreted as intestinal casts, after strings of up to 1 m were excavated (Broughton 1981).

Another Late Cretaceous occurrence, in southern Madagascar, is so far known only from commercial specimens. While showing the same morphological variations as the Washington coprolites, they are less valued: their surface is crackled because of secondary limonitization, making them less suited to be placed on the host's carpet for a practical joke. Such "popcorn" specimens are also represented in the Washington material (Spencer 1993: Fig. 4). Finally, one of us (T. T.) discovered a large number of Washington-type cololites (Fig. 5) in the late Paleocene of North Dakota. They occur in a massive, silty, kaolinitic unit of fluvial overbank deposits overlain by a coal seam.

These occurrences all share a fluvial or swamp origin. The only other associated fossils are plant remains—no vertebrate bones, teeth, or footprints. While the accumulation of carcasses yielding the cololites could be explained by the catastrophic origin of overbank deposits—what happened to the skeletons?

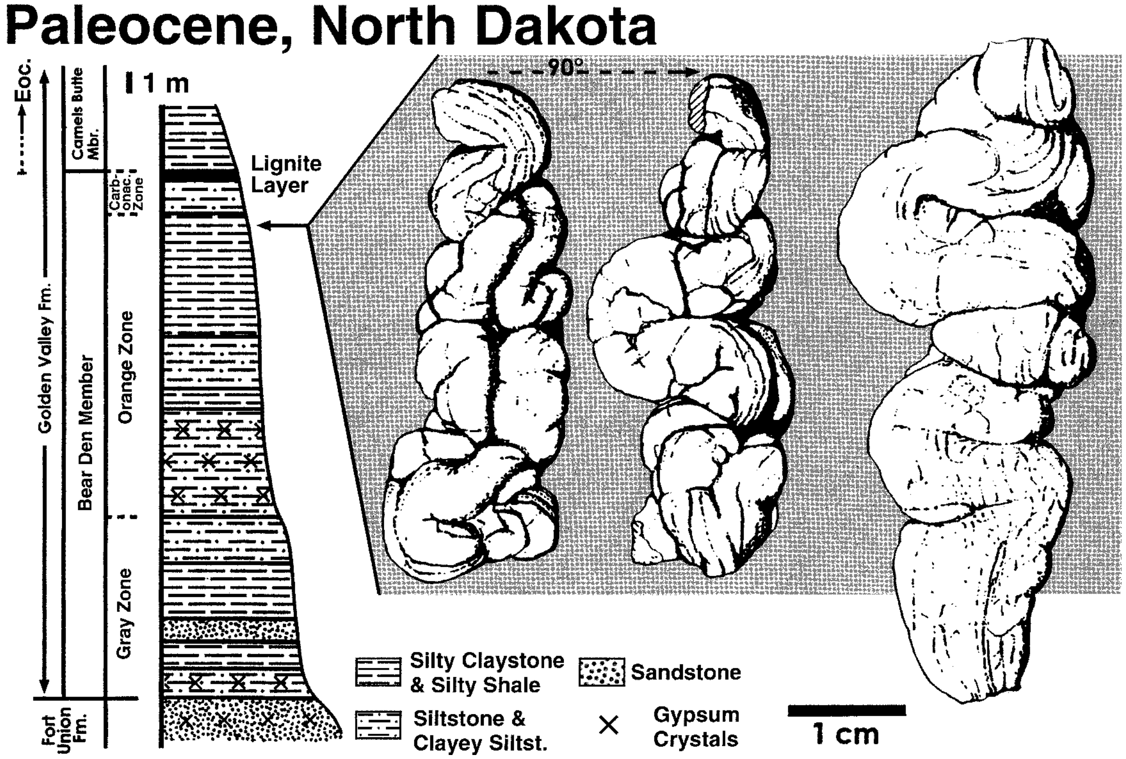

FIGURE 5. North Dakota cololites and their stratigraphic positions. Section from Hickey 1977. (YPM 56410 and 56411.)

Roll-Fronts as a Taphonomic Filter

A possible clue to help in this quandary comes from a hypothesis that Pennilyn Higgins (1999 and personal communication) proposed in another context. In the Cretaceous Hanna Formation of south-central Wyoming, vertebrate bones are restricted to certain intervals and are completely absent in other horizons, which appear bleached and contain an abundance of sideritic nodules. This phenomenon is referred to as secondary alteration by "roll-fronts" of oxidized groundwater (Goldhaber et al. 1979; Harris and King 1993). In organic-rich layers, these fronts dissolved pyrite. The resulting acidic conditions altered mineral phases and favored other species. Thus, calcite and phosphatic bones were destroyed, while Fe and CO_3 became reprecipitated as siderite. Since shapes, but not the internal structures, were retained in the sideritic cololites, their original mineralization was probably not purely phosphatic; otherwise they would have suffered the same fate as bones and teeth.

Conclusions

1. On morphological grounds we claim that twisted sideritic "coprolites" from fluvial deposits of various ages are intestinal casts (cololites). In the very special microenvironment of the gut, food contents must have become mineralized immediately after death—presumably by the bacteria already present.

2. Since no other vertebrate remains are preserved in the beds containing these fossils, another diagenetic event must have wiped out phosphatic bones and teeth and transformed the premineralized gut contents into siderite. Groundwater roll-fronts provide a possible mechanism.

3. These preliminary findings call for more systematic excavations and actuopaleontological, sedimentological, and geochemical studies of this remarkable taphofacies.

Sideritic cololites convey an important general message. It is clear that an intestinal cast can form only after death: a rare case indeed compared to the thousands of droppings the same individual has produced during its lifetime. Yet, taphonomy *is* a science of the rare cases, because in geological time organismic remains accumulate not according to original numbers, but in proportion to their relative fossilization potentials, whereby the rare event may become the common occurrence. So if you go to the next fair, stop not only for ‘‘coprolites’’ before their new interpretation raises the price level, but remember that unexpected discoveries are waiting for you at a much lower cost than the ticket to Madagascar

Acknowledgments

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