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GASTROLITHS IN COPROLITES - A CALL TO SEARCH!

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Abstract—Knowledge about gastroliths in coprolites is important because such finds can provide information for retention and utilization of stomach stones in certain taxa, the size of excreted sediment particles, and special surface features of gastroliths. Gastroliths could help to link coprolites with their producer. A review of published reports reveals that direct evidence of gastroliths within fossil feces appears to be extraordinarily rare and can almost exclusively be attributed to crocodilian and avian coprolites. Preliminary data of extant ostrich feces shows that 12.3% of the fecal mass was composed of sediment. A separation into grain sizes demonstrated that the vast majority (94.3%) of sediment particles excreted by ostriches is sand-sized (<2 mm in diameter), while the largest excreted ostrich gastroliths are <8 mm in diameter. This suggests that the rarity of gastroliths in coprolites may be partly attributed to collection bias or lack of research interest. A raised awareness for such finds will not only help to assess their true frequency, but might help solve paleobiological questions.

INTRODUCTION

Gastroliths, ingested sediment particles (geo-gastroliths *sensu* Wings, 2007), and coprolites, the fossilized remains of fecal material, are two types of trace fossils that constitute a valuable source of paleobiological information. Paleodiet, habitats, and the presence of certain taxa in areas otherwise lacking body fossils and/or other trace fossils may be deduced from their presence.

Coprolites commonly contain body fossils such as bacteria, plant remains, bones, and very rarely even soft tissue (Martin, 2001). Knowledge about gastroliths in coprolites might help tackle several paleobiological questions such as 1) evidence for retention and utilization of gastroliths in specific taxa; 2) the size of excreted pebbles in lithophagic animals; 3) special surface features valuable for gastroliths identification; and 4) help to link coprolites with their producer. Direct evidence of gastroliths within fossil feces, however, appears to be extraordinarily rare. This is puzzling not only because gastroliths might have been responsible for the fragmentary nature of common bone pieces in coprolites (Northwood, 2005), but especially because almost every stone swallowed during lithophagy eventually ends up in the feces (except when regurgitated or completely disintegrated). Furthermore, most gastroliths have an unsurpassed potential for fossilization.

This short review intends to raise awareness for this topic and encourage paleontologists to search for gastroliths in coprolites in order to guard against any potential collection bias.

IDENTIFICATION OF UNAMBIGUOUS FINDS

Caution should be used when identifying stones in coprolites as former gastroliths because feces with a soft, plastic consistency are likely to enclose surrounding material including sediment after defecation. Sediment particles can also adhere to the surface of coprolites, as shown by Rodríguez-de la Rosa et al. (1998) for vertebrate coprolites from the Late Cretaceous (Campanian) Cerro del Pueblo Formation of southeastern Coahuila, Mexico. Sediment can also become incorporated into feces after deposition via reworking by other organisms. Herbivorous dinosaur feces from the Late Cretaceous Two Medicine Formation of Montana, USA, for instance, were reworked by scarabaeine dung beetles (Chin and Gill, 1996). The coprolites contain burrows with a sediment/plant material mixture. The sediment in this mixture was probably removed from a burrow excavated below the dung pat (Chin and Gill, 1996). For identification of unambiguous gastroliths, the amount of the enclosing coprolite matrix is important. It is highly plausible that completely surrounded pebbles represent former gastroliths.

Inorganic components that have passed through the digestive tract may come from several sources. For herbivorous birds, for example, they are often a combination of accidental intake of sediments ingested during feeding (e.g., attached to roots, see Wings (2007) for more details), parts of gastroliths derived from the high mechanical erosion in the gastric mill (Wings and Sander, 2007), and possibly also biogenic silica from ingested plant matter.

The size of non-foodstuff particles passing the digestive tract can be impressively large, as shown by 0.5 l cola cans thrown by irresponsible visitors into animal enclosures of the Stuttgart Wilhelma Zoo several years ago (Fig. 1). Despite their size, the cans were swallowed by members of two large mammal taxa: a hippopotamus (*Hippopotamus amphibius*) and a southern elephant seal (*Mirounga leonina*). While the hippopotamus chewed on the can, reducing its size considerably, and excreted it normally, the elephant seal swallowed the can at full size (original diameter: 67 mm) followed by its regurgitation (written comm. W. Rietschel, 2011). Such large, non-organic objects swallowed by extant animals show the potential to find gastroliths within coprolites of extinct large vertebrates (i.e., herbivorous dinosaurs). However, feces of herbivorous vertebrates seem to have a much lower fossilization potential than these of carnivorous taxa (Bradley, 1946; Chin, 1997).

It is also important to distinguish coprolites with a distinct outline from entire layers of biogenically reworked sediments. Sediment feeders can produce vast quantities of fecal pellets. These pellets often disintegrate upon compaction, but are still aggregated in coprolitic sediments (Dapples, 1938).

OCCURRENCES IN THE FOSSIL RECORD OF FISHES

There is only one coprolite (OESM-10006-102; Fig. 2) with gastroliths which is tentatively attributed to fish. It has recently been found together with a number of other presumably phosphatic coprolites in the Lower Paleocene Danian limestone of Faxe Quarry, Denmark (Milàn, 2010). Albeit exoliths *sensu* Wings (2007) have been described from the Danian of Denmark (Noe-Nygaard, 1975), this is the first report of stones from the Danian of Denmark that are unambiguous gastroliths.

The spherical morphology of the coprolite bears very weak signs of spiral coiling suggesting a fish as producer. However, given the fragmentary status of the coprolite and its irregular surface, a crocodilian producer cannot be ruled out. The coprolite contains two embedded quartz pebbles, possibly composed of chert. The first gastrolith is a beige-greyish, well-rounded, highly spherical pebble with 3 mm length and a greasy luster. The second gastrolith is an orange-brownish, sub-

FIGURE 1. Cola cans regurgitated by an elephant seal *Mirounga leonina* (left) and retrieved from feces of a hippopotamus *Hippopotamus amphibius* (right) in the Zoological Garden Wilhelma (Stuttgart, Germany) show the large possible size of non-foodstuff particles within the digestive tract of vertebrates.

rounded pebble with 7 mm length, a low sphericity and a resinous luster. The luster of the gastroliths does not differ from polish found on chert beach shingle (Wings, pers. obs.). The occurrence of two pebbles with a considerable size difference indicates excretion after accidental ingestion, albeit the fragmentary preservation of the coprolite makes precise statements difficult. Gastroliths in fishes are usually attributed to accidental intake (Wings, 2007).

OCCURRENCES IN THE FOSSIL RECORD OF CROCODILIANS

Fossil coprolites with gastroliths are known almost exclusively from archosaurs (i.e., crocodilians and birds). Fossil and extant crocodilians often possess gastroliths (Taylor, 1993; Whittle and Everhart, 2000; Wings, 2007), but their documentation within coprolites is rare. Jepsen (1963) described coprolites from the Eocene Golden Valley Formation of North Dakota, some of which contained plant matter, sand grains and small pebbles. It remains unclear, however, if the stones indeed represent gastroliths, because they mostly appear on the surfaces of the coprolites and because there is evidence that the fecal masses must have been quite plastic when voided (Jepsen, 1963).

Weigelt (1927) described possible feeding grounds of crocodilians from the Eocene lignite deposits of Geiseltal, Germany. Among the fossils found in the open pit mine Mücheln-Westfeld were not only several individuals of the alligatoroid *Diplocynodon* with associated gastroliths, but also layers with *Diplocynodon* teeth as well as coprolites attributed to this taxon because of their high similarity to feces of modern alligators (Weigelt, 1927). Some coprolites from this locality contain bones and teeth (Walter and Weigelt, 1934), others contain gastroliths (Hellmund, 2001; Walter and Weigelt, 1934; Weigelt, 1927) and probably provide one of the best examples for their combined occurrence in the fossil record (Fig. 3).

FIGURE 2. Photograph of a phosphatic fish coprolite with gastroliths from the Danian limestone quarry Faxe in Denmark (OESM-10006-102, collection of the Geomuseum Faxe/Østsjællands Museum, Denmark). The coprolite is 17 x 13 x 10 mm in size and contains two quartz gastroliths with 3 mm (black arrow) and 7 mm (white arrow) length, respectively.

Crocodilian gastroliths in coprolites are also known from Asia: coprolites were associated with the type specimen of *Asiatosuchus nanlingensis* from the Paleocene Shanghu Formation of Nanxiong, Guangdong Province, China (Young, 1964). A total number of 22 coprolites varying in length from 45 – 115 mm were found. One of them, described as more flattened than the others, contained pebbles which could represent gastroliths.

DeKay (1836) reported a reptilian coprolite with a "convoluted spiral structure". A small cavity contained "minute siliceous pebbles". It remains unclear, however, if these pebbles just adhere to the surface of the coprolite.

OCCURRENCES IN EXTANT BIRDS AND THE FOSSIL RECORD OF BIRDS

Herbivorous birds represent the largest and ecologically most varied group of extant lithophagic vertebrates (Gionfriddo and Best, 1999; Wings, 2004, 2007) and can hence be expected to produce a large number of feces with gastroliths. Extant tetraonid birds (grouses) defecate stones when exposed to an excess of grit or excrete the grit involuntarily when fed with coarse food such as hard twigs (Porkert and Höglund, 1984). An increase in the number of gastroliths in feces of dunnocks (*Prunella modularis*) correlates with a change in diet from insects to both seeds and insects (Bishton, 1986). This has previously been interpreted as an indication for the assistance of gastroliths in the grinding of vegetable matter (Bishton, 1986).

Ratites, the largest living birds, regularly utilize relatively large gastroliths in a gastric mill (Wings, 2004) and are therefore especially qualified for studies of the coexistence of gastroliths and feces. A "quick and dirty" experiment revealed that gastroliths are indeed regularly excreted in ratites. During a study mainly concerning amounts and function of ostrich (*Struthio camelus*) gastroliths (Wings, 2004; Wings and Sander, 2007), the author randomly collected a sample of 1.5 kg of ostrich feces (semi-dried as well as fresh fecal matter) on a pasture of free-ranging farm ostriches near Remagen, Germany in May 2002. After washing, the sample revealed a total amount of 184.4 g (12.3% of the partially moist fecal mass) sediment. A separation into grain sizes demonstrated that the vast majority of the excreted sediment particles (94.3%) was sand-sized (Figs. 4, 5), whereas the stomachs of these birds commonly contain stones with a size of up to a few centimeters (Wings, 2004).

This is consistent with finds from coprolites of upland moas (*Megalapteryx didinus*) from South Island, New Zealand. An examina-

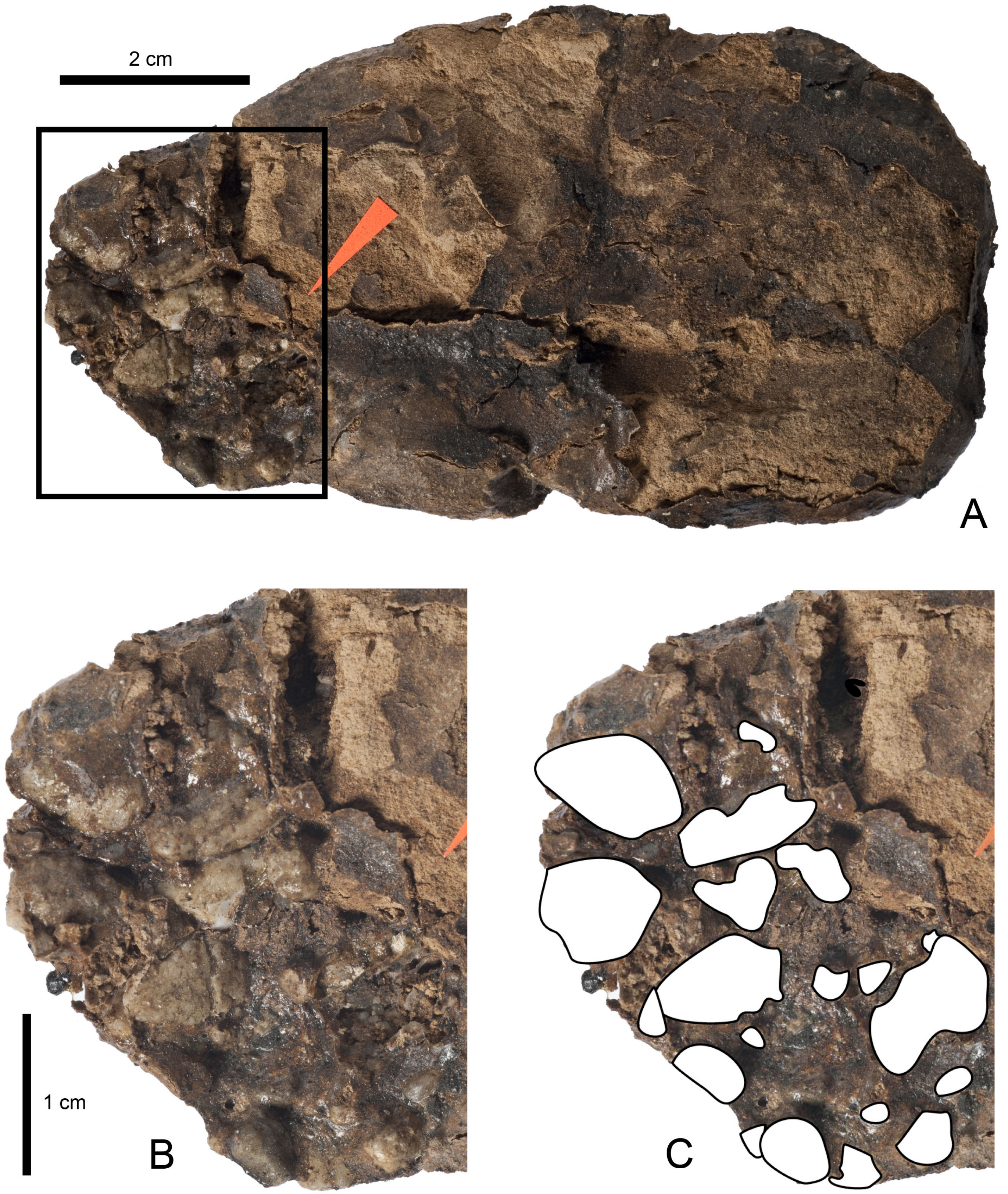

FIGURE 3. **A-C**, Photographs of a phosphatic crocodilian coprolite with gastroliths from the Eocene lignite deposit Geiseltal (Ce III-3637, collection of the Geiseltalmuseum, Halle (Saale), Germany). The coprolite is 100 x 54 x 18 mm in size and contains about 25 gastroliths sized between 1-10 mm. The gastroliths are concentrated on one end of the coprolite (**B**) and are mainly composed of white quartz, with feldspar and mudstone also being present. The originally smooth surface of the coprolite was consolidated with a thick lacquer layer with obscures the outlines (**C**) of the gastroliths.

tion of 35 coprolites showed that the organic content varied significantly from 27.2 – 69.8% (mean = 51.4%), but also that sediment particles (quartz grains, most as fine sand and silt, but occasionally up to 5.5 mm in diameter) occur on a regular basis (written comm., Jamie R. Wood, 2011).

A variety of moa gastroliths have been reported by Chapman (1884) from Mackenzie Country in the Central South Island (South Canterbury) region of New Zealand. Several finds of isolated sets of white exotic quartz pebbles (generally 3 – 4, but two sets contained nearly 30 pebbles) were attributed to former moa coprolites (Chapman, 1884). It remains unclear however, if these pebbles were still associated with coprolitic matter.

DISCUSSION AND CONCLUSIONS

Feces containing sediment particles may come not only from lithophagic vertebrate groups but also from vertebrates that accidentally ingested sediment particles. It remains unclear which group produces feces with a higher preservation potential: lithophagic animals usually possess an effective retention mechanism for gastroliths (especially in herbivorous birds, Gionfriddo and Best, 1999; Wings, 2004) whereas accidental ingestion of sediment particles in other vertebrates followed by their immediate defecation is a rare event. Gastroliths in lithophagic vertebrate clades without an avian-style gastric mill, such as pinnipeds or crocodilians, experience much less erosion and have consequently less ground-off sediment particles in their feces. This may explain why the majority of reports of large-sized gastroliths in coprolites come from crocodilians.

Since the uptake of gastroliths by farm ostriches takes place continuously, often even on a daily basis (personal observations 2000-2003), the excretion of rock material is expected to happen continuously too. The preliminary research on ostrich feces presented herein shows a typical size for excreted gastroliths of <2 mm and a maximum size of <8 mm (Figs. 4-5). The general rarity of grain sizes >2 mm is a result of the preferred excretion by the ostriches. Sand-sized gastroliths are probably too small to be of efficient use in the trituration of foodstuffs and/or are difficult to separate from pulped foodstuffs in the stomach and are thus excreted.

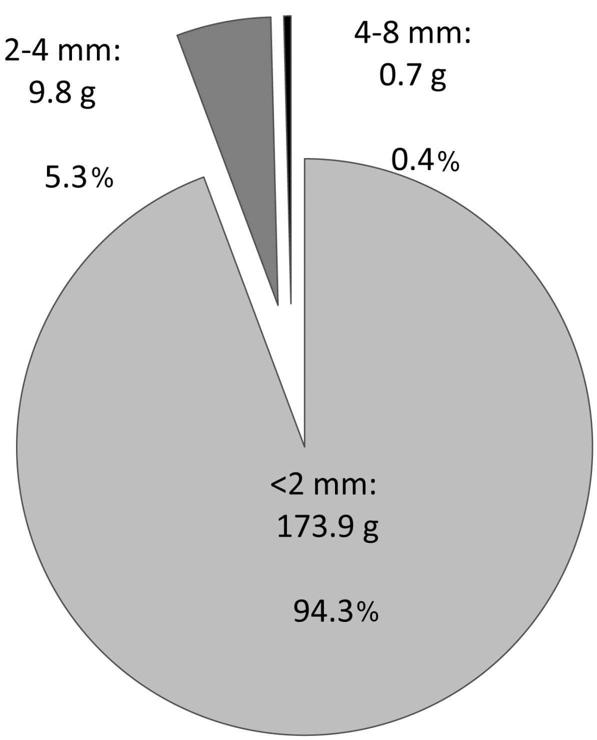

FIGURE 4. Circular chart showing mass distribution of different grain sizes of gastroliths in ostrich feces. The vast majority of gastroliths is sand-sized and hence smaller than the average gastrolith in the gizzard (Wings, 2004).

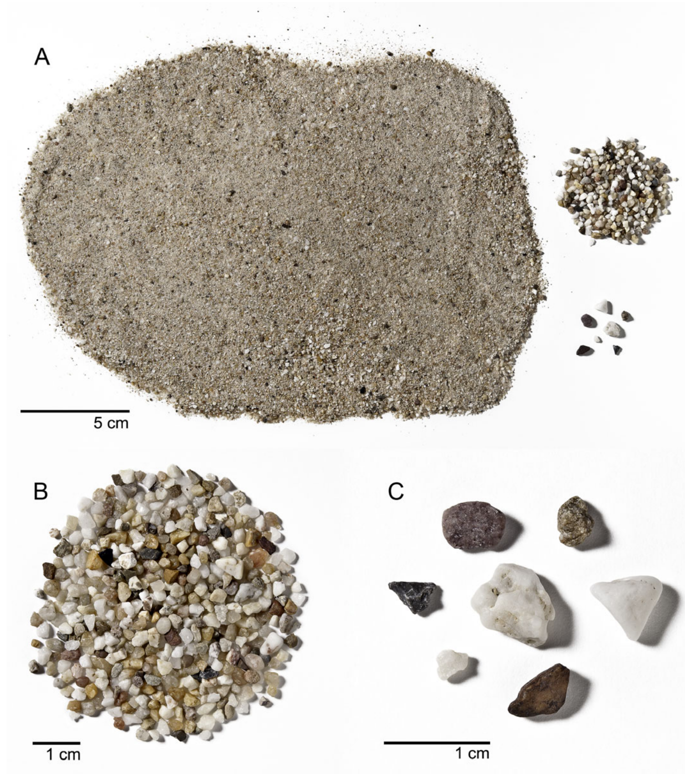

FIGURE 5. Photographs of the gastroliths retrieved from ostrich feces. **A**, Total mass, separated into grain sizes. Note the large amount of sand left of the larger grain sizes. **B-C**, Close-up photos of the gastroliths in the size-range **B**, 2 – 4 mm and **C**, 4 – 8 mm. Surface and general appearance of the gastroliths is similar to gastroliths retrieved directly from ostrich stomachs (Wings, 2004; Wings and Sander, 2007).

Interestingly, the gastroliths reported from crocodilian coprolites appear generally to have a larger size that the gastroliths retrieved from avian feces/coprolites. This is another indication for functional differences in gastrolith utilization between these two vertebrate groups (Wings, 2007).

A loss of "working size" gastroliths during life via regurgitation or defecation is possible in all lithophagic vertebrates, but seem not to occur on a regular basis, except in pinnipeds via regurgitation (Wings, 2004). Very small ground-off pieces of gastroliths, which are probably excreted continuously in taxa with a gastric mill, are difficult to detect macroscopically in coprolites. At least in birds, the stones are usually kept in the gizzard until they are totally eroded (Wings, 2004; Wings and Sander, 2007).

Numerous skeletal finds within Archosauria (i.e. Crocodylomorpha, Dinosauria, Aves) and Plesiosauria have been found with associated gastroliths. It is plausible to assume that these vertebrate groups have defecated gastroliths as well. In contrast, gastroliths are relatively rare in fishes (Whittle and Everhart, 2000; Wings, 2007), which is possibly the reason why the vast abundance of coprolites attributed to fishes has not yet shown any evidence of gastroliths.

The potential of feces of certain taxa for fossilization is also important. Not only do feces in certain environmental settings (i.e., shallow aquatic habitats) have a higher potential for fossilization than in other habitats (i.e., terrestrial settings), their initial chemical composition is also important (Chin, 1997).

The remarkable rarity of gastroliths in coprolites cannot be explained by their taphonomy. A high percentage of all gastroliths is composed of quartz, a mechanically resistant and chemically stable mineral (Wings, 2009; Wings and Sander, 2007). It is not plausible that sediment particles within feces prevent the fossilization of the latter. It remains unclear, however, if this rarity may be partly attributed to collection bias or lack of research interest. It is possible that many more gastroliths in coprolites are waiting to be discovered in the field and in fossil collections. A raised awareness for such finds will not only help to assess their true frequency, but might help solve paleobiological puzzles.

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