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COPROLITES OF *DEINOSUCHUS* AND OTHER CROCODYLIANS FROM THE UPPER CRETACEOUS OF WESTERN GEORGIA, USA

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Abstract—Associated with abundant bones, teeth and osteoderms of the giant eusuchian *Deinosuchus rugosus* are larger concretionary masses of consistent form and composition. It is proposed that these are crocodylian coprolites, and further, based on their size and abundance, that these are coprolites of *Deinosuchus*. The associated coprolite assemblage also contains additional types that may come from smaller crocodylians, most likely species of the riverine/estuarine genus *Borealosuchus*, which is represented by bones, osteoderms and teeth in fossil collections from the same site.

INTRODUCTION

The Upper Cretaceous Blufftown Formation in western Georgia contains a diverse perimarine and marine vertebrate fauna, including many sharks and bony fish (Case and Schwimmer, 1988), mosasaurs, plesiosaurs, turtles (Schwimmer, 1986), dinosaurs (Schwimmer et al., 1993), and of particular interest here, abundant remains of the giant eusuchian crocodylian *Deinosuchus rugosus* (Schwimmer and Williams, 1996; Schwimmer, 2002). Together with bite traces attributable to *Deinosuchus* (see Schwimmer, this volume), there are more than 60 coprolites recovered from the same formation, including ~30 specimens that appear to be of crocodylian origin. It is proposed here that the larger coprolites are from *Deinosuchus*, principally because that is the most common large tetrapod in the vertebrate bone assemblage from the same locality, and it is assumed that feces scale to the producer (Chin, 2002). The additional coprolites of apparently crocodylian origin considered here are tentatively assigned to an indeterminate species of *Borealosuchus*, which is the second most common crocodylian in the fossil assemblage.

Age and Paleoenvironment

The specimens in consideration come from a ~1.0-m thick bonebed in the uppermost Blufftown Formation, a detrital sedimentary unit that represents a mixture of marine coastal salt marshes, back-barrier embayments, and tidal estuaries along the southeastern coast of North America during the Late Cretaceous (Reinhardt and Donovan, 1986). This geographic position is significant because it was then at the boundary of the Atlantic and Gulf Coastal Plains, although the Cenozoic growth of Florida places it now in the easternmost Gulf Coastal region (Frazier and Schwimmer, 1987). The locality sampled for all of the material here is near the boundary of the States of Georgia and Alabama in the southeastern United States (Fig. 1), along the banks of Hannahatchee Creek, a major tributary to the Chattahoochee River, in Stewart County, western Georgia. The detailed site stratigraphy is presented in Schwimmer (1986), and the precise GPS coordinates are available by contacting DRS.

At the sampling locality, the Blufftown Formation is dated to the latest-early Campanian (78.0 ± 1.0 Ma) by the co-occurrence of numerous index taxa, including oysters (*Exogyra erraticostata*), ammonites (*Placenticeras dekayi*), planktonic foraminiferans, and by lithostratigraphic correlation with regional chalk formations containing abundant calcareous microfossils (Schwimmer et al., 1994). The Blufftown Formation is overall approximately 125 m thick and ranges down to ages of approximately 84 Ma (Schwimmer et al., 1994); however, the specimens here are from the very top of the formation.

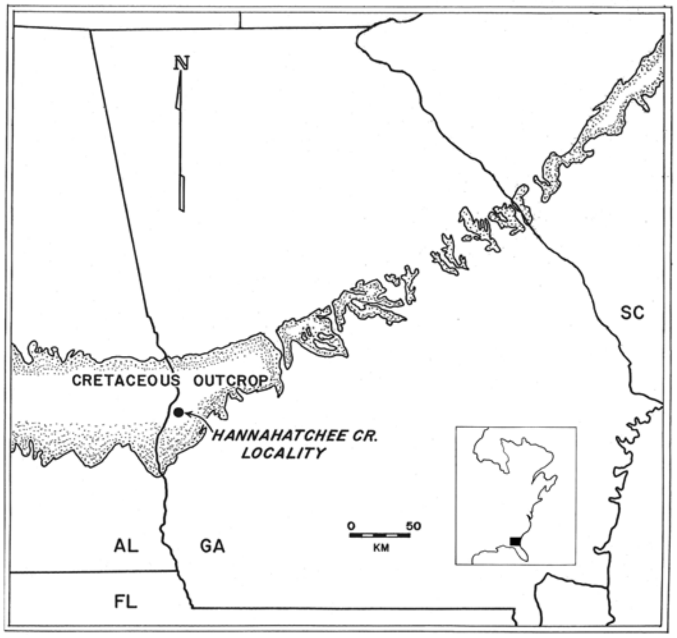

FIGURE 1. Locality map, showing the approximate position of the collecting site for all specimens in study. The study area is in western Georgia, USA, within the valley of Hannahatchee Creek, a tributary to the Chattahoochee River. The inset map of eastern North America shows the position of the locality map within the southeastern continent.

COPROLITES ATTRIBUTED TO *DEINOSUCHUS*

Identifying the source of a Mesozoic coprolite can be a daunting task. Of the general categories of sedimentary masses found in association with numerous *Deinosuchus* fossils in the Blufftown Formation, the six largest of these have shapes and large size (Fig. 2) most parsimoniously attributed to *Deinosuchus*. This attribution is based on several factors. First, *Deinosuchus* specimens extrapolated to 7-9 m total length are locally common and by far the most abundant larger tetrapods in the vertebrate assemblage from this site; indeed, this locality has the most abundant known assemblage of *Deinosuchus* bones and teeth in the eastern USA (Schwimmer, 2002). Second, the overall external form of these presumed coprolite masses, as discussed below, is reasonably close to crocodylian coprolites from other ages and settings (e.g., Sawyer, 1981; Milàn, this volume). Finally, these are relatively large masses (relative to other non-dinosaurian coprolites), and *Deinosuchus* is precisely a large, non-dinosaurian tetrapod.

These putative *Deinosuchus* coprolites are ellipsoidal and isopolar (*sensu* Thulborn, 1991), ranging from 9 to 11 cm in length (averaging 10.25 cm), with the average width of 5.25 cm, ranging from 4.5 cm to 8.0 cm. The six well-preserved masses are grossly uniform in being relatively wide in cross-section in proportion to length, but they range in outline

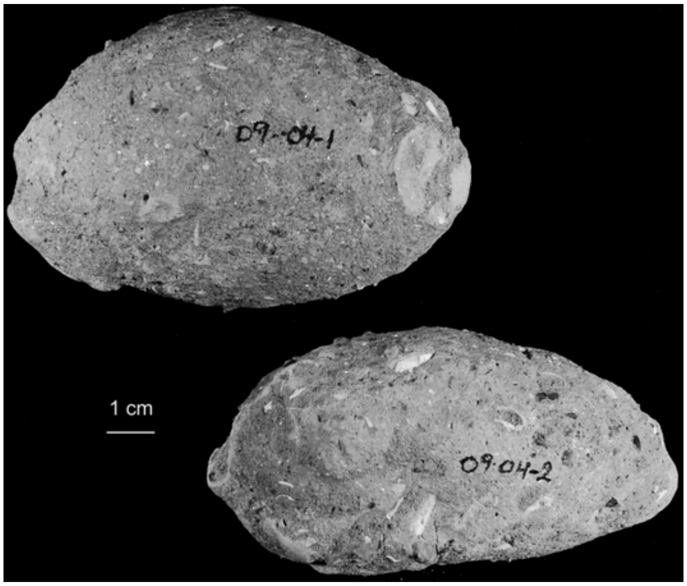

FIGURE 2. Representative coprolites of *Deinosuchus rugosus*, both are from the uppermost meter of the Blufftown Formation, Hannahatchee Creek locality, Stewart County, Georgia (all specimens to be figured here from the same locality). All specimens are catalogued in Columbus State University Cretaceous (CSUK) collections: these are (upper left) CSUK-09-04-1 and (lower right) CSUK-09-04-2. Scale bars in all figures = 1 cm (except Fig. 7). Note the surface accumulations of carbonate shell debris, siliceous detritus, and minor (darker) vertebrate material.

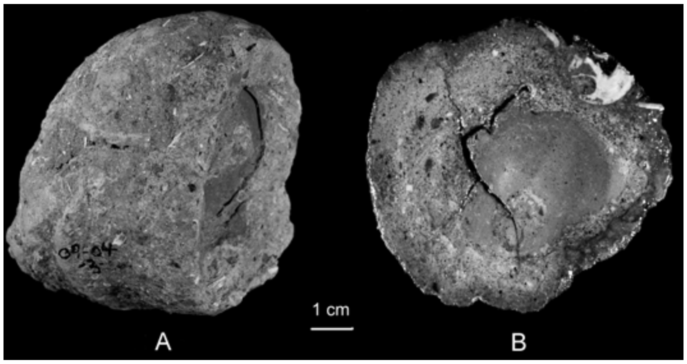

FIGURE 3. Largest (8.0 cm diameter) coprolite in the assemblage, CSUK-09-04-3, with one tapered end and broken surface showing distinctly separate core and cortex. In this specimen the cortex is relatively asymmetrical (compare with Figure 5), and incorporates some larger shells and detritus which are assumed to have accreted onto the original fecal mass.

from elongate cylinders to sub-ovals. All of these that are complete have tapering ends, but none show clearly-indicated sphincter marks. Structurally and sedimentologically they have many of the characteristics of common septarian concretions (McBride et al., 2003), but with open voids internally rather than the mineral-filled cracks found in septaria; however, we argue below that the origin of these concretions is fecal. In the discussion to follow, we divide the morphology of these putative coprolites into three distinct regions: outer surfaces (Fig. 3A), cortices and cores (Fig. 3B).

The outer surfaces of these presumed *Deinosuchus* coprolitic masses are mostly gray to tan, agglutinated quartz sand, carbonate clasts and mica, with invertebrate shell fragments, and osteichthyan and shark teeth comprising ~5% of the surface material. The cortices (i.e., the outer zones between surfaces and cores) comprise approximately the outer 0.8-1.0 cm volume in most specimens where they are visible, and contain materials similar to the surfaces but with increased amounts of carbonate clasts, bone fragments and small fish teeth. One specimen (Fig. 4) includes a well-preserved shark tooth (*Squalicorax yangaensis*) in the cortex.

The cores of these coprolites consist of a slightly darker, fine grained matrix (Fig. 5A), which is composed largely of microcrystalline calcite with a few, very small, empty vesicles, and minor inclusions of a wide variety of materials, including opaque, presumably organic substances. The notable feature evident in the cores of cut or broken specimens (Fig. 5B) is large fissures. These fissures are not as extensive as are typically found in septarian concretions, but they do resemble closely the radial fissure configuration present in some dinosaur coprolites (Thulborn, 1991). The presence of fissures in these presumed *Deinosuchus* coprolites, versus the more typical small gas vesicles found in smaller crocodylian coprolites (see below), is explained as follows: in smaller fecal masses, numerous small vesicles occur from gas bubbles, which are small and abundant, and which may escape to the surface. In the large fecal masses of dinosaurs (Thulborn, 1991) and presumably *Deinosuchus*-size crocodylians, large volumes of gases (principally methane and ammonia) would instead be confined by the large size of the mass, producing elongate voids, which would be preserved as radial fissures. It is also noteworthy that these fissures are generally open, rather than filled with calcite crystals, as in typical septarian concretions.

The mineralogical composition of the presumed *Deinosuchus* coprolites is unusual. To explain their makeup, it is here hypothesized that these masses, which are obviously concretionary, developed around the original *Deinosuchus* fecal masses, which are represented by the cores. Thus, the relatively homogeneous carbonate cores of the coprolites represent the approximate size and shape of the feces, which is approximately 7.0 to 10.0 cm long by ~ 5.0 cm diameter, whereas the "cortex" of each mass is mostly detrital sedimentary material that accumulated around the original fecal mass. Bacterial films would naturally form around the feces and would be sticky, attracting external material to the developing concretions (Hendry et al., 2006). Although coprolites from carnivores are typically mineralized by fluorapatite in terrestrial and freshwater environments (Chin, 2002), they may also become the nuclei for concretionary growth (Thulborn, 1991). Formation of a carbonate concretion around large feces in marine deposits may occur when the mass is buried just below the sediment-water interface in finer-gained, carbonate-rich sediment. In this model, anaerobic decomposition produces abundant NH_3, raising the local pH, and favoring precipitation of carbonate (Weeks, 1957). We hypothesize that marine sedimentary conditions of the Blufftown Formation, and the relatively large size of these *Deinosuchus*-size masses, favored this mode of preservation of the cores of these coprolites.

The distinctive cortices of these specimens are assumed to have accumulated well after the feces were excreted, during extensive marine transport and redeposition. The upper 1.0 m of the Blufftown Formation, where these coprolites are found, contains a concentrated bed of fragmentary bones of many organisms (Schwimmer, 1986) and very abundant, usually water-worn fish teeth (Case and Schwimmer, 1988). This type of sedimentary deposit is best explained as a marine transgressive lag concentration, where teeth and bones initially accumulated in the nearshore marine environment, and are subsequently carried by cyclical high-sea stands into sediment-starved bays and estuaries along the marine coast (Schwimmer, 2002). During the extensive transport and times of accumulation, it is assumed the developing concretionary masses would roll around, pick up detritus and bone fragments, and accrete largely in width. It is notable that the cores extend well to the ends of the masses (Fig. 5B), whereas the cross-sections show thick annular accumulation of the cortex (Fig. 5A). Some of the fish teeth embedded in the cortices and on the surfaces may also represent coprophagous feeding by bony fish and sharks (e.g., Fig. 4).

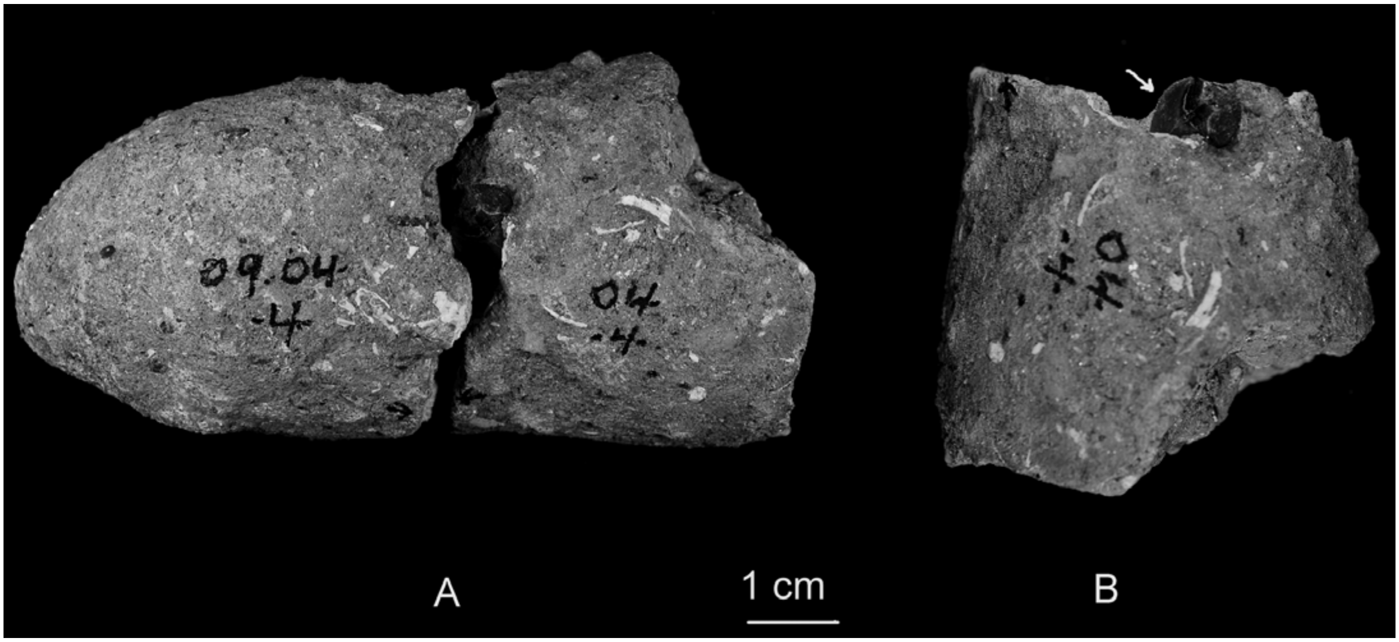

FIGURE 4. *Deinosuchus* coprolite including complete shark tooth (*Squalicorax yangaensis*), CSUK-09-04-4: **A**, overall coprolite morphology. **B**, broken end separated and rotated to show shark tooth (arrow). Note that preservation of the shark tooth is very good, suggesting that the tooth was implanted in the coprolite after it was transported back to the final depositional site (i.e., the shark may have been feeding on the coprolite).

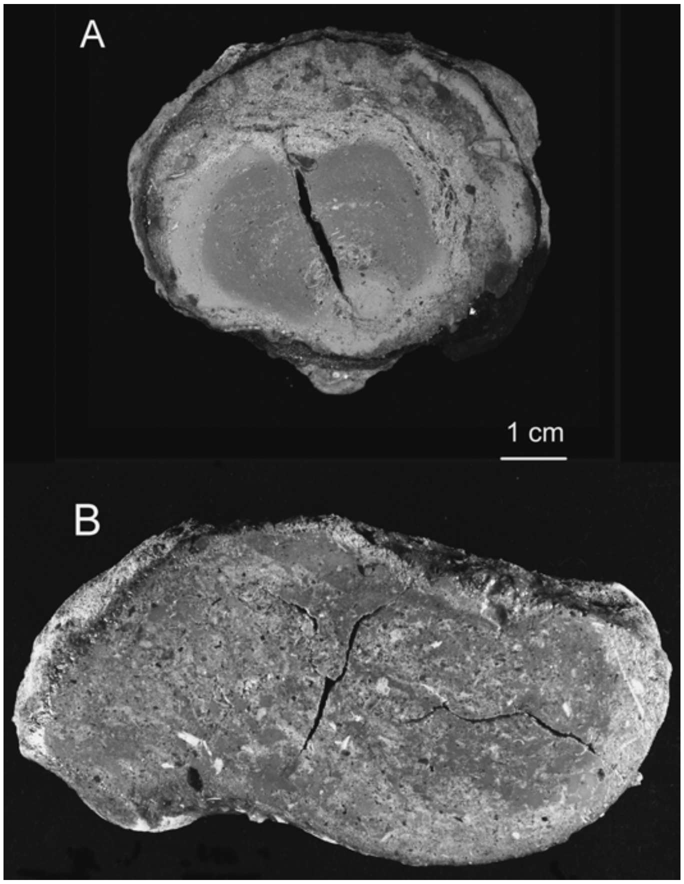

FIGURE 5. Cut specimens of assumed *Deinosuchus* coprolites: **A**, CSUK-09-02-2, cross-sectioned and polished specimen, showing the distinct core and relatively symmetrical cortex. **B**, CSUK-09-02-1, sagittally cut and polished specimen. Note the extensive fissure visible in both sections, and that the core in B persists close to the two ends.

ADDITIONAL COPROLITES ATTRIBUTED TO CROCODYLIANS

Smaller (relative to the above) coprolites in the Blufftown assemblage are generally more typical of the sizes, shapes, and surface features generally assumed for crocodylian coprolites (Fisher, 1981; Sawyer, 1981; Milan, this volume). These coprolites vary widely in size, averaging 4.0 cm in length by 2.2 cm width, and they are relatively dark and more uniform in texture than the *Deinosuchus* coprolites discussed above. The overall shapes vary (Fig. 6), with some showing strong coiled or ropy-textures, presumed to result from digestive compaction (Fig. 6A), which are quite typical of carnivorous tetrapod coprolites (Chin, 2002). Several of these smaller coprolites also show characteristic anisopolar morphology (Thulborn, 1991) with one strongly tapered end (Fig. 6B), typical of terrestrial carnivore scat. Several smaller isopolar coprolites in the assemblage have a J-shaped morphology (Fig. 6C), which may be representative of some smaller crocodylian feces (J. Milàn, pers. comm.).

The internal composition of these smaller coprolites appears relatively uniform and is composed of darker, microcrystalline phosphatic mineral (collophane), with abundant, well-demarcated voids (Fig. 7), presumed to be formed by gas bubbles entrapped while the masses were nonmineralized. No evidence of preserved bone or any invertebrate materials has been found either within or on the surfaces of these smaller coprolites. As discussed above, the associated Blufftown Formation vertebrate assemblage includes many types of tetrapod carnivores, which could hypothetically produce ~ 4.0 cm coprolites, ranging from smaller theropod dinosaurs (an indeterminate ornithomimisaur and cf. *Saurornitholestes* sp.), to mosasaurs, plesiosaurs, turtles, and crocodylians. There are also large fish in the assemblage (e.g., the 4-m-long teleost *Xiphactinus*: Schwimmer, et al., 1997, and the similar-sized coelacanth *Megalocoelacanthus*: Schwimmer, et al., 1994), which conceivably could produce some of these masses. Assuming they are crocodylian in origin, the fossil assemblage includes numerous teeth, osteoderms and a few vertebrae and jaw fragments attributed to an indeterminate species of *Borealosuchus*, which would be the mostly likely source of smaller crocodylian coprolites in this collection.

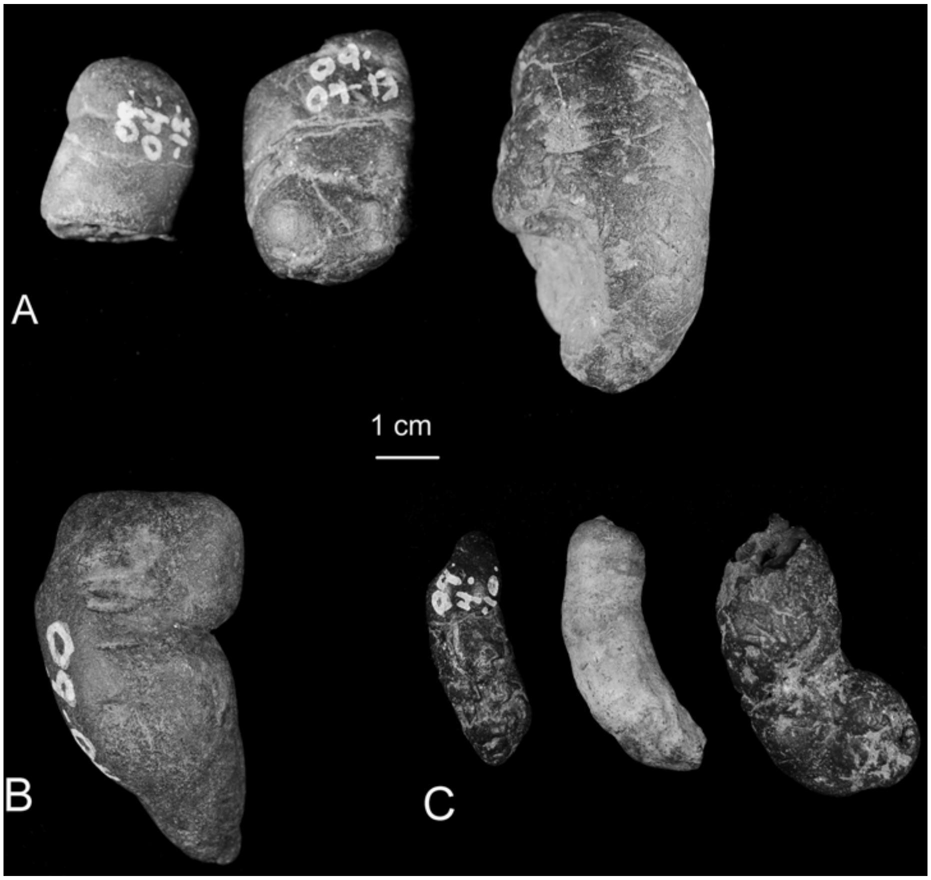

FIGURE 6. Smaller, more typical tetrapod coprolites from the Blufftown Formation, same locality as the preceding figures: **A**, (left to right) CSUK-09-04-12, -13, -14, masses of generalized coprolitic morphology, notably with ropy surfaces suggesting digestive compaction; **B**, CSUK-09-04-10 complete coprolite with tapered unipolar morphology; **C**, (left to right) CSUK-09-04-10, -8, -9, J-shaped coprolites, notably with more complex surface sculpting and relatively uniform shape.

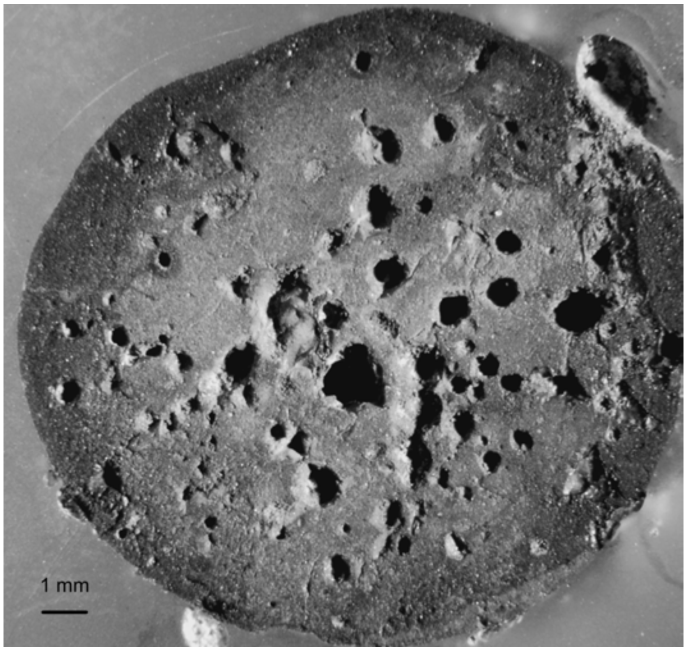

FIGURE 7. Cross-sectional view of smaller coprolite, CSUK-09-04-16, similar in size and morphology to the specimens in Figure 6C. The specimen is embedded in epoxy and polished, showing microcrystalline apatite composition with numerous ~ 1 mm diameter voids. Scale bar for this figure is 1 mm.

SUMMARY AND CONCLUSIONS

The larger masses proposed here as *Deinosuchus* coprolites are atypical crocodylian coprolites, in that they are preserved as carbonate-cored concretions with differentiated concentric internal structure, including internal fissures and a large amount of accumulated sedimentary material in the outer region. The explanation of all these unique characteristics is the combination of the large size of *Deinosuchus* feces and their marine depositional and transportation history. It is hypothesized that these *Deinosuchus* coprolites underwent some diagenetic processes more similar to the feces of dinosaurs rather than of smaller crocodylians, but their occurrence in nearshore marine environments favored replacement with calcite rather than the more typical mineralization by apatite. The smaller coprolites in the same deposit are typical of those from average-sized crocodylians, and derive from *Borealosuchus* or a similar-sized reptilian carnivore.

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Chinese alligator. Photo by Jesper Milàn.