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## Turtle Shell Impression in a Coprolite from South Carolina, USA

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### ABSTRACT

Coprolites (fossilized feces) can preserve a wide range of biogenic components. A mold of a hatchling turtle partial shell (carapace) referable to *Taphrosphys sulcatus* is here identified within a coprolite from Clapp Creek in Kingstree, Williamsburg County, South Carolina, USA. The specimen is the first-known coprolite to preserve a vertebrate body impression. The small size of the turtle shell coupled with the fact that it shows signs of breakage indicates that the turtle was ingested and that the impression was made while the feces were still within the body of the predator. The detailed impression could only have survived the act of defecation if the section of bony carapace was voided concurrently and remained bonded with the feces until the latter lithified. Exceptionally, the surface texture of the scutes is preserved, including its finely pitted embryonic texture and a narrow perimeter of hatchling scute texture. The very small size of the shell represented by the impression makes it a suitable size for swallowing by any one of several large predators known from this locality. The coprolite was collected from a lag deposit containing a temporally mixed vertebrate assemblage (Cretaceous, Paleocene and Plio-Pleistocene). The genus *Taphrosphys* is known from both sides of the Cretaceous–Paleogene (K–Pg) boundary so, based on the size of the coprolite and the locally-known predators, the juvenile turtle could have been ingested by a mosasaur, a crocodylian, or a theropod dinosaur. Unlike mosasaurs and theropod dinosaurs, crocodylian stomachs have extremely high acid content that almost always dissolves bone. Therefore, the likely predator of this turtle was a mosasaur or a (non-avian or avian) theropod dinosaur.

### KEYWORDS

Coprolite; Turtle shell impression; *Taphrosphys*; Bothremyidae; Testudines; Theropod; Dinosaur; Bird; Mosasaur; Crocodylian

### Introduction

An ever-increasing diversity of biogenic components is being found preserved within coprolites. Some of these include DNA fragments (Poinar et al., 2003), spores and pollen (Horrocks et al. 2004), filamentous fungi (Mahaney et al., 2013), phytoliths, other plant parts (Scott, 1977; Nambudiri and Binda, 1989) and wood fragments (Chin, 2007), cyanobacteria (Northwood, 2005), bacteria, bacterial endospores and bacterial residues, diatoms, radiolarians (Moodie, 1916; Hollocher et al., 2001; Mahaney et al., 2013; Souto, 2012), insects and other arthropods and vertebrate tissues including bones, muscle, teeth, scales, keratin and feathers (Wetmore, 1943; Waldman and Hopkins, 1970; Ash, 1978; Parris and Holman, 1978; Sohn and Chatterjee, 1979; Fisher, 1981; Martin, 1981; Thulborn, 1991; Hunt, Chin and Lockley, 1994; Davis and Briggs, 1995; Shimada, 1997; Chin et al., 1998, 2003; Chin, 2002, 2007; Northwood, 2005; Prasad et al., 2005; Everhart, 2007; Smith and Botha-Brink, 2011). Coprolites are also known to preserve external markings made by other organisms interacting with the feces, such as feeding traces

(Månsby, 2009, fig. 3I; Eriksson et al., 2011; Anagnostakis, 2013) or tooth impressions (Godfrey and Smith, 2010; Godfrey and Palmer, 2015).

Until now, no coprolite was known to preserve a vertebrate body impression. Here a single coprolite (Calvert Marine Museum Vertebrate collection, CMM-V-4524, Fig. 1) from Clapp Creek in Kingstree, Williamsburg County, South Carolina, USA is documented to preserve a natural mold of a partial turtle shell (carapace and scutes) referable to *Taphrosphys sulcatus* (Bothremyidae, Testudines). This occurrence provides another example of how coprolites can preserve evidence of trophic interactions that cannot be known solely from the study of body fossils.

### Geologic setting

This coprolite was found, along with many hundreds of other coprolites, along an underwater bank of Clapp Creek, a tributary of the Black River, within the city limits of Kingstree, Williamsburg County, South Carolina. The

underwater site is only about 2 m in length. It was recovered from a thick lag deposit of unconsolidated sediment, predominantly phosphatic quartz sands, comprising a “bone bed” that includes a temporally mixed vertebrate assemblage of Late Cretaceous, Paleocene and Plio-Pleistocene taxa (Cicimurri, 2010; Soehner, 2012). The vertebrate fauna includes Cretaceous chondrichthyans and dinosaurs; Paleocene chondrichthyans, actinopterygians, trionychid and chelonoid turtles and crocodylians (Purdy, 1998; Weems, 1998; Soehner, 2012); and Plio-Pleistocene chondrichthyans, equids, proboscideans and cetaceans (Cicimurri, 2007, 2010). Coprolites are the most abundant material occurring in this bone bed (Soehner, 2012).

The source of the Cretaceous fossils is probably Maastrichtian strata (either the Peedee or Steel Creek formations), whereas the Paleocene fossils likely derive from the Danian Rhems and Thanetian Williamsburg formations. Weems and Bybell (1998) and Cicimurri (2010) proposed that these fossils were probably concentrated together during a Plio-Pleistocene sea level highstand, at which time the Plio-Pleistocene vertebrate material was added to the mix.

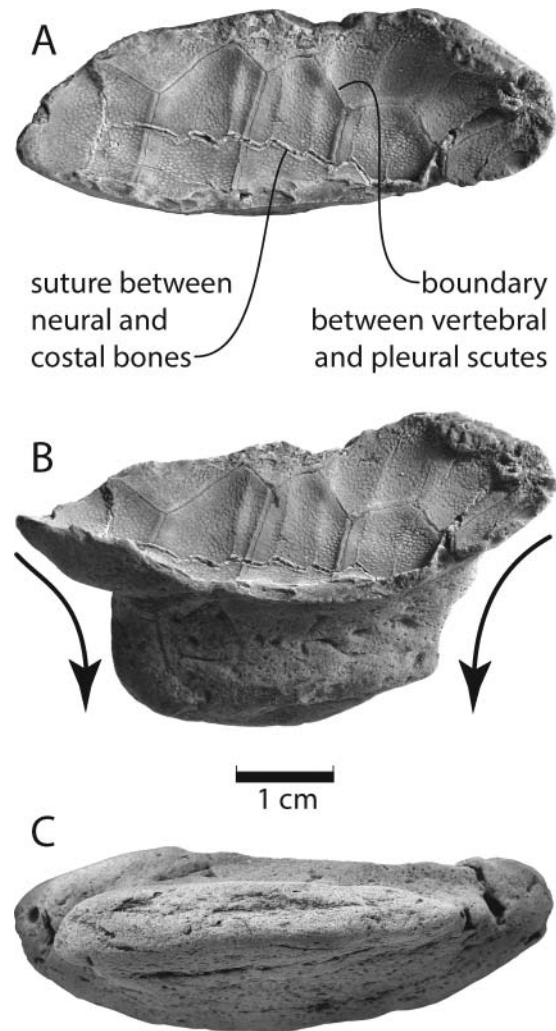
At all three times when these fossils were accumulating, the paleoenvironment in the Kingstree area was a nearshore coastal environment, with the coprolite-rich bone bed probably deposited in an estuary (Weems and Bybell, 1998; Soehner, 2012). This environment would have supported both the marine and terrestrial fauna occurring at this locality.

## Results

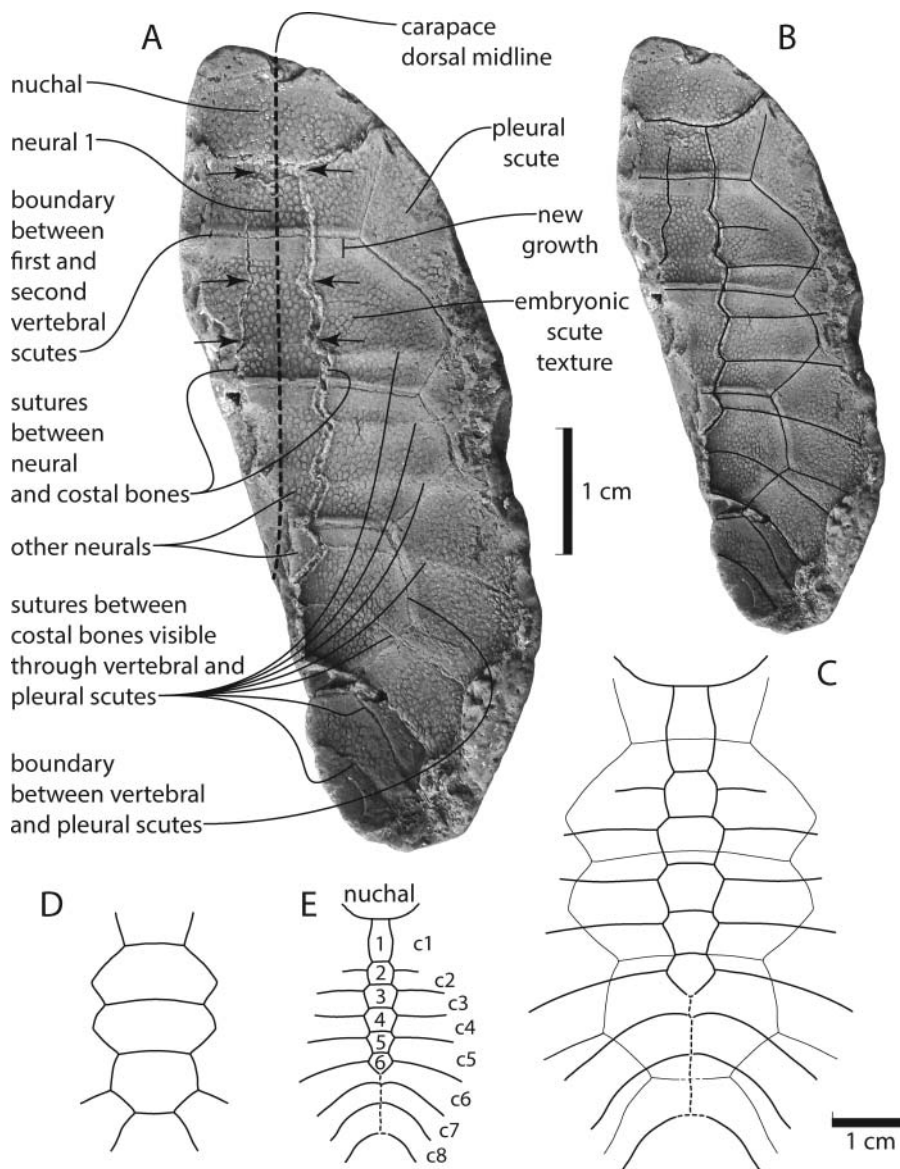
Coprolite CMM-V-4524 (Figs. 1 and 2) is irregularly shaped, unlike the cylindrical shape of most of the other coprolites known from this locality (Sawyer, 1998). As with the vast majority of the coprolites from Clapp Creek, it is very dark in color: between a dusky purple (5RP 2/2) and black (N1) in the Munsell Rock-Color Chart (2009 revision). In its natural state, the surface of the coprolite exhibits a somewhat reflective patina. CMM-V-4524 measures 57.5 mm long by approximately 20.5 mm wide and 33 mm deep. No inclusions are visible on the surface of this coprolite.

The overall shape of the coprolite approximates that of the hull of a sailboat with a very prominent keel. The impression of the outer surface of the turtle shell occupies the concave interior of the “hull” in this analogy (Fig. 1B). The unusual overall shape is attributed to the presence of the turtle shell and the direction in which the feces were voided. The arrows in Figure 1B indicate the direction the feces passed through the cloaca; the keel passing first before the cloaca stretched to

accommodate the shell. The impression (i.e., a natural mold of the external surface of the carapace) preserves a portion of the entire turtle shell, and there seems to be no way of knowing how much more of the shell may have been present at the time the impression in the feces was made. The impression preserves two zigzagging linear markings (Fig. 1A). The upper one in Figure 1A marks the boundary between vertebral and pleural scutes. The other represents an open suture between the neural and costal bones. Perhaps this open suture was



**Figure 1.** (A) CMM-V-4524, a vertebrate coprolite from Clapp Creek in Kingstree, Williamsburg County, South Carolina, USA, preserving an impression of most of a turtle carapace. Anterior of carapace is to the left. (B) Same specimen in profile showing that, beyond the area of the impression, the coprolite is reduced and more bilaterally compressed in proportions; probably more nearly approximating the normal size and shape of the cloacal aperture. The arrows indicate the direction the feces passed through the cloaca; the keel passing first before the cloaca stretched to accommodate the shell. (C) Ventral view of the same specimen, whitened with sublimed ammonium chloride to improve contrast.



**Figure 2.** (A) Details of the impression of a turtle carapace as preserved in vertebrate coprolite CMM-V-4524; anterior end is toward top of page. The opposing black arrows point out some of the symmetrical landmarks along the left and right sutures between neurals and pleurals. Specimen is whitened with sublimed ammonium chloride to improve contrast. (B) Sutures are highlighted between vertebral and pleural scutes, and between neural and costal bones. (C) Partial restoration of the carapace based on CMM-V-4524. (D) Conformation of the preserved scutes without the bony carapace elements. (E) Conformation of the preserved bony carapace elements without the scutes. 1–6 comprise the neurals; c1–c8 identify the costals.

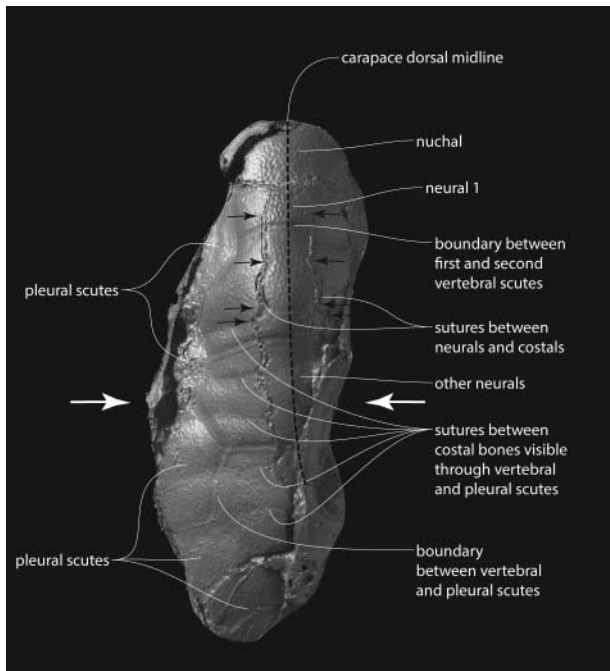
caused by oral “nutcracking” of the turtle shell by its predator or tight passage of the shell through the cloaca.

Papillate-textured impressions of portions of five vertebral scutes and four pleural scutes are visible (Figs. 1 and 2D). Furthermore, impressions of portions of at least 14 osseous carapace elements are preserved in CMM-V-4524 (Figs. 2E and 5A). These are interpreted to represent parts or all of the nuchal, neurals 1–6, costals 1–8 and possibly part of a suprapygal or pygal from the left side of the shell (Fig. 3, mirror reversed in the impression, Fig. 2).

The preserved surface of the natural mold of the shell (Figs. 1 and 2A) is textured by closely spaced, roughly circular papillae. An alginite cast shows the original texture to be reminiscent of the pitted or pocked surface of a golf ball (Figs. 3 and 4A), but on a smaller scale. The depressions vary in size, but most of them are approximately 0.5 mm in diameter.

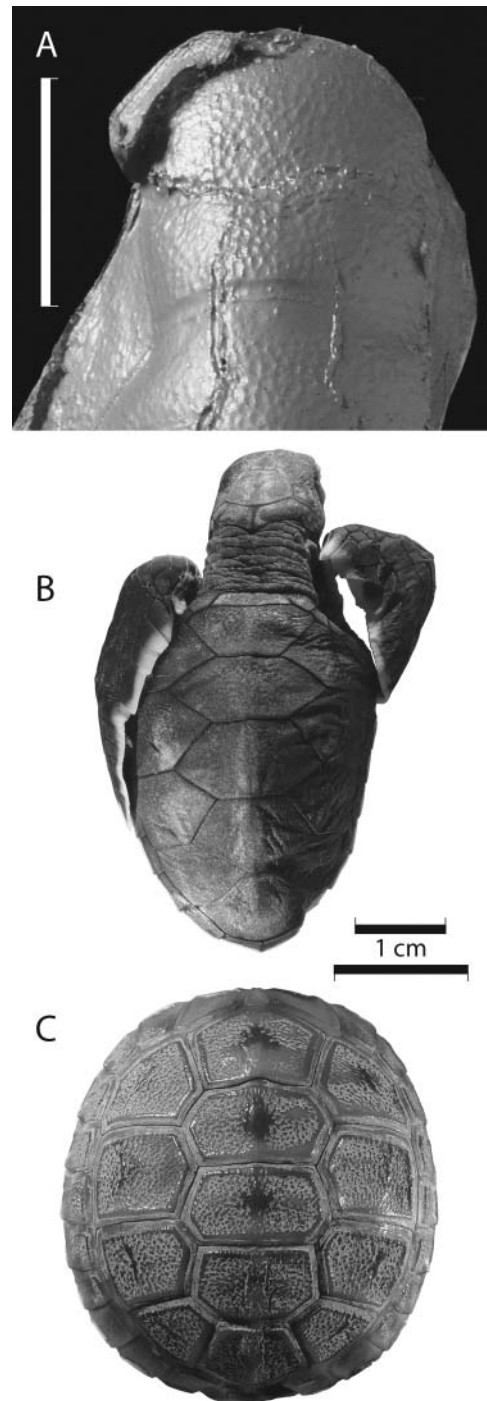
Typically, a fossil turtle carapace consists only of bones or bone impressions. In such specimens, the pattern of the scutes that overlay these bones can be documented only indirectly by grooves on the external



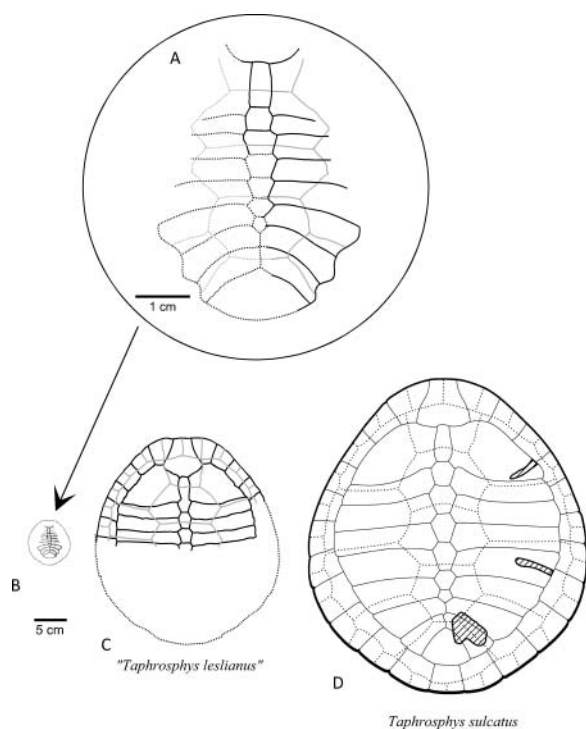


**Figure 3.** Alginite cast of the turtle carapace impression within vertebrate coprolite CMM-V-4524, whitened with ammonium chloride and in normal relief. Anterior end is toward top of page. The black dashed line marks the dorsal midline of the carapace. The opposing black arrows point out some of the symmetrical landmarks along the left and right sutures between neurals and costals. The white arrows show the direction in which the turtle shell was compressed, which resulted in opening the sutures between neurals and costals.

carapace bone surfaces that mark the boundaries of the scutes. If the carapace bones become somewhat offset during sediment compaction, the offsets are quite abrupt because the individual bones are hard. In this specimen, however, the scutes remained attached to the bony shell beneath them while this animal was being digested. This is indicated by the rather rounded offsets between carapace osseous elements where they are slightly offset because they were covered by a pliable covering above the osseous elements, i.e. the scutes. As a result, the surface texture of the carapace preserved in the coprolite is that of the scutes and not that of the osseous carapace elements beneath them. This unique mode of turtle scute preservation is absolutely novel for a fossil. This conclusion is further supported by the texture observed on the surface of this impression. Embryonic turtle scutes are usually ornamented with finely pitted (Fig. 4B) to crenulated or pustulate surface texture (Fig. 4C), which has no relationship with the texture of the underlying bones (W. Joyce, Personal communication, 17 October, 2016). Furthermore, as hatchling turtles begin to grow, the peripheral tissue that is added to the scute is smooth as



**Figure 4.** (A) Enlarged view of the anterior end of an alginite cast of the turtle shell impression within vertebrate coprolite CMM-V-4524, whitened with ammonium chloride to show the finely pocked surface texture of the embryonic scutes. Anterior end is toward top of page. (B) Embryonic/hatchling *Chelonia mydas* (USNM 292975) in dorsal view showing the pocked/pitted texture of its embryonic scutes. Shell length = 3.75 cm. (C) Hatchling *Testudo hermanni* (USNM 7717) in dorsal view showing the pustulate texture of its embryonic scutes, each of which is encircled by relatively smooth new-growth hatchling scute tissue. Shell length = 4.1 cm. Scale bars equal 1 cm.



**Figure 5.** (A) Partial restoration of the carapace of the hatchling *Taphrosphys sulcatus* preserved in coprolite CMM-V-4524, derived from Figure 2C. (B–D) Comparison of hatchling (B), juvenile (C) and adult (D) specimens of *T. sulcatus* to the same scale. Juvenile from Hay (1908, p.111) and adult from Gaffney, Tong and Meylan (2006, p. 557).

compared to that of the textured embryonic scute. This kind of hatchling new scute growth is illustrated here in Figure 4C (*Testudo hermanni*, USNM 7717), where a narrow band of smooth hatchling scute encircles the pustulate embryonic scute. Clearly visible hatchling scute growth-bands along the anterior and anterolateral scute borders are also preserved in CMM-V-4524 (Fig. 2A, “new growth”). That most of the surface area of the scutes is textured like those of extant embryonic turtles is compelling evidence that this turtle died soon after hatching as only a narrow band of hatchling scute growth had developed prior to it being ingested.

Judging from what is preserved of the length of the carapace, its overall shell length at the time of death would have been approximately 60 mm. If we subtract from 60 mm the midline length of the post-hatching new scute growth for each scute ( $\sim 1.4$  mm/scute), we can thereby approximate the length of the shell at birth. We measure a total minimum of 5.6 mm of hatchling scute growth ( $4 \text{ mm} \times 1.4 \text{ mm}$ ), so the fully ossified shell of this turtle when it emerged from its egg probably was no more than  $(60 - 5.6 = )$  54.4 mm long.

## Discussion

### Identity of the prey

Because CMM-V-4524 preserves the surface texture of the scutes and not the bones of this hatchling turtle, the surface texture of fossil turtle carapace bones from this region are not relevant to the identification of this hatchling. Instead, useful comparisons can only be made to the proportions and conformation of the carapace bone elements. The carapace impression preserved in CMM-V-4524 is that of a turtle with the following osteological characteristics: (1) the first neural element is anteroposteriorly long and narrow; (2) the first costals are also quite long anteroposteriorly; (3) the succeeding second through fourth costals are narrow anteroposteriorly, followed by wider fifth and sixth costals; (4) the neurals are hexagonal to pentagonal in shape; and (5) the vertebral scutes are very wide.

Among the twelve turtle taxa known from the Paleocene in South Carolina (Hutchison and Weems, 1998), and the nine or ten taxa known from the Late Cretaceous (Weems, 2015), only *Taphrosphys* has all of these characteristics (Fig. 5). While *Adocus* is similar in that it also has an elongate first neural and first costals, it differs in that it had a square-shaped second neural (Meylan and Gaffney, 1989) quite unlike the hexagonal second neural seen in the CMM-V-4524 carapace impression. Based on this identification, the stratigraphic origin of this specimen can be restricted either to the Late Cretaceous or early Paleocene (Danian), because *Taphrosphys* has never been reported from the Williamsburg Formation (Thanetian, upper Paleocene).

It is notable that “*Taphrosphys leslianus*,” now considered a junior synonym of *T. sulcatus*, has relatively wider vertebral scutes than are found in adult specimens. This suggests that, as *T. sulcatus* grew, its vertebral scutes became relatively narrower and its pleural scutes relatively wider. Carrying this trend back to hatchling size implies that hatchlings of *T. sulcatus* probably had very wide vertebral scutes as seen in CMM-V-4524 (Fig. 5). Identification of this specimen as *T. sulcatus* greatly expands our knowledge of the growth and developmental stages of this turtle from hatching to maturity. Based on the paleoenvironments in which specimens of *T. sulcatus* are found, this turtle probably was an inhabitant of both estuaries and shallow marine environments. Based on the hatchling or near-hatchling size of the specimen described here, it was probably living in an estuarine environment at the time it was eaten.

## Identity of the predator

Predators from the Late Cretaceous and Paleocene large enough to have swallowed this small turtle and produced coprolites of this size and general morphology include mosasaurs, crocodylians and theropod dinosaurs (including birds). Mosasaurs are not well known from this locality, but representative elements have been found by one of us (BP). Mosasaurs have been identified as possible producers of coprolites from other localities (Anagnostakis, 2013; Mahaney et al., 2013). The most likely crocodylian candidates are the large Cretaceous crocodylian *Deinosuchus* and the Late Cretaceous-Paleocene crocodylian genera *Hyposaurus*, *Bottosaurus* and *Thoracosaurus* (Schwimmer and Williams, 1996; Erickson, 1998; Harrell and Schwimmer, 2010). Because a large number of crocodylian bones were found in association with coprolites collected at the Clapp Creek site, Sawyer, (1998) proposed that most of the coprolites were crocodylian in origin and noted that most of the Black Mingo coprolites were not qualitatively different from coprolites previously attributed to crocodylians (Hantzschel, El-Baz and Amstutz 1968; Sawyer, 1981). The coprolite described here, however, is distinctly different in overall shape from most of the coprolites that have come from this site, and it also is different because it contained intact bone material. Crocodylian coprolites are characterized by a complete lack of bone tissue within them because crocodylians have very effective digestive systems, with hydrochloric acid concentrations (pH 1–2) that exceed those of mammalian carnivores by a factor of 50 (Coulson, Herbert and Coulson, 1989; Semeniuk et al., 2011). This concentration of acid decalcifies and dissolves all bone tissue completely before excretion (Fischer, 1981; Coulson, Herbert and Coulson, 1989; Trutnau and Sommerlad, 2006; Semeniuk et al., 2011). Semeniuk et al. (2011) report that ingested keratin (feathers, hair) and chitin (insect cuticle) are not digested, but even so they are mechanically broken down; stomach stones (gastroliths) are likely to assist in breaking down prey. Apparently, hairballs can be formed in the stomach, but if so they are eventually regurgitated. The shape of the coprolite discussed here and the presence of bone in the feces at the time of defecation both argue against a crocodylian predator.

In addition to a mosasaur, the predator may have been a theropod dinosaur (including avian theropods). The tyrannosauroids *Appalachiosaurus montgomeriensis* (Carr, Williamson and Schwimmer, 2005) and *Dryptosaurus aquilunguis* (Carpenter et al., 1997) are among the known Late Cretaceous theropod dinosaurs from eastern North America that would have been large enough to produce coprolites of this size (Weishampel, 1990), so one of these animals could have been the

predator if the coprolite is of Late Cretaceous age. If the coprolite is of Paleocene age, however, then it most likely was produced by a large bird. Although poorly known, there were a number of species of Late Cretaceous and Paleocene birds large enough to produce coprolites of this size, including a Paleocene pelagornithid (relevant literature summarized in Mayr, 2007). Bird predation is a major factor limiting turtle hatchling survival today (e.g., Janzen, Tucker and Paukstis, 2000), so it is likely that a similar pattern existed in the Late Cretaceous and early Paleocene.

The small (i.e., young post-hatchling) size of the turtle shell and the fact that the shell shows signs of breakage both indicate that the turtle was ingested and that the shell impression was made while the feces were still within the body of the predator. The way in which the feces tapers immediately beyond the turtle shell impression (Fig. 1B) suggests that as the shell was voided, the cloacal aperture was stretched more than it might ordinarily have been. CMM-V-4524 is the first-known coprolite to preserve a largely complete body impression; though turtle vertebrae have been reported from Late Cretaceous shark coprolites (Anagnostakis, 2013, fig. 9J; Schwimmer, Weems and Sanders, 2015). This specimen also represents the first-known record of embryonic and early post-hatchling turtle scute texture preserved in the fossil record.

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