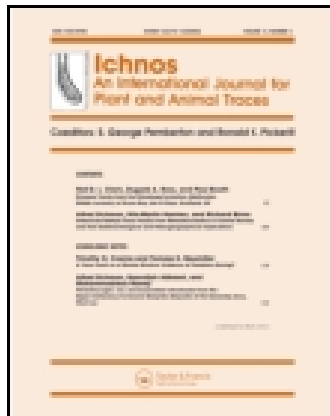


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# Gar-Bitten Coprolite From South Carolina, USA

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**Coprolites can preserve a wide range of biogenic components. Of all the coprolites known from the fossil record, hitherto only two are known to preserve vertebrate tooth impressions (i.e., those of chondrichthyans). Here, a coprolite, from a thick lag deposit that includes a mixture of late Cretaceous, early Paleocene, and Plio-Pleistocene taxa at Clapp Creek in Kingstree, Williamsburg County, South Carolina, USA, preserves bite marks most consistent with having been made by a gar, *Lepisosteus* sp. (Lepisosteidae, Actinopterygii). This is the first-known coprolite to preserve actinopterygian tooth/bite marks. Aborted coprophagy seems unlikely; an accidental or serendipitous strike more likely describes the origin of the score marks over the surface of the coprolite. This coprolite also preserves small paired striations interpreted as evidence of coprophagy by an unknown organism.**

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**Keywords** Coprolite, Cretaceous, Paleocene, *Lepisosteus*, Crocodylian, Dinosaur

## INTRODUCTION

Coprolites are now known to preserve a wide range of biogenic components, including DNA fragments (Poinar et al., 2003), spores, pollen (Horrocks et al., 2003), phytoliths, other plant parts (Nambudiri and Binda, 1989) and wood fragments (Chin, 2007), cyanobacteria (Northwood, 2005), bacteria, diatoms, radiolarians (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; Paris and Holman, 1978; Sohn and Chatterjee, 1979; Fisher, 1981; Martin, 1981; Thulborn, 1991; Hunt et al., 1994; Davis and Briggs, 1995; Chin et al., 1998, 2003; Chin, 2002, 2007; Northwood, 2005; Prasad et al., 2005). Coprolites are also known to preserve external markings, like feeding traces (Månsby, 2009, fig. 3I) or tooth impressions (Godfrey and Smith, 2010) made by other organisms interacting with the feces. Of all the coprolites known from the fossil record, only two have been formally recognized as

preserving vertebrate (i.e., carchariniform shark) tooth impressions (Godfrey and Smith, 2010). Here we describe another unique coprolite, CMM-V-4480 (Calvert Marine Museum Vertebrate collection), (Figs. 1-3), that preserves bite marks and tooth impressions most consistent with having been made by a gar, *Lepisosteus* sp. (Lepisosteidae, Actinopterygii), as well as diminutive paired striations interpreted as evidence of coprophagy by an unknown organism.

## Geological Setting

The coprolite was found by one of the authors (B.T.P.) 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. 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, early Paleocene, and Plio-Pleistocene taxa (Cicimurri, 2010; Soehner, 2012). The vertebrate fauna includes Cretaceous marine 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 from Maastriichtian strata (either the Peedee or Steel Creek formations), whereas the Paleocene fossils likely derive from the Danian Rhems and Williamsburg formations. Weems and Bybell (1998) and Cicimurri (2010) proposed that these fossils were probably concentrated together during Plio-Pleistocene sea level highstand, at which time the Plio-Pleistocene vertebrate material was added to the mix.

The paleoenvironment in the Kingstree area was a near-shore 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.

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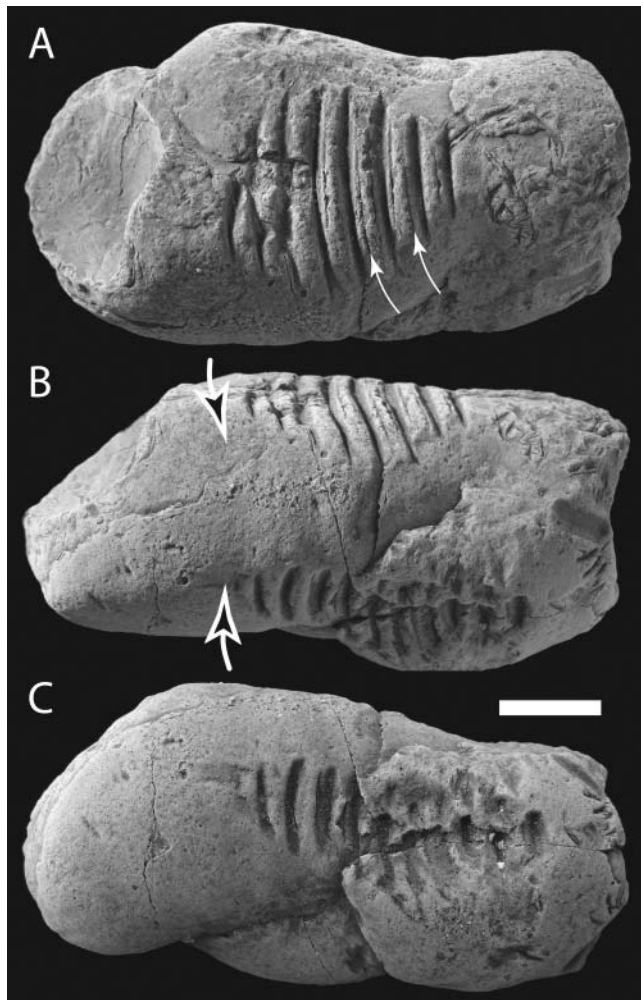


FIG. 1. Coprolite (CMM-V-4480) from Clapp Creek in Kingstree, Williamsburg County, South Carolina, showing two series of tooth scarrings over its surface, the origin of which is interpreted to have come from a glancing bite by a gar (*Lepisosteus* sp.). **A.** Tooth-mark primary furrows and finer associated striations (two of the striations are indicated by small white arrows). **B.** Coprolite rotated upwards approximately  $90^\circ$  about its long axis to show both sets of tooth marks, which resulted from the upper and lower teeth raking the surface of the feces. The bold arrows show the direction the teeth raked the surface of the feces. **C.** Coprolite rotated upwards approximately  $90^\circ$  from its position in B, showing the shorter series of tooth scarrings. Specimen whitened with sublimed ammonium chloride to improve contrast and highlight detail. White scale bar equals 10 mm.

## RESULTS

CMM-V-4480 (Fig. 1) has an elongate, irregularly cylindrical shape characteristic of many of the other coprolites known from that locality (Sawyer, 1998). As with the vast majority of the coprolites from Clapp Creek, it is very dark in color, between a dusky purple (SRP 2/2 in the Munsell Color Rock-Color Chart 2009 revision) and black (N1 in the same chart), not apparent in Figures 1–3 because the coprolite was coated (i.e., whitened) with sublimed ammonium chloride to improve contrast. In its natural state, the surface of the coprolite

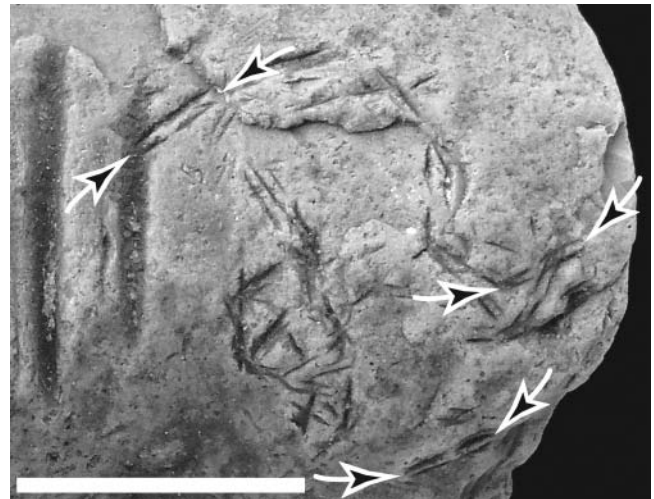


FIG. 2. Enlarged view of one end of the gar-bitten coprolite (CMM-V-4480, i.e., right side of Figure 1A) showing isolated paired striations. The three pairs of opposing arrows highlight six pairs of parallel troughs interpreted as evidence of coprophagy by an as yet unknown organism. Specimen whitened with sublimed ammonium chloride. White scale bar equals 10 mm.

exhibits a somewhat reflective patina. Neither end of the coprolite is complete, but the general morphology implies that not much is missing from its original length. CMM-V-4480 measures 62.5 mm long and 33.5 mm in diameter at the point of its greatest girth. No inclusions are visible on its surface.

On approximately opposite sides of the coprolite, two separate series of parallel primary furrows mark its surface (Fig. 1). The primary furrows are 3 mm apart and curve slightly over the uneven, but generally cylindrically-shaped coprolite. The longer furrows (Fig. 1A), up to 21.5 mm in length, consist of eight parallel and gently curving gouges. The other series (Fig. 1C) preserves ten shorter primary furrows, the longest of which is 10.5 mm. An oblique view of both series of primary furrows is shown in Figure 1B. The furrows begin on opposite sides of the coprolite and course towards one another, as indicated by the bold arrows in Figure 1B. However, the proximate ends of the two series of furrows do not abut or overlap. In the shorter series, the proximate ends of some of the furrows terminate as conical impressions, preserving the shape of the very pointed end of the tooth and indicating the direction the teeth passed over the surface of the coprolite (Fig. 1B).

In addition to the aforementioned primary furrows, some finer but associated striations are visible on four of the intervening ridges between primary furrows. Two of these associated striations are indicated by the small white arrows in Figure 1A. The fine associated striations parallel the larger ones and appear on one or both sides of the intervening ridge. No associated striations are visible with the shorter series of furrows (Figs. 1B and C). The striations described here are in no way related to the longitudinal striations/ridges present in many fossil and recent coprolites attributed to crocodylians or archosauromorphs (Young,

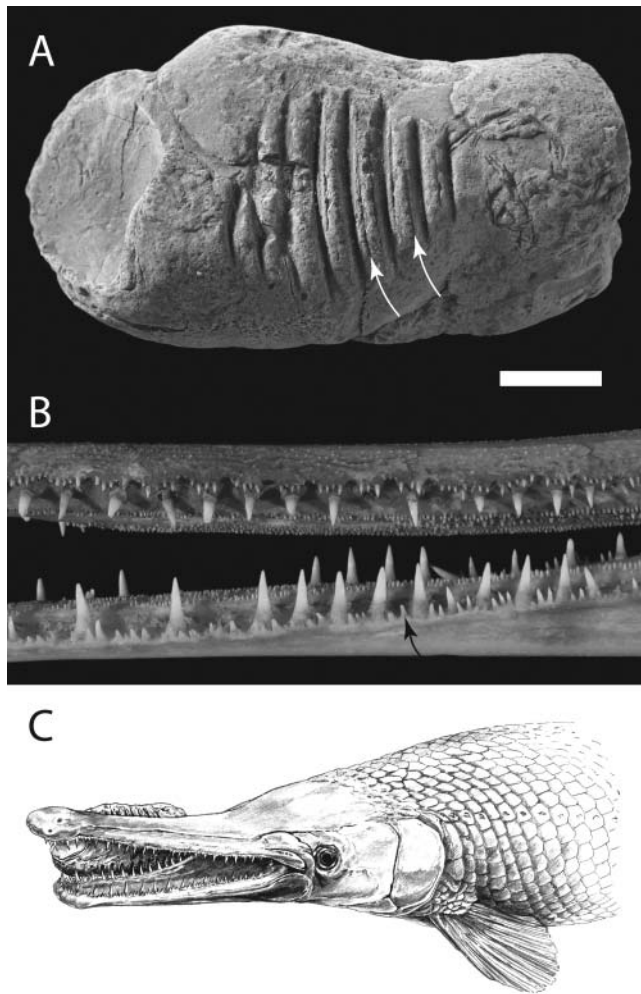


FIG. 3. A. Tooth-marked coprolite (CMM-V-4480) highlighting the finer associated striations (two of which are indicated by small white arrows). B. Left lateral view of the mid-section of the rostrum of an extant gar (*Lepisosteus osseus*, CMM-O-33) showing the presence of small peripheral teeth (one of which along the lower jaw is highlighted by a black arrow) adjacent to the fewer larger fangs in both the upper and lower jaws. White scale bar equals 10 mm. C. Drawing showing the way in which we interpret the coprolite (CMM-V-4480) to have been scored, i.e., by a glancing bite from a gar, *Lepisosteus* sp.

1964; Rodriguez-de la Rosa et al., 1998; Northwood, 2005; Milàn, 2010, 2012, fig. 4a-b; Souto, 2010).

At one end of CMM-V-4480 (Fig. 2), adjacent to the longer furrows (Fig. 1A), is a clustering of approximately 35 much smaller mostly paired but variously scattered striations (six of these paired striations are marked by the opposing arrows in Fig. 2). These tiny paired striations range between 2–3.5 mm long and when paired are separated from their twin by approximately 0.3 mm.

## DISCUSSION

Because a large number of crocodylian bones, including those of *Hyposaurus*, *Bottosaurus*, and *Thoracosaurus* (Erickson, 1998)

and *Alligator* (Soehner, 2012) were found in association with the coprolites collected from the Clapp Creek site, Sawyer (1998) proposed that most of the coprolites were crocodylian in origin. Although Sawyer (1998) noted that most of these coprolites were not qualitatively different from coprolites previously attributed to crocodylians (Hantzschel et al., 1968; Sawyer, 1981; Hunt and Lucas, 2010; Milàn, 2010), it is not yet possible to distinguish between crocodylian and predatory dinosaur coprolites, unless specimens are too large to have been produced by crocodylians (Chin, personal communication, February 15, 2011). CMM-V-4480 is not nearly large enough to fall into the exclusively dinosaur-coprolite size range. Therefore, since Cretaceous dinosaur remains have also been collected at the Clapp Creek site, albeit very few, a dinosaurian origin for CMM-V-4480 cannot be ruled out. Neither can we rule out the possibility that this coprolite was produced by one of the actinopterygian (see below) nor chelonians (Hutchison and Weems, 1998) known from this site. The regularity of the primary furrows and associated fine striations and the presence of conical impressions at the proximate ends of some of the furrows attest to their exogenous origin (vs. compression folds or striations in the feces that formed in vivo). The way in which the associated striations parallel the primary furrows strongly suggests that they were made concurrently by much smaller denticles in a single pass of teeth over the feces. The presence of two discrete series of furrows indicate an origin from opposing teeth in the upper and lower jaws from one side of an animal (Fig. 3C), (although it is not known which series was made by which jaw). When the furrows in each series are viewed perpendicular to the plane in which they course over the surface of the coprolite (Fig. 1A and C), notice that they arc across the coprolite with a radius of curvature indicating that the angle of the jaw of the biter was to the right (the bold arrows in Figure 1B were deliberately curved to draw attention to the curve in the furrows). Therefore, the furrows in the two series are not parallel to one another, suggesting that they were not made by teeth at the front of the jaws, but rather by teeth on the side of the jaws. That the furrows within the respective series lie in approximately the same plane indicates an animal with a nearly straight and elongate jaw with different-sized teeth or cusplets in a single row or that the biter possessed teeth offset from one another in lateral and medial rows. Differences in the lengths of the tooth furrows are simply an artefact of the way in which the teeth grazed the curved surface of the feces. In the longer series (Fig. 1A), the teeth did not stop as they raked the surface. However, in the shorter series (Fig. 1C), the presence of tooth-tip impressions (in the six furrows on the right-hand side of this series) indicates that these teeth did not make a clean sweep of the surface of the feces, but rather penetrated a short distance into the feces, stopped, and were then withdrawn.

The following actinopterygians (genera and then families listed here alphabetically) are known from the Clapp Creek

locality: *Albula* sp., *Cylindracanthus* sp., *Egertonia* cf. *isodonta*, *Enchodus* sp., *Hadrodus* sp., *Lepisosteus* sp., cf. *Progygnodon* sp., cf. *Scomberomorus*, Labridae and Ostraciidae, (Weems, 1998; Cicimurri, 2007; Soehner, 2012), although existing collections have not yet been fully studied (Cicimurri, pers com., May 18, 2011). Of these, only *Lepisosteus* sp. possesses the jaw and dental morphology [i.e., elongate, nearly parallel-sided jaws with several rows (medial and lateral) of closely spaced, needle-like teeth (Figs. 3B and C)] capable of having produced these bite marks.

In Figure 4, modelling clay was fashioned into a mass comparable in size and shape to that preserved in CMM-V-4480. Then the bony jaw of an extant gar, *Lepisosteus osseus*, was raked over its surface. In Figure 4A, the fangs of the inner medial row of teeth formed the deep primary furrows, whereas the finer associated striations were made by the outer row of teeth along the perimeter of the jaws. In Figure 4B, the jaw was pressed more forcefully into the clay such that a greater number of tiny peripheral teeth raked its surface. The gouges preserved in CMM-V-4480 (Figs. 1 and 3A) more closely resemble those in Figure 4A. The absence in CMM-V-4480 of more intervening tiny associated striation, as seen

in Figure 4B, is explained either by the jaws not having penetrated the feces deeply enough for more peripheral teeth to have gouged the feces, or that this bite mark was not made by *Lepisosteus* sp. Chondrichthyans are known from Clapp Creek (Purdy, 1998), including the lamniform sharks *Carcharias* sp. and *Odontaspis* sp., both of which possess sharply pointed teeth that include accessory cusplets. Although we have not been able to duplicate or even approximate the gouge pattern preserved in CMM-V-4480 by raking shark dentitions over modelling clay, prudence precludes us from excluding a chondrichthyan origin for the bite marks preserved on CMM-V-4480.

Nevertheless, *Lepisosteus* sp. appears to be the best fit and we propose that the evenly spaced primary furrows and conical impressions were made by the largest teeth in the jaws, that is, the so-called fangs of the inner medial row of teeth in *Lepisosteus* (Grande, 2010, p. 74; Fig. 3B). At only about 3 mm apart, the primary furrows are well within the range for the distance separating adjacent fangs in gars. The smaller associated striations would have been made as the smaller outer row of teeth along the perimeter of the jaws raked the tops of the fecal ridges pushed up between the more deeply indented primary furrows.

Extant gars are voracious ambush predators that feed on a wide variety of fishes (Grande, 2010). Depending on the species, they also variously feed on decapods, insects, and even snails (Kodera et al., 1994; Grande, 2010), but plant material can also form part of their diets, if only incidentally, taken in while feeding on fishes (Lambou, 1961; Knight and Hastings, 1987). Prey capture is accomplished by a lateral movement of the head towards the prey as the jaws open widely and then snap shut extremely rapidly (Lauder, 1980; Grande, 2010). Gars are not known to engage in coprophagy, so it would seem unlikely that these tooth marks represent evidence of an aborted attempt to consume the fecal mass. Gars are also not known to assess the palatability of potential prey through exploratory biting as some sharks seemingly do (Klimley, 1994; Collier et al., 1996; Ritter and Levine, 2004). A more likely explanation would be that the bite marks represent evidence of an accidental strike; the feces were perhaps momentarily mistaken as prey or they were snagged unintentionally by the teeth as the gar snapped at another genuine prey in close proximity to the obstructing feces. Either way, the feces were not eaten.

The origin of the very small often paired striations (Fig. 2) remains unknown. That they typically occur as couplets strongly suggests a biogenic origin, and because there are so many suggests a certain level of intent, possibly coprophagy by a fish or an invertebrate. Markings like these also characterize many of the coprolites found within the Lower and Middle Miocene Calvert Formation along Calvert Cliffs, Maryland, USA (SJG, personal observation). In Figure 2, the arrow furthest to the left, points at one of the paired striations that overlaps the relatively much larger primary furrow; evidence that

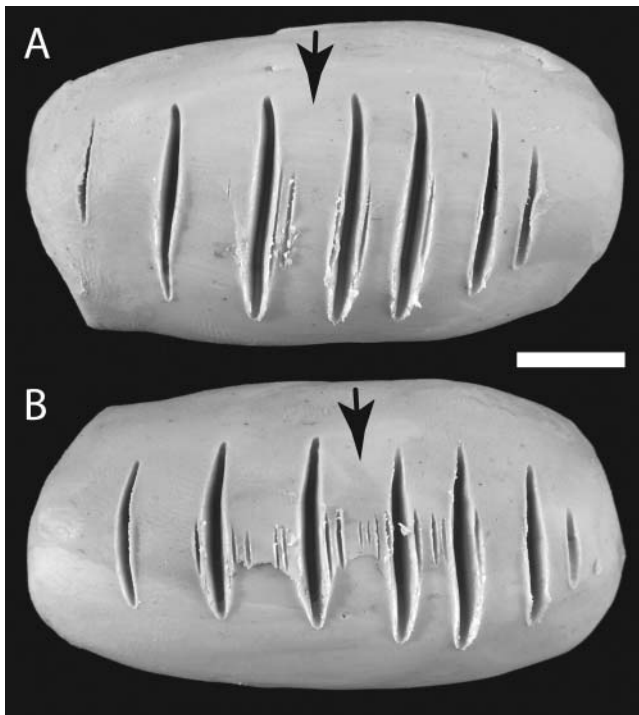


FIG. 4. A.-B. Modelling clay in the approximate size and shape of CMM-V-4480. In both, the bony lower jaw of an extant gar, *Lepisosteus osseus*, was raked over its surface as indicated by the direction of the arrows. In A, the fangs of the inner medial row of teeth gouged the deep primary furrows, whereas the finer associated striations immediately adjacent to the furrows were made by the outer row of teeth along the perimeter of the jaws. In B, the jaw was pressed more forcefully into the clay such that a greater number of tiny peripheral teeth raked the surface of the modelling clay. White scale bar equals 10 mm.

this couplet gouged the surface of the feces after the primary furrows had been made.

There seems to be no way of knowing from an examination of the coprolite when the primary furrows were made—whether it was bitten while still in the water column versus laying on, or buried in the sediment below. The scenario we favor but cannot prove, is that the furrows were made while in the water column (Fig. 3C). Perhaps a more compelling case could be made that the tiny isolated paired striations (Fig. 2) happened while the coprolite was at the bottom of the water column or completely buried in the sediment; by virtue of the number of paired striations, and that they marked the surface of the coprolite after the primary furrows were made.

All of these bite, or feeding marks represent the unusual occurrence of trace fossils (bite marks) on a trace fossil (a coprolite), resulting in the creation of a compound trace fossil. There is now no doubt that coprolites have been either deliberately (i.e., at least mouthed by exploring or foraging animals), or accidentally bitten by vertebrates (here and Godfrey and Smith, 2010). These occurrences are still exceedingly rare, but as more coprolites are collected and existing museum specimens carefully examined, doubtless other examples will surface showing behavioural interactions between organisms and feces.

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## REFERENCES

Ash, S. R. 1978. Coprolites. *Brigham Young University Geological Studies*, 28:498–508.

- Chin, K. 2002. Analyses of coprolites produced by carnivorous vertebrates. In Kowalewski, M. and Kelley, P. H. (eds.). *Predation in the Fossil Record. Paleontological Society Special Paper*, 8:43–49.
- Chin, K. 2007. The paleobiological implications of herbivorous dinosaur coprolites from the Upper Cretaceous Two Medicine Formation of Montana: Why eat wood? *Palaio*, 22:554–566.
- Chin, K., Eberth, D. A., Schweitzer, M. H., Rando, T. A., Sloboda, W. J., and Horner, J. R. 2003. Remarkable preservation of undigested muscle tissue within a Late Cretaceous tyrannosaurid coprolite from Alberta, Canada. *Palaio*, 18:286–294.
- Chin, K., Tokaryk, T. T., Erickson, G. M. and Calk, C. L. 1998. King-sized feces: A probable tyrannosaur coprolite from Saskatchewan. *Nature*, 393:680–682.
- Cicimurri, D. J. 2007. A late Campanian (Cretaceous) selachian assemblage from a classic locality in Florence County, South Carolina. *Southeastern Geology*, 45(2):59–72.
- Cicimurri, D. J. 2010. Fossil chimaeroid remains (Chondrichthyes: Holocephali) from Williamsburg County, South Carolina, USA. *Paludicola*, 8:37–48.
- Collier, R. S., Marks, M. and Warner, R. W. 1996. White shark attacks on inanimate objects along the Pacific coast of North America. In Klimley, A. P. and Ainley, D. G. (eds.). *Great White Sharks: The Biology of *Carcharodon carcharias**. Academic Press, San Diego, pp. 217–222.
- Davis, P. G. and Briggs, D. E. G. 1995. Fossilization of feathers. *Geology*, 23:783–786.
- Erickson, B. R. 1998. Crocodylians of the Black Mingo Group (Paleocene) of the south Carolina Coastal Plain. In Sanders, A. E. (ed.). *Paleobiology of the Williamsburg Formation (Black Mingo Group; Paleocene) of South Carolina, U.S.A.*, *Transactions of the American Philosophical Society*, 88 (4):196–214.
- Fisher, D. C. 1981. Crocodylian scatology, microvertebrate concentrations, and enamel-less teeth. *Paleobiology*, 7:261–275.
- Godfrey, S. J. and Smith, J. 2010. Shark-bitten vertebrate coprolites from the Miocene of Maryland. *Naturwissenschaften*, 97:461–467.
- Grande, L. 2010. An empirical synthetic pattern study of gars (Lepisosteiformes) and closely related species, based mostly on skeletal anatomy. The resurrection of Holosteï. American Society of Ichthyologists and Herpetologists Special Publication 6, Supplementary Issue of Copeia Volume 10, Number 2A.
- Hantzschel, W., El-Baz, F., and Amstutz, G. C. 1968. Coprolites: An annotated bibliography. *Geological Society of America*, Memoir 108, Boulder, Colorado, 121 p.
- Horrocks, M., Irwin G. J., McGlone, M. S., Nichol, S. L., and Williams, L. J. 2003. Pollen, phytoliths and diatoms in prehistoric coprolites from Kohika, Bay of Plenty, New Zealand. *Journal of Archaeological Science*, 30:13–20.
- Hunt, A. P., Chin, K., and Lockley, M. G. 1994. The palaeobiology of vertebrate coprolites. In Donovan, S. K. (ed.). *The Palaeobiology of Trace Fossils*. John Wiley & Sons, Chichester, pp. 221–240.
- Hunt, A. P. and Lucas, S. G. 2010. Crocodylian coprolites and the identification of the producers of coprolites. *New Mexico Museum of Natural History and Science, Bulletin*, 51:219–226.
- Hutchison, H. J. and Weems, R. E. 1998. Paleocene turtle remains from South Carolina. In Sanders, A. E. (ed.). *Paleobiology of the Williamsburg Formation (Black Mingo Group; Paleocene) of South Carolina, U.S.A.* *Transactions of the American Philosophical Society*, 88 (4):165–195.
- Klimley, A. P. 1994. The predatory behaviour of the white shark. *American Scientist*, 52:122–133.
- Knight, C. L. and Hastings, R. W. 1987. A comparison of the food habits of spotted gar (*Lepisosteus oculatus*) from two habitats in the Lake Pontchartrain drainage system. *Proceedings of the Los Angeles Academy of Science*, 50:27–31.

- Kodera, H., Igarashi, T., Kuroiwa, N., Maeda, H., Mitani, S., Mori, F., and Yamazaki, K. 1994. Jurassic Fishes: Selection, Care, Behavior. T. F. H. Publications, Neptune, NJ.
- Lambou, V. W. 1961. Utilization of macrocrustaceans for food by freshwater fishes in Louisiana and its effects on the determination of predator-prey relations. *Progressive Fish-Culturist*, 23:18–25.
- Lauder, G. V., Jr. 1980. Evolution of the feeding mechanism in primitive actinopterygian fishes: A functional anatomical analysis of *Polypterus*, *Lepisosteus*, and *Amia*. *Journal of Morphology*, 163:283–317.
- Månsby, U. 2009. Late Cretaceous coprolites from the Kristianstad Basin, southern Sweden. *Examensarbeten i geologi vid Lunds universitet*, Nr. 246, 16 p., 15 points.
- Martin, J. E. 1981. Contents of coprolites from Hemphillian sediments in northern Oregon, and their significance in paleoecological interpretations. *Proceedings of the South Dakota Academy of Science*, 60:105–115.
- Milà, J. 2010. Coprolites from the Danian limestone (Lower Paleocene) of Faxø Quarry, Denmark. *New Mexico Museum of Natural History and Science, Bulletin*, 51:215–218.
- Milà, J. 2012. Crocodylian scatology – a look into morphology, internal architecture, inter- and intraspecific variation and prey remains in extant crocodylian feces. *New Mexico Museum of Natural History and Science, Bulletin*, 57:65–72.
- Nambudiri, E. M. V. and Binda, P. L. 1989. Dicotyledonous fruits associated with coprolites from the Upper Cretaceous (Maastrichtian) Whitemud Formation, southern Saskatchewan, Canada. *Review of Palaeobotany and Palynology*, 59:57–66.
- Northwood, C. 2005. Early Triassic coprolites from Australia and their palaeobiological significance: *Palaentology*, 48:49–68.
- Parris, D. C. and Holman, J. A. 1978. An Oligocene snake from a coprolite. *Herpetologica*, 34:258–264.
- Poinar, H., Kuch, M., McDonald, G., Martin, P., and Pääbo, S. 2003. Nuclear gene sequences from a Late Pleistocene sloth coprolite. *Current Biology*, 13:1150–1152.
- Prasad, V., Strömberg, C. A. E., Alimohammadian, H., and Sahni, A. 2005. Dinosaur coprolites and the early evolution of grasses and grazers. *Science*, 310:1177–1180.
- Purdy, R. W. 1998. Chondrichthyan Fishes from the Paleocene of South Carolina. In Sanders, A. E. (ed.). Paleobiology of the Williamsburg Formation (Black Mingo Group; Paleocene) of South Carolina, U.S.A. *Transactions of the American Philosophical Society*, 88(4):122–146.
- Ritter, E. and Levine, M. 2004. Use of forensic analysis to better understand shark attack behaviour. *Journal of Forensic Odonto-Stomatology*, 22:40–46.
- Rodríguez-de la Rosa, R. A., Cevallos-Ferriz, S. R. S., and Silva-Pineda, A. 1998. Paleobiological implications of Campanian coprolites. *Palaogeography, Palaeoclimatology, Palaeoecology*, 142:231–254.
- Sawyer, G. T. 1981. A study of crocodylian coprolites from Wannagan Creek Quarry (Paleocene—North Dakota), Ichnofossils II, Minnesota. *Scientific Publication of the Science Museum*, 5(2):1–29.
- Sawyer, G. T. 1998. Coprolites of the Black Mingo Group (Paleocene) of South Carolina. In Sanders, A. E. (ed.). Paleobiology of the Williamsburg Formation (Black Mingo Group; Paleocene) of South Carolina, U.S.A., *Transactions of the American Philosophical Society*, 88(4):221–228.
- Soehner, J. R. 2012. Why is there such a high concentration of vertebrate remains within a bone-bed along Clapp Creek, Williamsburg County, South Carolina? MS thesis, Department of Earth and Environmental Sciences, Wright State University.
- Sohn, E. G. and Chatterjee, S. 1979. Freshwater ostracods from Late Triassic coprolites in central India. *Journal of Paleontology*, 53:578–586.
- Souto, P. R. F. 2010. The crocodylomorph coprolites from Baru Basin, Upper Cretaceous, Brazil. *New Mexico Museum of Natural History and Science, Bulletin*, 51:201–208.
- Souto, P. R. F. 2012. The Brazilian coprolites; an unexpected journey to the past. *Publit*, Rio de Janeiro, Brazil, 101 p.
- Thulborn, R. A. 1991. Morphology, preservation and palaeobiological significance of dinosaur coprolites: *Palaogeography, Palaeoclimatology, Palaeoecology*, 83:341–366.
- Waldman, M. and Hopkins, Jr., W. S. 1970. Coprolites from the Upper Cretaceous of Alberta, Canada, with a description of their microflora. *Canadian Journal of Earth Sciences*, 7:1295–1303.
- Weems, R. E. 1998. Actinopterygian fish remains from the Paleocene of South Carolina. In Sanders, A. E. (ed.). Paleobiology of the Williamsburg Formation (Black Mingo Group; Paleocene) of South Carolina, U.S.A. *Transactions of the American Philosophical Society*, 88(4):147–164.
- Weems, R. E. and Bybell, L. M. 1998. Geology of the Black Mingo Group (Paleocene) in the Kingstree and St. Stephen areas of South Carolina. In Sanders, A. E. (ed.). Paleobiology of the Williamsburg Formation (Black Mingo Group; Paleocene) of South Carolina, U.S.A. *Transactions of the American Philosophical Society*, 88(4):9–27.
- Wetmore, A. 1943. The occurrence of feather impressions in the Miocene deposits of Maryland. *Auk*, 60:440–441.
- Young, C. C. 1964. New fossil crocodiles from China. *Vertebrate Palasiatica*, 8:190–208.