COPROLITES FROM THE UPPER CRETACEOUS FRUITLAND, KIRTLAND AND OJO ALAMO FORMATIONS, SAN JUAN BASIN, NEW MEXICO

ROBERT M. SULLIVAN 1 AND STEVEN E. JASINSKI1,2

¹ Section of Paleontology and Geology, The State Museum of Pennsylvania, 300 North Street Harrisburg, PA 17120-0024; ² Department of Biology and the Don Sundquist Center of Excellence in Paleontology, East Tennessee State University, Johnson City, TN 37614

Abstract—Coprolites from the Upper Cretaceous Fruitland, Kirtland and Ojo Alamo formations in the vertebrate paleontology collection of the State Museum of Pennsylvania consist of different forms that are identified as morphotypes A-G. These coprolites are attributed to carnivorous vertebrates (fishes, turtles and crocodylians). At least four unique Upper Cretaceous coprolite morphotypes (B, D, F and G) are recognized. Four different surface textures are also recognized (smooth, slightly blistered, wrinkled and striated), but only partially coincide with the morphotypes. Bone inclusions are common in about half of the coprolites, and one contains the ?astragalus and ?calcaneum of an anuran, the first record of an anuran in a Late Cretaceous coprolite. A large, irregular bony mass containing large and small fragments of a ?scapula blade, ?vertebral centra and partially digested bone is identified as a probable tyrannosauroid coprolite. The large ?scapula blade fragment appears to be from a sub-adult hadrosaurid. This specimen potentially represents the third record of a carnosaur coprolite, and the first from the United States and New Mexico.

INTRODUCTION

Skeletal remains of fossil vertebrates have been collected from the Upper Cretaceous strata of the San Juan Basin for over 100 years. Yet little has been published on trace fossils (footprints and coprolites) from the Fruitland, Kirtland and Oio Alamo formations, Fossilized hadrosaur footprints from the Fruitland Formation have been previously reported by Wolberg et al. (1988), Williamson (2000), Hunt and Lucas (1993, 2003), and most recently by Lucas et al. (2011). Hunt (1991) hypothesized that the scarcity or absence of coprolites of large reptiles and dinosaurs in the Fossil Forest region (Fruitland-Kirtland formation transition) was due to efficient digestive processes that destroyed all traces of bones and teeth. However, it appears that this conclusion is based, in part, on the limited geographic extent of the Fossil Forest study area, as well as local preservation factors. Hunt (1991) did not specifically cite or illustrate any coprolites from the Fossil Forest region. Sullivan (2006) briefly reported on two coprolites from the Fossil Forest Member of the Fruitland Formation (now known to be the Hunter Wash Member of the Kirtland Formation) in Ah-shi-sle-pah, San Juan Basin, New Mexico. More recently, in an abstract, Hunt et al. (2011) briefly mentioned the presence of Late Cretaceous coprolites from the San Juan Basin in the collections of the New Mexico of Natural History and Science. The only other mention of coprolites from the Upper Cretaceous San Juan Basin of New Mexico is by Jasinski et al. (2011), who briefly reported on, and illustrated, two coprolites from the Ojo Alamo Formation (Naashoibito Member) that are described below in more detail.

Here we review, describe, and assess the gross morphology of coprolites from the Fruitland, Kirtland and Ojo Alamo formations, collected over a 15 year period. The specimens are cataloged in the collections of the State Museum of Pennsylvania (SMP), Harrisburg, Pennsylvania.

GEOLOGIC SETTING

The Upper Cretaceous rocks of the Fruitland and Kirtland formations and the Naashoibito Member (Ojo Alamo Formation) are part of a regressive sequence that varies from paludal to alluvial origin (Fassett and Hinds, 1971; Lucas, 1981; Lehman, 1985; Hunt, 1991). Generally, the more marshy part of the depositional sequence, the Fossil Forest Member of the Fruitland Formation and the Hunter Wash Member of the Kirtland Formation, transition to the more "terrestrial" strata of the Dena-zin Member (Kirtland Formation) and the Naashoibito Member (Ojo Alamo Formation). The sediments are largely fluvial in origin, and are characterized by coaly intervals in the Fruitland Formation and lower part of the Hunter Wash Member of the Kirtland Formation (Reeside, 1924; Fassett and Hinds, 1971; Hunt and Lucas, 1992). Channel sandstones are frequently encountered in the Fossil Forest Member (Fruitland Formation) and the lower part of the Hunter Wash Member (Kirtland Formation). The Farmington (Sandstone) Member is stratigraphically between the lower Hunter Wash Member (= lower shale member) and the higher De-na-zin Member (= upper shale member) (Fassett and Hinds, 1971; Brown, 1983; Hunt and Lucas, 1992). Vertebrate fossils from the Farmington Member are not well-known because of limited collecting in the unit, as well as its limited exposure. We note that there is disagreement as to the placement of the boundary between the upper part of the Hunter Wash Member and the lower part of the Farmington Member. We accept the mapping of the Farmington Member by Brown (1983), where the Farmington Member pinches out in the Alamo Mesa East quadrangle. Southeast of the pinch-out, the De-na-zin Member overlies the upper part of the Hunter Wash Member, which contradicts the conclusions of Lucas and Sullivan (2000).

Coprolites are found throughout the Fossil Forest Member (Fruitland Formation), the Hunter Wash and De-na-zin members (Kirtland Formation) and the Naashoibito Member (Ojo Alamo Formation). Most of the coprolites are known from the Hunter Wash and De-na-zin members, but we attribute this, in part, to collecting bias.

FRUITLAND/KIRTLAND AND OJO ALAMO COPROLITES

There have been a number of studies dealing with the description and categorization of vertebrate coprolites based on morphology (Thulborn, 1991; Hunt et al., 1994, 1998; Chin, 2002; Jouy-Avantin et al., 2003; Hunt and Lucas, 2010; Eriksson et al., 2011). Perhaps the most persistent problem with coprolites and their identification is attributing them to a specific coprolite producer. Thus, not all coprolites are readily attributed to a particular taxon, so we feel a conservative approach based on gross morphology is more descriptive and less controversial.

We categorize coprolites mainly by morphotype (form), which is arguably the most important criterion. Surface texture is considered a secondary feature and may be related to dietary factors, inner surfaces of the gastrointestinal tract (i.e., surface striations), and cuts across morphologies. Size and inclusions in coprolites vary within the recognized morphotypes. Coprolites are difficult to measure due to their variable nature, and their relative orientation is often difficult to determine. Here, we define "length" as the distance between the leading end (the end that emerges from the anus first), and the terminal end or terminus (the end that comes out last). The "thickness" (width) is measured perpendicular to the axis of the length, but there is no other meaningful orientation. In tightly coiled coprolites, the length cannot be measured with any degree of certainty due to its configuration and, therefore, is not attempted.

Morphotype "A"

Coprolites designated morphotype "A" are characterized by a "Jshaped" morphology (Fig. 1A-D). These coprolites are similar to those "J-shaped" coprolites reported by Harrell and Schwimmer (2010, p. 211, fig. 6C) from the Upper Cretaceous Blufftown Formation (Georgia). However, the Kirtland Formation coprolites have a smooth outer texture, unlike the "complex surface sculpting" noted on those of the Blufftown Formation. Bone inclusions are generally uncommon in the Kirtland Formation coprolites of this morphotype. Morphotype "A" coprolites from the Fruitland and Kirtland formations range in size from 34.34 mm (maximum length) and 16.74 mm (maximum thickness) for SMP VP-1928, to 72.78 mm (maximum length) and 26.36 mm (maximum thickness) for SMP VP-2024. We note that a similar-shaped coprolite (SMP VP-3459) has a "slight blistering," texture, or tiny raised bumps, on its outer surface, and this coprolite is from the overlying Naashoibito Member (Ojo Alamo Formation).

Morphotype "B"

A distinctive coprolite, designated morphotype "B," is known from only one specimen (SMP VP-2473) from the De-na-zin Member of the Kirtland Formation (Fig. 2). It is characterized as being unipolar and slightly sinuous, with a strong tapered end. It is silicified, and the surface texture is wrinkled, with the wrinkles parallel to the sinuous form of the fecal unit. It measures 21.24 mm in maximum length and has a maximum thickness of 9.48 mm.

Two other similar coprolites (SMP VP-2582 and VP-739) from the Fruitland and Nacimiento (Paleocene) formations, respectively, are both small (approximately 7.5 mm maximum length and 6.7 mm maximum thickness). However, the former is characterized by a smooth surface texture on one side, mechanically pitted on the other, and is latterly compressed. SMP VP-739, on the other hand, is characterized by a more bulbous shape with an irregular textured surface. The only common feature they share is the tapered end, which is not unusual. Therefore, we consider these two coprolites to only superficially resemble what we consider morphotype "B."

Morphotype "C"

Morphotype "C" is the most common and largest type of coprolite from the Kirtland Formation (Fig. 3). It has the earmarks of the classic carnivoran, similar to "dog-like" feces, composed of several (segmented) concavo-convex units, distinguished by a tapered end and a concave terminus at the other end. The surface texture is characterized by being smooth to "slightly blistered." These coprolites range in size from 21.35 mm (maximum length) by 13.1 mm (maximum thickness) for SMP VP-2621 to 91.8 mm (maximum length) by 37.8 mm (maximum thickness) for SMP VP-1739 (Fig. 3D). Bone inclusions are common, and in two specimens they can be identified. SMP VP-1811 has a number of well-preserved lepisosteid scales, whereas SMP VP-2446 has two nearly complete bones that we have identified as the ?left calcaneum and ?left astragalus of an indeterminate anuran (Fig. 3A). Both ends of the former bone are visible, but only one end of the latter is visible, with its opposite end buried in the matrix of the coprolite. The ?calcaneum has a maximum length of 12.64 mm. The visible end of the ?astragalus measures 8.84 mm in length. There is also a tiny third bone fragment that measures 2.6 mm long.

Morphotype "D"

SMP VP-2008 consists of two coprolites, one of which is complete. The other is a broken medial section of a slightly larger coprolite. They were collected together, but it is uncertain whether they were produced by the same animal. Morphotype "D" is represented by the more complete specimen (Fig. 4). It is small (maximum length of 16.40 mm), with a smooth external surface, and contains inclusions of either bone and/or minerals. It is unipolar with a blunt end, differing from morphotype "B," but similar to the blunt ends seen in morphotypes "A" and "C." The coprolite is constricted around its middle, thus appearing slightly bulbous at both ends. The coprolite has two termini, one at the polar end and one on the lateral side of the opposite end. These terminal scars indicate that this was a medial part in a chain of coprolite segments from a single defecating event. The incomplete fragment is a cross-section of a segment, displaying the internal surface of the coprolite on both sides. In cross-section there are numerous hair-like ?manganese inclusions. There are no obvious inclusions of bone. The external surface is the same as in the more complete coprolite.

Morphotype "E"

Morphotype "E" (Fig. 5) is characterized by coprolites that are tightly twisted with a single terminus. The surface texture consists of intermittent longitudinal striations with incipient blistering. Bone inclu-



FIGURE 1. Vertebrata indeterminate. "Morphotype A" coprolites. **A**, SMP VP-1928; **B**, SMP VP-2754; **C**, SMP VP-1329 and **D**, SMP VP-2024. See Appendix for measurements and stratigraphic information.

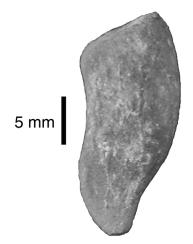
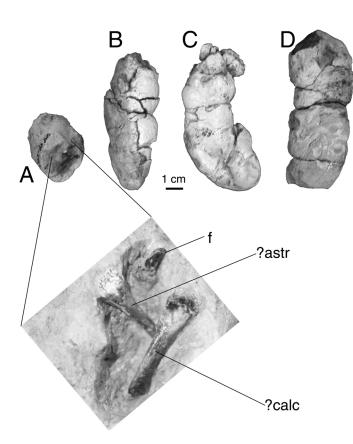


FIGURE 2. Vertebrata indeterminate. "Morphotype B" coprolite. SMP VP-2473. See Appendix for measurements and stratigraphic information.



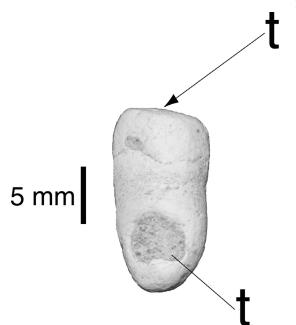


FIGURE 4. Vertebrata indeterminate. "Morphotype D" coprolite. SMP VP-2008. Abbreviation: t, terminus. See Appendix for measurements and stratigraphic information.

7C) measures approximately 95 mm maximum length and 22.50 mm maximum thickness. Bone inclusions (fish scales) are present only in SMP VP-2200 (Fig. 7C).

COPROLITES OF UNCERTAIN MORPHOLOGY

Three specimens are coprolites of uncertain morphologies. The first, SMP VP-1597, consists of numerous broken fragments, presumably from a single defecation event. Two segments have blunt leading ends, whereas the other two sections consist of broken segments. The external texture is relatively smooth, but the largest section, measuring 18.8 mm maximum length and 15.02 mm maximum thickness, has faint longitudinal striations. There are no bone inclusions present.

The second coprolite in this category, SMP VP-2081, is unipolar, compressed, and fractured with most of the external surface spalled off. The area where the surface is preserved exhibits a slightly wrinkled texture. The coprolite seems to represent a complete fecal segment and measures 26.4 mm maximum length, 16.12 mm maximum thickness, and 9.4 mm minimum thickness. There are no inclusions present.

The third specimen, SMP VP-2879, consists of numerous, isolated, tiny coprolites and coprolite fragments, obtained from an anthill. The largest one measures approximately 4.4 mm in diameter. The texture of these coprolites ranges from smooth to slightly blistered. No bone inclusions are present in any of these coprolites.

QUESTIONABLE COPROLITES

Two specimens, SMP VP-2524 and SMP VP-3276, are tentatively considered to be coprolites based on the overall preservation and kaolinitic-like/phosphatic? composition. Neither specimen has a distinct form nor do they have any bone inclusions. These specimens are not considered further.

TYRANNOSAUROID COPROLITE

SMP VP-3329 (Fig. 8) is a large aggregate, consisting of part of a medial section of an indeterminate ?hadrosaurid ?scapula blade, ?vertebral centra and angular bone fragments, forming an irregular fused bony mass, and is interpreted as a coprolite from a tyrannosauroid. Cancellous bone, possibly pertaining to vertebral centra, is also a fused component

FIGURE 3. Vertebrata indeterminate. "Morphotype C" coprolites. A, SMP VP-2446, (with close-up of bone inclusions from an indeterminate anuran); B, SMP VP-1615; C, SMP VP-1616 and D, SMP VP-1739. Abbreviations: ?astr, astragalus; ?calc, calcaneum; f, bone fragment. See Appendix for measurements and stratigraphic information.

sions are uncommon in this form, identifiable in only one (SMP VP-1521) of seven specimens assigned to this morphotype. Based on SMP VP-2117 (Fig. 5B), this morphotype consists of a series of segmented units, similar to morphotype "C," but is distinguished from that morphotype by its twisted nature and external sculpturing. The segmented units vary is size and complexity based on SMP VP-2117. The largest complete segment (Fig. 5B) measures 12.97 mm (maximum thickness), while the smallest complete segment measures 11.54 mm (maximum thickness).

Morphotype "F"

Morphotype "F" is represented by a single specimen, SMP VP-1673 (Fig. 6), characterized by a loose spiral form at the leading end that transitions to a crescent–shape and becomes unipolar towards the other (terminal) end. The terminal end is broken and the leading end is blunt. Surface texture is smooth and there are no bone inclusions. The maximum length is approximately 60 mm and the maximum thickness is 16.65 mm.

Morphotype "G"

Morphotype "G" is distinguished by a loose to tight, crescentshaped coil (Fig. 7). The surface sculpturing consists of prominent longitudinal grooves. Each coil represents a single segment, based on the leading end and the prominent single terminus. The two smaller coprolites (SMP VP-2149, Fig. 7A and SMP VP-2502, Fig. 7B) are coiled in the same direction. SMP VP-2200 (Fig. 7C), the largest of this morphotype, is coiled in the opposite direction. SMP VP-2149 (Fig. 7A) measures approximately 50 mm maximum length and 14.14 mm maximum thickness, while SMP VP-2502 (Fig. 7B) measures approximately 55 mm maximum length and 10.54 mm maximum thickness. SMP VP-2200 (Fig.

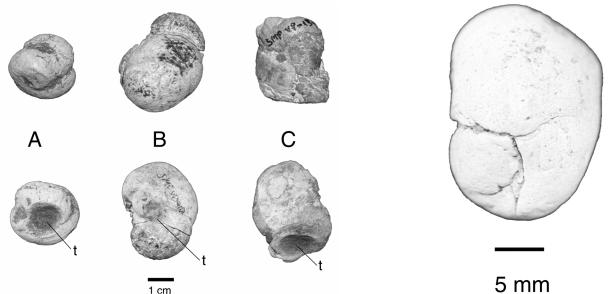


FIGURE 5. Vertebrata indeterminate. "Morphotype E" coprolites (showing two different sides, upper row displaying coil and lower row displaying the terminus). **A**, SMP VP-1461; **B**, SMP VP-2117; and **C**, SMP VP-1341. **Abbreviation: t**, terminus. See Appendix for measurements and stratigraphic information.

of this peculiar structure. It measures 31 cm (maximum length) by 15.8 cm (maximum "thickness"). There is no evident orientation to the mass. Angular fragments, presumably from the ?scapula blade, occur interspersed along the opposite side of the exterior surface of the main section (Fig. 8). There are no explicit bite marks evident on the external surface of the ?scapula blade or on any of the preserved fragments.

DISCUSSION

Upper Cretaceous coprolites have been documented in a few papers, most notably Matley (1941), Broughton et al. (1978), Hunt (1991), Thulborn (1991), Coy (1995), Chin et al. (1998, 2003), Seilacher et al., (2001), Månsby (2009), Harrell and Schwimmer (2010), Hunt and Lucas (2010), Souto (2010) and Eriksson et al. (2011). The majority of these articles have discussed morphology and the potential fecal producers, which have mostly been considered to be carnivores.

In the Upper Cretaceous strata of the San Juan Basin in New Mexico, there are several common potential carnivorous animals, including, fishes, crocodylians and carnivorous dinosaurs. Other possible candidates might include amphibians, turtles, champsosaurs, pterosaurs, birds, and small mammals. However, based on known studies, most Upper Cretaceous coprolites have been attributed to fishes and crocodylians.

Morphotype "A" most closely resembles coprolites figured by Harrell and Schwimmer (2010, p. 211, fig. 6C), which they hypothesized may have been produced by small crocodylians, but this is not known for certain. Several of the New Mexico "J-shaped" specimens (morphotype "A") have bone inclusions (see Appendix). Small- to medium-sized crocodylians such as *Brachychampsa*, cf. *Leidyosuchus* sp. and *Denazinosuchus* are known from the Upper Cretaceous of the San Juan Basin, New Mexico (Lucas et al., 2006), and any one of these crocodylians may have been the coprolite producer.

Morphotype "B" is represented by a single specimen (SMP VP-2473, Fig. 2) that appears to be unique in morphology, distinguished by a slightly sinuous shape and covered with longitudinal wrinkles. Based on its very small size and shape we feel confident that is was not produced by either a crocodylian or dinosaur.

Morphotype "C" is the most common of the morphotypes, and a high percentage of these coprolites have bone inclusions. Although

FIGURE 6. Vertebrata indeterminate. "Morphotype F" coprolite. SMP VP-1673. See Appendix for measurements and stratigraphic information.

they differ from those illustrated by Thulborn (1991) and Harrell and Schwimmer (2010), and differ slightly from those illustrated by Souto (2010), we attribute morphotype "C" to crocodylians. The occurrence of lepisosteid and anuran remains is consistent with the presumed diets of crocodylians in a swampy environment. The anuran remains in SMP VP-2446 (Fig. 3A) are significant as being only the third record of an anuran in the Upper Cretaceous of New Mexico, the first two being fragments of maxillae assigned to the discoglossid *Scotiophryna pustulosa* and the pelobatid *?Eopelobates* sp. (Armstrong-Zeigler, 1980). These bones may be attributable to either taxon, but due to their undiagnostic nature, a more precise identification is not possible. Although anuran remains have recently been reported in Pleistocene snake coprolites (Bader and Martin, 2011), SMP VP-2446 represents the first remains (postcrania) in a coprolite of an anuran from the Upper Cretaceous.

Morphotype "D" is represented by a single specimen (SMP VP-2008, Fig. 4) and is similar to other small unipolar coprolites illustrated by Harrell and Schwimmer (2010), except for its blunt end and location of the terminus on its side. Therefore, it is another unique morphotype and is from an unknown fecal producer.

Morphotype "E" is characterized by tightly and irregularly coiled coprolites (Fig. 5). These coprolites are similar to those reported and figured by Broughton et al. (1978), and refigured by Thulborn (1991, fig. 5d), from the Upper Cretaceous Whitemud Formation in western Canada, which were considered fish coprolites. Morphotype "E" coprolites are attributed to fishes based on similarities to those reported and figured by Broughton et al. (1978).

Morphotype "F" is represented by a single coprolite (SMP VP-1673, Fig. 6), uniquely characterized by its loose spiral form at the leading end and transitions to a crescent–shape unipolar form towards the other (terminal) end. In some respects, it is similar to morphotype "A," although it is coiled in on itself rather than being "J-shaped." We are unable to identify its producer, although its small size may suggest some indeterminate fish.

Morphotype "G" coprolites are distinguished by a loose- to tightcrescent shaped coil (Fig. 7) and vary in size. The longitudinal grooves in this morphotype are more prominent and wider than the longitudinal striations seen in morphotype "E." These grooves are similar to those seen on purported reptilian coprolites figured by Matley (1941, pl. 36, figs. 3-4), re-figured by Thulborn (1991, 7e-f) and later named *Alococopros indicus*, and re-figured, in part, by Hunt et al. (2007, fig. 3D). The distinguishing features of morphotype "G" are its coil, as well as its

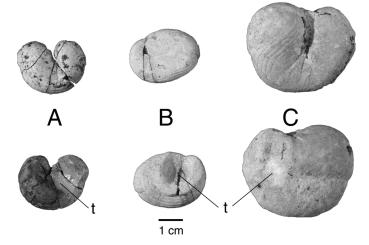


FIGURE 7. Vertebrata indeterminate. "Morphotype G" (showing two different sides, upper row displaying striated surface texture and lower row displaying the terminus). A, SMP VP-2149; B, SMP VP-2502 and C, SMP VP-2200. Abbreviation: t, terminus. See Appendix for measurements and stratigraphic information.

prominent grooves, which have been attributed to turtles, based on longitudinal pleats that occur in the intestines of some living turtles (Matley, 1941; Thulborn, 1991) and also to archosauromorphs and crocodylians (Young, 1964; Northwood, 2005). Indeed, there are numerous turtles known throughout the Fruitland, Kirtland and Ojo Alamo formations (Jasinski et al., 2011; Sullivan et al., in press), so there is a strong possibility that a turtle was the fecal producer.

SMP VP-3329 (Fig. 8) is a large aggregate of fossil bone, consisting of part of a medial section of indeterminate ?hadrosaurid ?scapula blade, ?vertebral centra and angular bone fragments, forming an irregular fused bony, matrix-supported, mass. The specimen was found in the typical soft mudstone of the De-na-zin Member (Kirtland Formation) as an isolated structure with no associated skeletal remains. This fact precludes it from being considered a cololite, as stated by Seilacher et al. (2001), since one would expect part of the tyrannosauroid skeleton to be preserved. Nearby, numerous other vertebrate remains, such as isolated carnosaur teeth, have been found and collected in adjacent rivulets within meters of SMP VP-3329.

We interpret this entire mass to represent a bony inclusion of a probable coprolite with the supporting matrix prepared away. There is no evidence that this is a pathologic structure. The isolated bony fragments embedded in it would preclude that interpretation. Nor is there evidence for it being a natural aggregate, formed from some natural depositional process.

The large size and massive bony nature further suggest that this structure may be from a tyrannosauroid. Broken-up bone, consisting of smaller angular bone fragments, suggests a scavenging behavior for the animal that produced this mass. The angular bone fragments were probably broken-up in the carcass prior to ingestion. It is difficult to imagine these bones were broken internally in the digestive track of the dinosaur.

Chin et al. (1998) attributed a large coprolite in the collections of the Royal Saskatchewan Museum (SMNH P2609.1) to a tyrannosaurid from the Maastrichtian Frenchman Formation of Canada, based on its large size and "temporal and geographic context." This coprolite is composed of a mass of bone fragments and digested (to partially digested) bone. Although larger, the specimen resembles SMP VP-3329 in both its size (>30 cm) and general composition. As with SMNH P2609.1, the matrix-supported bone fragments in SMP VP-3329 point to its coprolitic origin, rather than to it being a product of a regurgitation event or fluvial deposition. The size of SMP VP-3329 (approximately 31 cm) is consistent with a smaller tyrannosauroid, such as *Bistahieversor sealeyi* (Carr and Williamson, 2010), which is known from the Kirtland Formation.

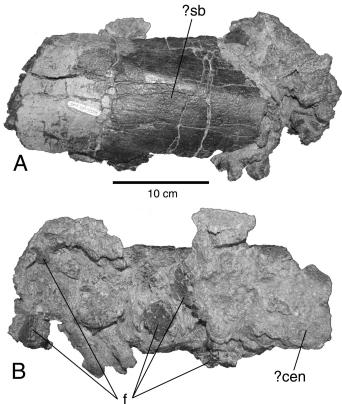


FIGURE 8. Dinosauria indeterminate, questionable coprolite or regurgitalite. SMP VP-3329, **A**, side showing large section of the ?scapula blade (external side) and with fused bony mass; and **B**, opposite side showing cancellous bone as a fused bony mass with isolated angular ?scapula fragments fused to the internal side of the ?scapula blade. **Abbreviations: ?cen**, ?vertebral centrum; **f**, bone fragments; **?sb**, medial section of ?scapula blade (external view). See Appendix for measurements and stratigraphic information.

Chin et al. (2003) used the same criteria to identify another tyrannosaurid coprolite in the collections of the Royal Tyrell Museum (TMP 98.102.7), this one from the upper Campanian Dinosaur Park Formation. TMP 98.102.7 is largely composed of fossilized soft-tissue, unlike SMNH P2609.1 and SMP VP-3329, and is further characterized by one side exhibiting "uneven topography" that varies in thickness, similar to SMP VP-3329. Chin et al. (2003) attributed this uneven form to expulsion of the feces in a "viscous state on uneven terrain." We doubt the terrain played a major factor in the "uneven topography" of the specimen, rather it's more likely due to its viscous state and the loss of the supporting coprolitic matrix before fossilization. The presence of small bone fragments and the fossilized soft-tissue in TMP 98.102.7 suggest incomplete digestion as a result of a shorter gut-residence time (Chin et al., 2003). The more porous cancellous centra appear to have been partly "digested," unlike the sections of the ?scapula blade and associated fragments. This suggests that the entire mass probably spent a fair amount of time in the digestive track prior to expulsion. Although lacking soft-tissue, both SMNH P-2609.1 and SMP VP-3329 contain small and large bone fragments. Indeed, the unusually large ?scapula blade in SMP VP-3329 suggests gorging, or rapid food ingestion, as hypothesized by Chin et al. (2003). The ?scapula blade (Fig. 5A) may be from a subadult hadrosaurid based on its overall morphology (?scapula blade length approximately 21 cm, width 11.12 cm, thickness 2.25 cm). Thus, SMP VP-3329 appears to be the third record of a large tyrannosauroid coprolite, and the first from the United States.

CONCLUSIONS

The SMP collection of coprolites from the Upper Cretaceous, San Juan Basin, New Mexico is attributed to carnivorous vertebrates,

260

including fish, turtle, crocodylian and dinosaur. Seven morphotypes are recognized, and an eighth is identified as being a large tyrannosauroid coprolite, but lacking a supporting coprolitic matrix, presumably because it was expelled in a viscous state. The identification of the tyrannosauroid coprolite is based mainly off elimination of other possibilities and the most parsimonious remaining one, although without direct correlation of a coprolite with a distinct tyrannosauroid specimen, we cannot be completely certain. Still, this is the first record of a purported tyrannosauroid coprolite from the United States and from New Mexico. The contents of the coprolite (?scapula blade, ?vertebrae centra and angular bone fragments) are tentatively identified as belonging to a subadult hadrosaur, based on size and external scapular morphology. The anuran bones in SMP VP-2446 are the first to be identified from an Upper Cretaceous coprolite. At least four unique Upper Cretaceous coprolite morphotypes (B, D, F and G) are recognized from New Mexico. Some of these morphotypes may be from the same taxon, but the identity of the fecal producers is still highly conjectural. Although some of the coprolites may be attributed to known fecal producers based on previous studies, none of these new morphotypes can be attributed to any known fecal producer with any degree of certainty.

ACKNOWLEDGMENTS

We thank Arjan Boere, Michael Burns, John H. Burris, Denver W. Fowler, James C. Hartley, Elliott J. Karetny, James W. Murphy, and James Nikas for their assistance in the field. We thank Walter Meshaka (State Museum of Pennsylvania) for comparative frog material. Spencer G. Lucas and Adrian P. Hunt read an earlier version of this paper and we thank them for their comments and suggestions.

REFERENCES

- Armstrong-Ziegler, J.G., 1980, Amphibia and Reptilia from the Campanian of New Mexico: Fieldiana: Geology, New Series, no. 4, 39 p.
- Bader, K.S. and Martin, L.D., 2011, Snake coprolites from the Pleistocene Angus local fauna, Nebraska: Abstracts of the 2011 Kansas Academy of Science, Baldwin City, Kansas.
- Broughton, P.L., Simpson, F. and Whitaker, S.H., 1978, Late Cretaceous coprolites from western Canada: Palaeontology, v. 21, p. 443-453.
- Brown, J., 1983, Geologic and isopach maps of the Bisti, De-na-zin and Ahshe-sle-pah [sic] Wilderness Study areas, New Mexico: Department of the Interior, Geological Survey, Reston, VA, Map MF-1508-A, scale 1:50,000, 2 sheets.
- Carr, T.D. and Williamson, T.E., 2010, *Bistahieversor sealeyi*, gen. et sp. nov., a new tyrannosauroid from New Mexico and the origin of deep snouts in Tyrannosauroidea: Journal of Vertebrate Paleontology, v. 30, p. 1-16.
- Chin, K., 2002, Analyses of coprolites produced by carnivorous vertebrates: Paleontological Society Papers, v. 8, p. 43-49.
- Chin, K., Tokaryk, T.T., Erickson, G.M. and Calk, L.C., 1998, A king-sized theropod coprolite: Nature, v. 393, p. 680-682.
- 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: PALAIOS, v. 18, p. 286-294.
- Coy, C.E., 1995, The first record of spiral coprolites from the Dinosaur Park Formation (Judith River Group, Upper Cretaceous) southern Alberta: Journal of Paleontology, v. 69, p. 1191-1194.
- Eriksson, M.E., Lindgren, J., Chin, K. and Månsby, U., 2011, Coprolite morphotypes from the Upper Cretaceous of Sweden: novel views on an ancient ecosystem and implications for coprolite taphonomy: Lethaia, 10.1111/j.1502-3931.2010.00257.x.
- Fassett, J.E. and Hinds, J.S., 1971, Geology and fuel resources of the Fruitland Formation and Kirtland Shale of the San Juan Basin, New Mexico: U.S. Geological Survey, Professional Paper 676, p. 1-76.
- Harrell, S. and Schwimmer, D.R., 2010, Coprolites of *Deinosuchus* and other crocodylians from the Upper Cretaceous of western Georgia, USA: New Mexico Museum of Natural History and Science, Bulletin 51, p. 209-213.
- Hunt, A.P., 1991, Integrated vertebrate, invertebrate and plant taphonomy of the Fossil Forest area (Fruitland and Kirtland formations: Late Cretaceous), San Juan County, New Mexico, U.S.A.: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 88, p. 85-107.
- Hunt, A.P. and Lucas, S.G., 1993, Cretaceous vertebrates of New Mexico: New Mexico Museum of Natural History and Science, Bulletin 2, p. 77-91.
- Hunt, A.P. and Lucas, S.G., 2003, A new hadrosaur track from the Upper Cretaceous Fruitland Formation of northwestern New Mexico: New Mexico Geological Society, Guidebook 54, p. 379-381.

- 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, New York, John Wiley and Sons, p. 221-240.
- Hunt, A.P. and Lucas, S.G., 1992, Stratigraphy, paleontology and age of the Fruitland and Kirtland formations (Upper Cretaceous), San Juan Basin, New Mexico: New Mexico Geological Society, Guidebook 43, p. 217-239.
- 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, p. 219-226.
- Hunt, A.P., Lucas, S.G. and Lockley, M.G., 1998, Taxonomy and stratigraphic and facies significance of vertebrate coprolites of the Upper Triassic Chinle Group, western United States: Ichnos, v. 5, p. 225-234.
- Hunt, A.P., Lucas, S.G. and Spielmann, J.A., 2011, New Mexico Museum of Natural History and Science and the vertebrate coprolite record from New Mexico: New Mexico Geology, v. 33, p. 55.
- Hunt, A.P., Lucas, S.G., Spielmann, J.A. and Lerner, A.J, 2007, A review of vertebrate coprolites of the Triassic with descriptions of new Mesozoic ichnotaxa: New Mexico Museum of Natural History and Science, Bulletin 41, p. 88-107.
- Jasinski, S.E., Sullivan, R.M. and Lucas, S.G., 2011, Taxonomic composition of the Alamo Wash local fauna from the Upper Cretaceous Ojo Alamo Formation (Naashoibito Member), San Juan Basin, New Mexico: New Mexico Museum of Natural History and Science, Bulletin 53, p. 216-271.
- Jouy-Avantin, F., Debenath, A., Moigne, A.-M., and Moné, H., 2003, A standardized method for description of the study of coprolites: Journal of Archaeological Science, v. 30, p. 367-372.
- Lehman, T.M., 1985, Depositional environments of the Naashoibito Member of the Kirtland Shale, Upper Cretaceous, San Juan Basin, New Mexico: New Mexico Bureau of Mines and Mineral Resources, Circular 195, p. 55-79.
- Lucas, S.G., 1981, Dinosaur communities of the San Juan Basin: a case for lateral variations in the composition of Late Cretaceous dinosaur communities; *in* Lucas, S.G., Rigby, J.K., Jr. and Kues, B.S., eds., Advances in San Juan Basin paleontology: Albuquerque, University of New Mexico Press, p. 337-393.
- Lucas, S.G. and Sullivan, R.M., 2000, Stratigraphy and vertebrate biostratigraphy across the Cretaceous-Tertiary boundary, Betonnie Tsosie Wash, San Juan Basin, New Mexico: New Mexico Museum of Natural History and Science, Bulletin 17, p. 95-104.
- Lucas, S.G., Spielmann, J.A., Sullivan, R.M. and Lewis, C., 2006, Late Cretaceous crocodylians from the San Juan Basin, New Mexico: New Mexico Museum of Natural History and Science, Bulletin 35, p. 249-252.
- Lucas, S.G., Sullivan, R.M., Jasinski, S.E. and Ford, T.L., 2011, Hadrosaur footprints from the Upper Cretaceous Fruitland Formation, San Juan

Basin, New Mexico, and the ichnotaxonomy of large ornithopod footprints: New Mexico Museum of Natural History and Science, Bulletin 53, p. 357-362.

- Månsby, U., 2009, Late Cretaceous coprolites from the Kristianstad Basin, southern Sweden: Examensarbeten I geologi vid Lunds inuversitet, Nr. 246, 16 p.
- Matley, C.A., 1941, The coprolites of Pijdura, Central Provinces: Records of the Geological Survey of India, v. 74, p. 535-547.
- Northwood, C., 2005, Early Triassic coprolites from Australia and their palaeobiological significance: Palaeontology, v. 48, p. 49-68.
- Reeside. J.B., Jr., 1924, Upper Cretaceous and Tertiary formations of the western part of the San Juan Basin of Colorado and New Mexico: U.S. Geological Society, Professional Paper 134, p. 1-70.
- Seilacher, A., Marshall, C., Skinner, H.C.W. and Tsuihiji, T., 2001, A fresh look at sideritic "coprolites": Paleobiology, v. 27, p. 7-13.
- Souto, P.R.F., 2010, Crocodylomorph coprolites from the Bauru Basin, Upper Cretaceous, Brazil: New Mexico Museum of Natural History and Science, Bulletin 51, p. 201-208.

Sullivan, R.M., 2006, Ah-shi-sle-pah Wilderness Study Area (San Juan Ba-

sin, New Mexico): a paleontological (and historical) treasure and resource: New Mexico Museum of Natural History and Science, Bulletin 34, p. 169-174.

- Sullivan, R.M., Jasinski, S.E. and Lucas, S.G., in press, Re-assessment of Late Campanian (Kirtlandian) turtles from the Upper Cretaceous Fruitland and Kirtland formations, San Juan Basin, New Mexico; *in* Brinkman, D., Gardner, J. and Holdroyd, P., eds., Morphology and evolution of turtles: Dordrecht, Springer.
- Thulborn, R.A., 1993. Morphology, preservation and palaeobiological significance of dinosaur coprolites: Palaeogeography, Palaeclimatology, Palaeoecology, v. 83, p. 341-366.
- Williamson, T.E., 2000, Review of Hadrosauridae (Dinosauria, Ornithischia) from the San Juan Basin, New Mexico: New Mexico Museum of Natural History and Science, Bulletin 17, p. 191-213.
- Wolberg, D.L., Hall, J.P. and Bettis, D., 1988, First record of dinosaur footprints from the Fruitland Formation, San Juan County, New Mexico: New Mexico Bureau of Mines and Mineral Resources, Bulletin 122, p. 33-44.
- Young, C.C., 1964, New fossil crocodiles from China: Vertebrata PalAsiatica, v. 8, p. 190-208.

| 2 | |
|----------|--|
| Ĥ | |
| ρ | |
| Z | |
| E | |
| P | |
| - | |
| ₹, | |

List of coprolites, grouped by morphotype, from the Fruitland, Kirtland and Ojo Alamo formations, in the collections of the State Museum of Pennsylvania.

| BONE | None | None | Yes | Yes | ?Yes | None | None | None | None | Yes | None | None | None | Yes | None | Yes | Yes | None | None | None | Yes | None | None | None | None | Yes | None | None | None | None | None | None |
|-----------------|-------------|-----------|-------------|-------------|-----------|-----------|-------------|--------------------|-------------|-------------|-----------|--------------------|--------------------|--------------------|--------------------|--------------------|--------------------|--------------------|--------------------|--------------------|--------------------|--------------------|--------------------|--------------------|-----------|------------------------------------|------------------------------------|--------------------|-------------|-----------|-----------|-------------|-------------|-----------|-------------|-------------|-------------------|--------------------|---------------------------------|--------------------|
| TEXTURE | smooth | smooth | smooth | smooth | smooth | smooth | smooth | slightly blistered | smooth | smooth | wrinkled | slightly blistered | smooth | slightly blistered and striated | slightly blistered and striated | slightly blistered | striated | striated | striated | smooth | striated | striated | striated | ć | slightly wrinkled | slightly blistered | smooth to slightly blistered | slightly blistered |
| MAX THICKNESS | 16.76 mm | 16.74 mm | 26.36 mm | 10.20 mm | 17.00 mm | 7.15 mm | 18.71 mm | 12.12 mm | 9.37 mm | 10.00 mm | 9.48 mm | 6.45 mm | 12.74 mm | 22.95 mm | 36.00 mm | 16.02 mm | 37.79 mm | 28.47 mm | 22.51 mm | 21.93 mm | 25.93 mm | 30.40 mm | 13.10 mm | 38.29 mm | 8.47 mm | 15.01 mm | 1 3.04 mm | 14.25 mm | 10.83 mm | 12.97 mm | 7.33 mm | 16.65 mm | 14.14 mm | 22.50 mm | 10.54 mm | 15.02 mm | 16.12 mm | 6.25 mm | >4.50 mm | 25.85 mm |
| MAX LENGTH | 47.33 mm | 34.35 mm | 72.78 mm | 17.85 mm | 43.00 mm | 15.61 mm | 35.35 mm | 20.88 mm | 12.85 mm | 17.63 mm | 21.24 mm | 8.35 mm | 18.05 mm | 78.11 mm | 86.88 mm | 29.55 mm | 91.80 mm | 58.88 mm | 16.63 mm | 33.61 mm | 33.56 mm | 39.88 mm | 21.35 mm | 72.78 mm | 16.40 mm | ذ | ż | ż | 2 | ć | ~13.10 mm | ~60.00 mm | ~50.00 mm | ~95.00 mm | ~55.00 mm | 18.80 mm | 26.40 mm | 7.95 mm | >4.5 mm | 27.05 mm |
| MEMBER | Hunter Wash | De-na-zin | Hunter Wash | Hunter Wash | De-na-zin | De-na-zin | Hunter Wash | Naashoibito | Hunter Wash | Hunter Wash | De-na-zin | | Hunter Wash | Hunter Wash | Hunter Wash | Hunter Wash | De-na-zin | Hunter Wash | De-na-zin | Naashoibito | De-na-zin | Hunter Wash | De-na-zin | De-na-zin | Hunter Wash | De-na-zin | De-na-zin | Hunter Wash | Hunter Wash | De-na-zin | Naashoibito | Hunter Wash | De-na-zin | Fossil Forest | Fossil Forest | Enssil Enrest |
| FORMATION | Kirtland | Kirtland | Kirtland | Kirtland | Kirtland | Kirtland | Kirtland | Ojo Alamo | Kirtland | Kirtland | Kirtland | Nacimiento | Kirtland | Ojo Alamo | Kirtland | Kirtland | Kirtland | Kirtland | Kirtland | Kirtland | Kirtland | Kirtland | Kirtland | Kirtland | Ojo Alamo | Kirtland | Kirtland | Fruitland | Fruitland | Fruitland |
| LOCALITY NO. | 228 | 382 | 419 | 228 | 319a | 350 | 228 | 370b | 228 | 421 | 319a | 351 | 452 | 400 | 400 | 397 | 363a | 365 | 283 | 419 | 421 | 228 | 313a | 410b | 350 | 372 | 358 | 376a | 365 | 361 | 319a | 399 | 281 | 319a | 370b | 398 | 309a | 450 | 450 | 463 |
| SMP VP- | 1329 | 1928 | 2024 | 2138 | 2178 | 2417 | 2754 | 3459 | 1926 | 2040 | 2473 | 739 | 2524 | 1615 | 1616 | 1659 | 1739 | 1792 | 1811 | 1974 | 2063 | 2446 | 2621 | 2700 | 2008 | 1134 | 1341 | 1461 | 1521 | 2117 | 2615 | 1673 | 2149 | 2200 | 2502 | 1597 | 2081 | 2582 | 2879 | 3776 |
| MORPHOTYPE | A | A | A | A | A | A | A | A | 3A | 3A | В | ?B | ?B | U | U | U | U | U | U | U | U | U | U | U | D | ш | ш | Ш | E | ш | ш | ш | 0 | J | 9 | 2 | : | 2 | \$ | ۲ |