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DESCRIPTIVE TERMINOLOGY OF COPROLITES AND RECENT FECES

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Abstract—Vertebrate coprolites and Recent feces display a wide range of morphological variation. A relatively small number of authors have explicitly addressed the terminology used to describe coprolites. Spiral coprolites externally have the appearance of a ribbon coiled around a long axis, but internally they consist of stacked, and spiraling, cones. Scroll coprolites are more analogous to a rolled sheet of paper in structure. These two morphologies reflect two architectures of valvular intestines of which Type D (mucosa forming spiraling cones, pointed anteriorly) is most common, and these intestines form coprolites of spiral morphology. The oldest possible spiral coprolites are from the Late Ordovician of South Africa. It is possible that some putative spiral vertebrate coprolites from the Ordovician-Permian might have been made by eurypterids. Spiral coprolites are amphipolar if the posterior spire constitutes more than 75% of the length; otherwise they are heteropolar. Heteropolar coprolites are microspiral, if the posterior spire constitutes less than 50% of the length of the coprolite in lateral view, and macrospiral if it represents 50% or more. The end of a spiral coprolite that externally appears to be more tightly spiraled is the posterior end. Scroll coprolites are very uncommon. *Eucoprus cylindratus* ichnogen. et ichnosp. nov. is a cylindrical coprolite with no inclusions. We recognize 27 morphotypes of coprolites and Recent vertebrate feces in 11 main categories: A, Cylindrical, elongate (length > 5 x diameter); B, Cylindrical, short (length < 5 x diameter); C, Subrounded; D, Flattened rounded plates that accumulate in circular piles; E, Reniform; F, Spiral; G, Elongate coiled cylinder; H, Thin and ovoid; I, Thin and linear; J, Splatter; and K, Irregular in shape.

INTRODUCTION

Vertebrate coprolites display a wide range of morphological variation, although the majority are elongate, and, if preserved uncrushed, they are commonly sub-cylindrical. This gross morphology reflects the fact that most vertebrate coprolites represent fossilized carnivore feces (e.g., Hunt et al., 1994). Recent vertebrate feces (and some cave samples of late Pleistocene coprolites: Mead and Swift, 2012) display a much wider range of morphologies, as they include many herbivore traces (e.g., Chame, 2003). Herbivore coprolites are much less common prior to the Pleistocene but some are preserved--for example, Mesozoic specimens produced by orthithischian and sauropod dinosaurs (e.g., Chin, 2007; Chin and Gill, 1996; Chin and Kirkland, 1998; Ghosh et al., 2004). What all vertebrate coprolite morphologies require is a consistent and standardized descriptive terminology.

A relatively small number of papers have explicitly addressed the terminology of describing coprolites (e.g., Neumayer, 1904; Häntzschel et al., 1968; Jain, 1983; McAllister, 1985; Thulborn, 1991; Jouy-Avantin et al., 2003; Hunt et al., 2007) (Fig. 1). Spiral coprolites are among the most distinctive, and they preserve a suite of morphological features that allow for ease of description. The purpose of this paper is to briefly review aspects of the morphology of vertebrate coprolites and Recent feces and the nomenclature applied to in order to advocate a standard descriptive terminology.

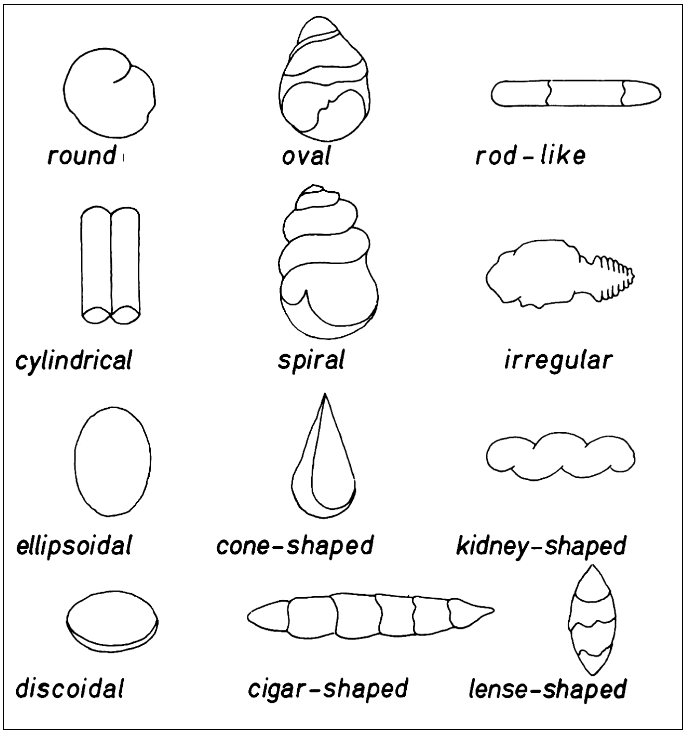

FIGURE 1. Classification of coprolites (vertebrate and invertebrate) by Häntzschel et al. (1968, fig. 1).

SPIRAL AND SCROLL COPROLITES

Introduction

Spiral coprolites were among the first to be recognized by Buckland (1829), and they are very common in aquatic paleoenvironments, notably before the Cenozoic. Two distinct morphologies are often considered spiral: (1) spiral *sensu stricto*, hereafter referred to as spiral, which externally have the appearance of a ribbon coiled around a long axis, but internally they consist of stacked, and spiraling, cones (e.g., Jain, 1983, pl. 82, figs. 7-8); and (2) scroll, which are more analogous to a rolled sheet of paper in structure. These two morphologies reflect two architectures of valvular intestines: *valvula voluta* (scroll valve) and *valvula spiralis* (spiral valve) (Parker, 1885; Owen, 1886; McAllister, 1987). Parker (1885) distinguished four types of spiral valves, based on studies of the skate *Raja*, of which his Types C and D have the mucosa forming spiraling cones that would result in coprolites of spiral morphology (Fig. 2). In Type C, the apices of the cones are directed posteriorly (caudally), whereas in Type D they are pointed anteriorly (cranially) – Type D is the most common type (Parker, 1885; McAllister, 1985, 1987). The

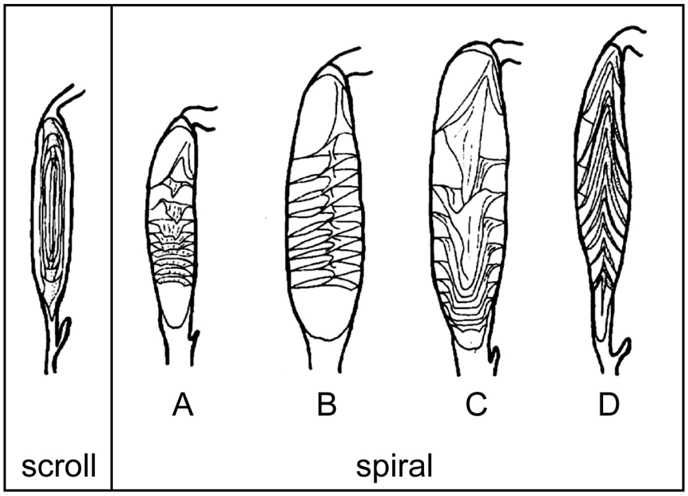

FIGURE 2. The morphologies of valvular intestines: *valvula voluta* (scroll valve) and four types (**A-D**) of *valvula spiralis* (spiral valve) (modified from McAllister, 1987, after Parker, 1885).

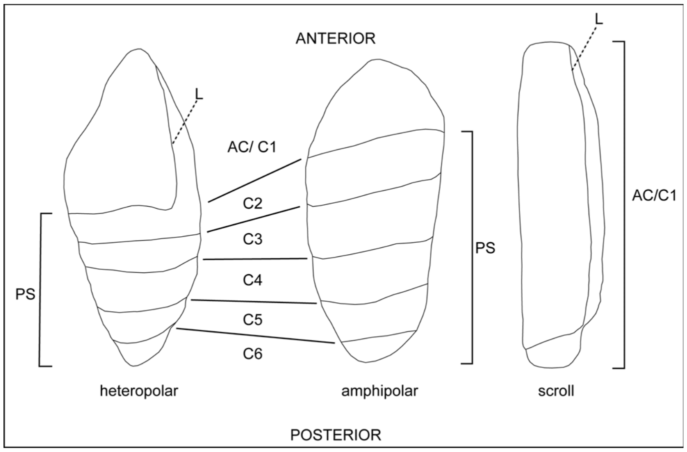

FIGURE 3. Terminology of spiral coprolites. **AC** is anterior coil, **C** is coil, **L** is lip, **PS** is posterior spire.

phylogenetic distribution of valvular intestines is not totally understood. McAllister (1987) presented evidence that that some or all agnathans, placoderms, dipnoans, actinistians and chondrichthyans have valvular intestines. However, the evidence for valvular intestines in acanthodians is not strong and consists of the co-occurrence of spiral coprolites and fish in the Mississippian of Montana, USA and the Upper Carboniferous of the Czech Republic, one of which may be enclosed in acanthodian scales (Zidek, 1980; McAllister, 1987). Only two fossil actinopterygians have evidence of this structure, and McAllister (1987) hypothesized that this group progressively reduced the valvular intestine. Teleosts do not exhibit this kind of intestinal structure (McAllister, 1987).

The oldest described spiral coprolites are from the Late Ordovician of South Africa (Aldridge et al., 2006). Because spiral valves are restricted to less derived fish they might be expected to be restricted to, or at least to be much more common, in the Paleozoic. However, this is not the case in marine environments where spiral coprolites are locally abundant in the Cenozoic (e.g., Diedrich and Felker, 2012; Stringer and King, 2012). In contrast, spiral coprolites are markedly less common in post-late Carnian (Late Triassic) ichnofaunas from freshwater settings. Evidence exists that eurypterids possessed a spiral intestinal structure (Waterson et al., 1985; Sumner, 1993), and many eurypterids reached a large body size, so it is possible that some putative spiral vertebrate coprolites from the Ordovician-Permian might pertain to this invertebrate group.

Terminology

Several authors have proposed different descriptive terminologies for spiral coprolites (e.g., Jain, 1983, fig. 2; McAllister, 1985, fig. 1; Laojumpon et al., 2012, fig. 5c). We have synthesized aspects of these schemes and recognize some new terms that we consider useful in the description of spiral coprolites (Fig. 3). The number of apparent spirals visible on the lateral aspect of the coprolite has been described as the spiral count (McAllister, 1985, fig. 1), the number of whorls (Jain, 1983, fig. 2) or the number of coils (Laojumpon et al., 2012, fig. 5c). We prefer the term "coils" for the external expression of the spiral, conular elements of the coprolite. In heteropolar coprolites the posterior segment of the coprolite consists of a number of closely spaced coils, which we term the posterior spire (Fig. 3). The anterior end consists of a single, antero-posteriorly elongate coil. This anterior coil was not considered in the count of the number of coils by McAllister (1985, fig. 1) but it was included by Jain (1983, fig. 2) and Laojumpon et al. (2012, fig. 5c), and we follow the latter authors. We use the numbering scheme of Jain (1983, fig. 2) and Laojumpon et al. (2012, fig. 5c) in considering the anterior coil to be coil 1 and numbering the remaining coils from anterior to posterior. In heteropolar coprolites the anterior coil (coil 1) includes an exposed edge of a flap of the coprolite that we term the lip, following Jain (1983, fig. 2) and Laojumpon et al. (2012, fig. 5c). We propose analogous terminology for amphipolar coprolites (Fig. 3). Scroll coprolites essentially consist of a single coil (Fig. 3).

Spiral Coprolites

Based on his study of samples from the Early Permian of Texas, Neumayer (1904) introduced a terminology for spiral coprolites that has been extremely durable. He recognized that some spiral coprolites have spirals that are distributed roughly evenly along the long axis in lateral view (amphipolar), while others have the spirals concentrated at one end (heteropolar). Heteropolar coprolites are much more common throughout the fossil record than amphipolar forms. True amphipolar coprolites (*sensu* Neumayer, 1904), such as *Hyronocoprus* (Hunt et al., 2005, fig. 3), preserve spirals (posterior spire) that extend for the majority of the length of the coprolite (>75%); some specimens that have been considered amphipolar are actually heteropolar (e.g., Jain, 1983, fig. 3A). The living lungfishes *Protopterus annectans* and *Neoceratodus forsteri* produce amphipolar feces (Williams, 1972, fig. 7; Jain, 1983, fig. 7). Recently, Hunt et al. (2007) recognized two forms of heteropolar morphology-- microspiral, in which the posterior spire constitutes less than 50% of the length of the coprolite in lateral view, and macrospiral, in which it represents 50%-75% the length of the coprolite.

One fundamental question with regard to spiral coprolites is which end is anterior/cranial? Since the early 19th Century it has been a fairly consistent practice to illustrate spiral coprolites with the long axis vertical and with the more tightly coiled end oriented upwards (e. g., Mantell, 1822, pl. 9, figs. 5, 8; DeKay, 1830, pl. 3, fig. 6; Buckland, 1835, pl. 34, figs. 1-5, 9-11; 1836, pl. 15, figs. 3, 5, 7, 8, 10-14), although Buckland was not totally consistent in his style (e.g., Buckland, 1835, pl. 28, figs. 4-8). This convention has generally been followed since (e.g., Neumayer, 1904; Jain, 1983; Thulborn, 1991; Laojumpon et al., 2012). Based on the convention of scientific illustration this would imply that the tightly coiled end is anterior. However, in most cases this is incorrect. In the most common Type D spiral valves, which are the most common chondrichthyan forms, the apices of the cones of the spiral are directed cranially, so the resultant coprolites would have both external and internal structures showing the appearance of smaller conular spirals being added inside the previous ones in a posterior direction; thus, the termination with the more closely-spaced external spirals is actually the posterior end (Diedrich and Felker, 2012, fig. 2). This is apparently the correct orientation for most spiral coprolites based on evidence of: (1) external morphology – the diameter of the exterior expression of the conular spirals decreases towards the posterior end; and (2) internal structure – the V-shaped cross sections of the spiral are open towards the posterior end (e.g., Jain, 1983, pl. 82, figs. 7-8; Hunt et al., 2012c, fig. 2D). Thus, the end of a spiral coprolite that externally appears to be the more tightly spiraled end (in lateral view) is to the posterior and should be oriented downward in scientific illustrations.

Williams (1972) was aware of the correct orientation of spiral coprolites but was inconsistent in his illustrations (compare Williams, 1972, figs. 2 and 6 with his pl. 1). Stewart (1978, fig. 4) and two papers in this volume (Diedrich and Felker, 2012, figs. 2-6; Stringer and King, 2012, figs. 7, 9) also used the correct orientation. But, note that Type C spiral valves have the apices of the spiral cones directed caudally, so that the tightly coiled end would be anterior.

Scroll Coprolites

Scroll coprolites are usually very uncommon (e.g., Hunt et al., 2012e; but see Stringer and King, 2012), except in the Middle-Late Silurian of Ireland and Scotland (Gilmore, 1992). The Silurian coprolites are unusual in that they are infilled with fine sediment of a different grain size from the surrounding matrix, indicating they were produced by a detritus feeder. Thus, it seems extremely unlikely that the putative agnathan producers had scroll valves homologous to those of some Recent fish. The only spiral coprolites that appear to be composed of sediment grains are from the Permian of Antarctica (Retallack and Krull, 1999).

NON-SPIRAL COPROLITES

Non-spiral coprolites display a wide range of morphologies (e.g., Häntzschel et al., 1968, fig. 1), which are discussed below. Nevertheless, many are simple cylinders with rounded terminations. We discern the need for an ichnotaxon to refer to this form. Because this morphology is manufactured by a large and diverse number of vertebrates, this ichnotaxon will undoubtedly be widespread in space and time (it will thus be homeomorphic), but, much like *Skolithos*, it will have great utility in describing ichnofaunas. Thus, we name this ichnotaxon *Eucoprus cylindratus* ichnogen. et ichnosp. nov. (Fig. 4; Appendix).

Thulborn (1991) noted that many coprolites have terminations of different shapes. He applied the term anisopolar to this type of coprolite and the term isopolar to forms in which the two ends are of the same shape. Typically, the posterior end of an anisopolar coprolite (Fig. 5), which emerges first from the anus/cloaca, is broadly rounded, and the anterior end is tapered to a point (mucro of Thulborn, 1991). The trailing end is pinched by the constriction of the cloaca/anal margins as it closes (Thulborn, 1991). We propose the term "segments" for the discrete longitudinal elements of a coprolite (pellets of Diedrich, 2012), well seen, for example, in felid and hyena specimens (e.g., Hunt et al., 2012a, fig. 5).

MORPHOLOGICAL CLASSIFICATION OF COPROLITES AND RECENT FECES

Several popular or semi-technical field guides have categorized modern vertebrate feces from different geographic areas (e. g., Murie, 1974; Stuart and Stuart, 2000). Chame (2003) compiled data from these guides and other technical literature and produced a morphological classification of the feces of Recent terrestrial mammals, recognizing nine morphotypes. Studies of Recent excrement are directed at aligning feces with producers, so they commonly include a miscellaneous category for the excrement of taxa that produce multiple morphotypes (e. g., Group IX of Chame, 2003). Herein, we are interested primarily in documenting the range of morphotypes present and only secondarily in assigning them to a producer following standard paleoichnological practice. Building on Chame's (2003) work we have attempted a first classification of the morphotypes of coprolites and Recent feces of vertebrates (Fig. 6;

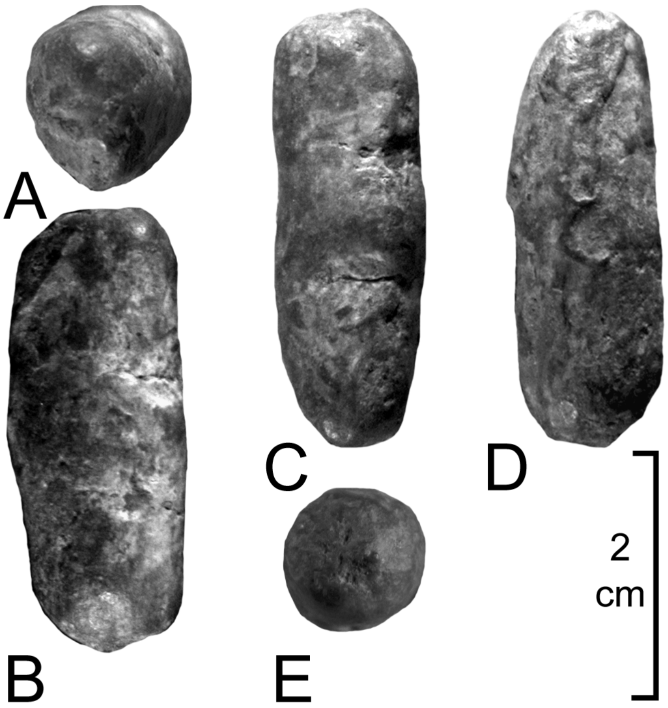

FIGURE 4. *Eucoprus cylindratus*, ichnosp. nov. from the Upper Triassic Redonda Formation of New Mexico, USA. **A-E**, NMMNH P-66582, coprolite in terminal (**A**, **E**) and lateral (**B**, **C**, **D**) views.

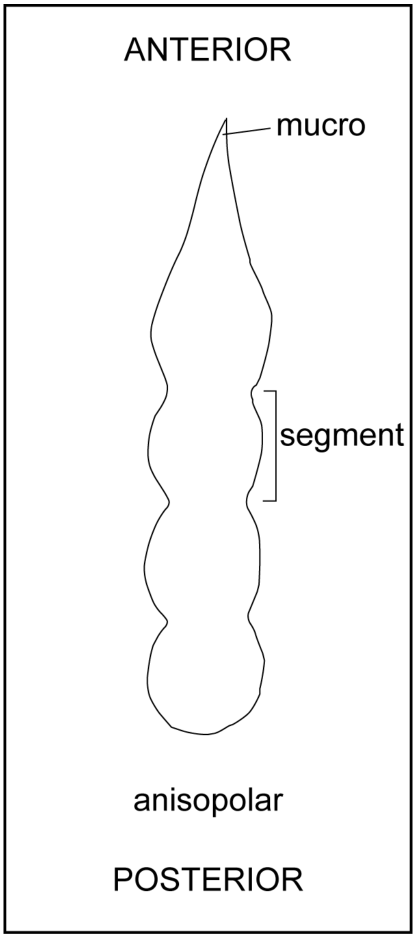

FIGURE 5. Terminology of a non-spiral coprolite.

TABLE 1. A morphological classification of coprolites and Recent feces.

Morphotype	Morphology	Sub-morphotype	Morphology	Producers (fossil and Recent)	Ichnotaxa	Demonstrated stratigraphic range	Notes and principal references
A	Cylindrical, elongate (length >5 x diameter)	A1	Tapered at one end with distinct rounded segments	Most Recent and Pleistocene felids Recent and Pleistocene Hyaenidae	*Hyaenacoprus bucklandi*	Pleistocene–Recent	Group I of Chame (2003) in part. Hunt et al. (2012a).The tapered end is probably commonly rounded off prior to fossilization.
		A2	Tapered at one end without distinct rounded segments	Most canids Most Chiroptera (some are segmented) Some mongooses Some otters Civet Genet Hedgehog		Pleistocene–Recent	Group II of Chame (2003) in part. The tapered end is probably commonly rounded off prior to fossilization.
		A3	Acutely tapered at both ends	Many snakes and lizards (Recent forms have a hard cap of white or yellowish uric acid at one end) Some felids Some mongooses Mustelids		Pleistocene–Recent	Stuart and Stuart (2000). Found in Early Permian and Late Cretaceous nonmarine settings.
		A4	Rounded ends and constant diameter	Some fishes Toads Tortoises Iguanas Crocodylians Theropoda Many Recent birds (often have a partial white calcium coating) Pinnipeds Some otters Ursidae Most Suidae Some primates	*Eucoprus cylindratus* *Costacoprus chinae*	Permian– Recent	Murie (1974), Stuart and Stuart (2000), Hunt and Lucas (2007, 2012b), Chin et al (2008), Hunt et al. (2012c), Milan (2012). Includes most terrestrial coprolites from the Cretaceous to Miocene.
		A5	Rounded ends, tapering in diameter to one	?Fish Pleistocene and Recent *Bassariscus astutus*	*Falcatocoprus oxfordiensis*	Triassic–Jurassic	Hunt et al. (2007).
		A6	Ovoid in lateral view	Dicynodont	*Dicynodontocoprus maximus*	Triassic	Hunt et al. (1998).
B	Cylindrical, short (length < 5x diameter)	B1	Two rounded ends or one slightly tapered	Some fish Most Pleistocene (e.g., *Erethizon* , *Neotoma*), and Recent Rodentia Insectivores Insectivorous bats	*Crustacopus tinajaensis*	Carboniferous–Recent	Group III of Chame (2003). Stuart and Stuart (2000), Huntet al. (2012g). Vary in size from small to medium.
		B2	Strongly tapering from one end to other (tear drop shape)	?Fishes	*Dakyronocoprus arroyoensis*	Permian	Hunt and Lucas (2005).
		B3	Inflected, with two rounded ends and a furrow along the length (coffee bean shape)	Recent African (Thrynomyidae) and South American (Caviomorpha) rodents		Recent	Group IV of Chame (2003).
		B4	Large cylindrical, unsegmented	Many Pleistocene and Recent Proboscidea Hippopotamidae Rhinocerotidae		Pleistocene–Recent	Group VIII of Chame (2003).
		B5	Large cylindrical, segmented	Pleistocene ground sloths (e.g., *Nothrotheriops shastensis* and South American forms) Some large artiodactyls (e.g., elk, caribou)		Pleistocene–Recent	Large artiodactyls also can produce C3.

TABLE 1. Continued.

C	Subrounded	C1	Small pellets (< 2 cm in diameter) often in large groups	Pleistocene and Recent Lagomorpha Some ungulates, Hyracoidea and aardvark (*Orycteropus afer*)		Pleistocene–Recent	Group II of Chame (2003).
		C2	Large masses (> 5 cm in diameter) can be subspherical or with two opposing flattened sides	Some Pleistocene and Recent proboscideans Armadillo		Pleistocene–Recent	Murie (1974), Mead et al. (2006). Personal observation at Woodland Park Zoo. *Loxodonta, Elephas* and *Mammuthus* can produce subspherical forms.
		C3	Rounded or segments of cylinders usually concavo-convex, one end may be acute	Pleistocene (*Oreamnos harringtoni, Ovis canadensis*, *Euceratherium collinum*) and Recent artiodactyls except Bovini		Pleistocene–Recent	Group V of Chame (2003). Knopf et al. (2007). Can be condensed to form large patties.
D	Flattened rounded plates that accumulate in circular piles	n/a	n/a	Recent Bovini Pleistocene *Bison*		Pleistocene–Recent	Group VI of Chame (2003)
E	Reniform	E1	Unstriated	Pleistocene and Recent Equidae Warthog (*Phacochoerus africanus*) Some Suidae		Pleistocene–Recent	Group VII of Chame (2003). They occur united, or in cake-like deposits in humid areas or during summer in temperate countries.
		E2	Longitudinally striated	Permian reptiles(?) Crocodylomorphs (?)	*Alococoprus triassicus* *A. indicus*	Permian–Recent	Hunt et al. (2007). Often conjoined.
F	Spiral	F1	Scroll	Fishes less derived than teleosts or advanced actinopterygians	*Bibliocoprus beemanensis*	Silurian–Recent	Hunt et al. (2012e).
		F2	Amphipolar spiral	Fossil (?) and Recent Dipnoi Other Fishes less derived than teleosts or advanced actinopterygians	*Hyronocoprus amphipola* *Iuloeidocoprus mantelli* *Kalocoprus oteroensis* *Elacacoprus williamsi*	Carboniferous–Recent	Hunt et al. (2005b, 2012b, e, g).
		F3	Heteropolar microspiral	Fishes less derived than teleosts or advanced actinopterygians	*Heteropolacoprus texaniensis* *Saurocoprus bucklandi* *Strabelocoprus liassicus* *Malericoprus matleyi* *Megaheteropolacoprus sidmacadami*	Carboniferous–Recent	Hunt et al. (1998, 2005a, 2007, 2012a)
		F4	Heteropolar macrospiral	Fishes less derived than teleosts or advanced actinopterygians	*Liassocoprus hawkinsi* *Crassocoprus mcallisteri* *Speiracoprus socorroensis*	Carboniferous–Recent	Hunt et al. (2007, 2012g).
		F5	Elongate coiled	Fishes less derived than teleosts or advanced actinopterygians	*Elongatocoprus amadoensis*	Carboniferous	Hunt et al. (2012g)

TABLE 1. Continued.

G	Elongate coiled cylinder	n/a	n/a	Plesiosaur or ichthyosaur(?)	*Plektecoprus whitbyensis*	Jurassic	Hunt et al. (2012a). Ends rounded or acute.
H	Thin ovoid	n/a	n/a	Some fishes	*Ostracocoprus snowyensis* *Conchobromus kinneyensis*	Carboniferous–Recent	Hunt et al. (2012d, f). Carboniferous fishes in lagoonal settings (Kinney, Bear Gulch, Tinajas).
I	Thin linear	n/a	n/a	Some fishes		Carboniferous–Recent	Hunt et al. (2012f). Carboniferous fishes in lagoonal settings (e.g., Kinney)
J	Splatter	n/a	n/a	Many birds Frugivorous bats			Produced by excrement of low viscosity. Stuart and Stuart (2000).
K	Irregular shape	n/a	n/a	Many fishes Plesiosaurs(?) Some primates Some bovids	*Ichthyosaurolites duffini*	Carboniferous–Recent	Hunt et al. (2012a).

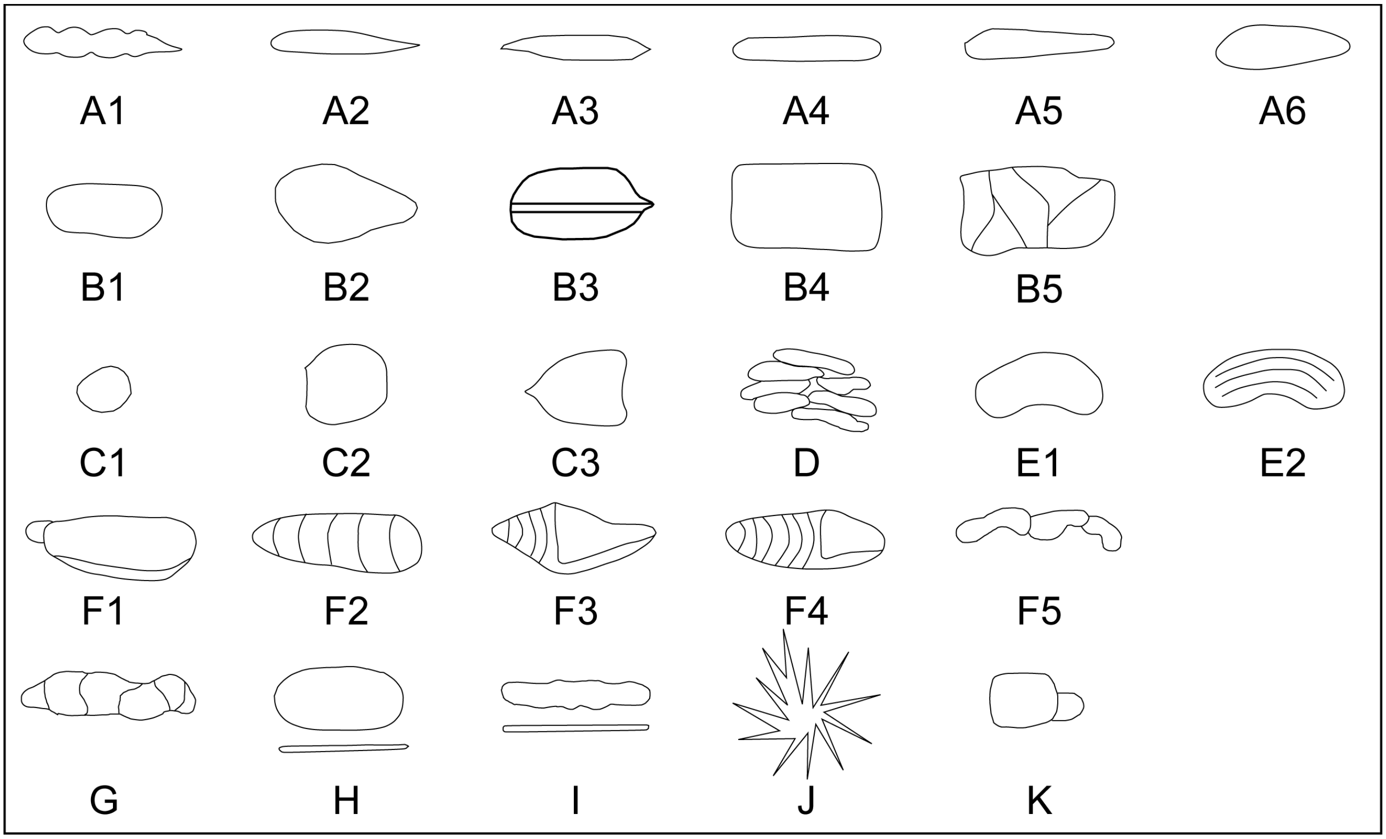

FIGURE 6. Morphological classification of coprolites and Recent feces.

Table 1):

- A, Cylindrical, elongate (length > 5 x diameter)
  - A1, Tapered at one end with distinct rounded segments
  - A2, Tapered at one end without distinct rounded segments
  - A3, Acutely tapered at both ends
  - A4, Rounded ends and constant diameter
  - A5, Rounded ends, tapering in diameter to one
  - A6, Ovoid in lateral view
- B, Cylindrical, short (length < 5 x diameter)
  - B1, Two rounded ends or one slightly tapered
  - B2, Strongly tapering from one end to other (tear drop shape)
  - B3, Inflected, with two rounded ends and a furrow along the length (coffee bean shape)
  - B4, Large cylindrical, unsegmented
  - B5, Large cylindrical, segmented
- C, Subrounded
  - C1, Small pellets (< 2 cm in diameter), often in large groups
  - C2, Large masses (> 5 cm in diameter) that can be subspherical or with two opposing flattened sides
  - C3, Rounded or segments of cylinders usually concavo-convex,

one end may be acute

D, Flattened rounded plates that accumulate in circular piles

E, Reniform

- E1, Unstriated
- E2, Longitudinally striated

F, Spiral

- F1, Scroll
- F2, Amphipolar spiral
- F3, Heteropolar microspiral
- F4, Heteropolar macrospiral
- F5, Elongate coiled

G, Elongate coiled cylinder

H, Thin ovoid

I, Thin linear

J, Splatter

K, Irregular shape

CONCLUSIONS

Increased study of vertebrate coprolites in the last few years has created a need for a consistent terminology. Analyses of coprolites have not generally considered comparisons with Recent feces (cf. Jain, 1983). However, actualistic studies of Recent feces (e.g, Milàn, 2012) are clearly of great potential, and we believe that a more holistic approach to the study of fossil and modern excrement will be of great value.

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REFERENCES

Aldridge, R.J., Gabbott, S.E., Siveter, L.J. and Theron, J.N., 2006, Bromalites from the Soom Shale Lagerstätte (Upper Ordovician) of South Africa: Palaeoecological and palaeobiological implications: Palaeontology, v. 49, p. 857–871.

Buckland, W., 1835, On the discovery of coprolites, or fossil faeces, in the Lias at Lyme Regis, and in other formations: Transactions of the Geological Society of London, v. 3 (series 2), p. 223-238.

Buckland, W., 1836, Geology and mineralogy considered with reference to natural theology. London, Pickering, 2 volumes, 599 p. and 128 p.

Chame, M., 2003, Terrestrial mammal feces: A morphometric summary and description: Memórias do Instituto Oswaldo Cruz, v. 98, supplement 1, p. 71-94.

Chin, K., 2007, The paleobiological implications of herbivorous dinosaur coprolites from the Upper Cretaceous Two Medicine Formation of Montana: why eat wood?: Palaios, v. 22, p. 554–566.

Chin, K. and Gill, B.D., 1996, Dinosaurs, dung beetles, and conifers: Participants in a Cretaceous food web: Palaios, v. 11, p. 280–285.

Chin, K. and Kirkland, J.I., 1998, Probable herbivore coprolites from the Upper Jurassic Mygatt-Moore Quarry, western Colorado: Modern Geology, v. 23, p. 249–275.

Chin, K., Tokaryk, T.T., Erickson, G.M. and Calk, L.C., 1998, A king-sized theropod coprolite: Nature, v. 393, p. 680–682.

DeKay, J.E., 1830, On the extinct reptiles of the genera *Mosasaurus* and *Geosaurus* found in the secondary formation of New Jersey; and on the occurrence of a substance recently named coprolite by Dr. Buckland in the same locality: Annals of the Lyceum of Natural History of New York, v. 3, p. 134-141.

Diedrich, C., 2012, Typology of Ice Age spotted hyena *Crocuta crocuta spelaea* (Goldfuss, 1823) coprolite aggregate pellets from the European Late Pleistocene and their significance at dens and scavenging sites: New Mexico Museum of Natural History, Bulletin 57, this volume.

Diedrich, C.D. and Felker, H., 2012, Middle Eocene shark coprolites from shallow marine and deltaic coasts of the pre-North Sea Basin in Central Europe: New Mexico Museum of Natural History and Science, Bulletin 57, this volume.

Ghosh, P., Bhattacharya, S.K., Sahni, A., Kar, R.K., Mohabey, D.M. and Ambwani, K., 2004, Dinosaur coprolites from the Late Cretaceous (Maastrichtian) Lameta Formation of India: Isotopic and other markers suggesting a C3 plant diet: Cretaceous Research, v. 24, p. 743–750.

Gilmore, B., 1992, Scroll coprolites from the Silurian of Ireland and the feeding of early vertebrates: Palaeontology, v. 35, p. 319-333.

Häntzschel, W., El-Baz, F. and Amstutz, G.C., 1968, Coprolites: An annotated bibliography: Geological Society of America, Memoir 108, 132 p.

Hunt, A.P. and Lucas, S.G., 2005, A new coprolite ichnotaxon from the Early Permian of Texas: New Mexico Museum of Natural History and Science, Bulletin 30, 121-122.

Hunt, A.P. and Lucas, S.G., 2007, Ichnological and taphonomic notes on Recent tetrapods from the Galápagos Islands: New Mexico Museum of Natural History and Science, Bulletin 42, p. 43-50.

Hunt, A.P., Chin, K. and Lockley, M.G., 1994, The paleobiology of coprolites; *in* Donovan, S.K., ed., The paleobiology of trace fossils: London, John Wiley, p. 221 240.

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., 2005a, Biochronology of Early Permian vertebrate coprolites of the American Southwest: New Mexico Museum of Natural History and Science, Bulletin 31, p. 43-45.

Hunt, A.P., Lucas, S.G. and Spielmann, J.A., 2005b, Early Permian vertebrate coprolites from north-central New Mexico with description of a new ichnogenus: New Mexico Museum of Natural History and Science, Bulletin 31, p. 39-42.

Hunt, A.P., Lucas, S.G. and Spielmann, J.A., 2012a, New coprolite ichnotaxa from the Buckland Collection at the Oxford University Museum of Natural History: New Mexico Museum of Natural History, Bulletin 57, this volume.

Hunt, A.P., Lucas, S.G. and Spielmann, J.A., 2012b, The bromalite collection at the National Museum Of Natural History (Smithsonian Institution), with descriptions of new ichnotaxa and notes on other significant coprolite collections: New Mexico Museum of Natural History, Bulletin 57, this volume.

Hunt, A.P., Lucas, S.G. and Spielmann, J.A., 2012c, The vertebrate coprolite collection at The Natural History Museum (London): New Mexico Museum of Natural History, Bulletin 57, this volume.

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.

Hunt, A.P., Lucas, S.G., Spielmann, J.A. and Lockley, M.G., 2012d, Bromalites from the Mississippian Bear Gulch lagerstätte of Central Montana, USA: New Mexico Museum of Natural History, Bulletin 57, this volume.

Hunt, A.P., Lucas, S.G., Spielmann, J.A., Cantrell, A. and Suazo, T., 2012e, A new marine coprofauna from the Beeman Formation (Late Pennsylvanian: Late Missourian), Sacramento Mountains, New Mexico, USA: New Mexico Museum of Natural History, Bulletin 57, this volume.

Hunt, A.P., Lucas, S.G., Spielmann, J.A., Suazo, T. and Cantrell, A., 2012f, A re-evaluation of Late Pennsylvanian bromalites from the Kinney Brick quarry lagerstätte, New Mexico, USA: New Mexico Museum of Natural History, Bulletin 57, this volume.

Hunt, A.P., Lucas, S.G., Spielmann, J.A., Cantrell, A., Suazo, T. and Lerner, A.J, 2012g, Bromalites from the Tinajas Lagerstatte (Late Pennsylvanian: Late Missourian), central New Mexico, USA: New Mexico Museum of Natural History, Bulletin 57, this volume.

Jain, S.L., 1983, Spirally coiled “coprolites” from the Upper Triassic Maleri

Formation, India: Palaeontology, v. 26, p. 813-829.

Jouy-Avantin, F., Debenath, A., Moigne, A.-M. and Moné, H., 2003, A standardized method for the description and the study of coprolites: Journal of Archaeological Science, v. 30, p. 367-372.

Kropf, M., Mead, J.I. and Anderson, R.C., 2007, Dung, diet, and the paleoenvironment of the extinct shrub-ox (*Euceratherium collinum*) on the Colorado Plateau, USA: Quaternary Research, v. 67, p. 143-151.

Laojumpon, C., Matkhammee, T., Wathanapitaksakul, A., Suteethorn, V., Suteethorn, S., Lauprasery, K., Srisuk, P. and LeLoeuff, J., 2012, Preliminary report on coprolites from the Late Triassic of Thailand: New Mexico Museum of Natural History and Science, Bulletin 57, this volume.

Mantell, G.A., 1822, The fossils of the South Downs: Or illustrations of the geology of Sussex: London, Lupton Relfe, 305 p.

McAllister, J.A., 1985, Reevaluation of the origin of spiral coprolites: University of Kansas Palaeontological Contributions, v. 114, p. 1-12.

McAllister, J.A., 1987, Phylogenetic distribution and morphological reassessment of the intestines of fossil and modern fishes: Zoologische Jahrbücher Abtheilung für Anatomie und Ontogenie der Thiere, v. 115, p. 281-294.

Mead, J.I., Agenbroad, L.D., Davis, O.K. and Martin, P.S., 1986, Dung of *Mammuthus* in the arid Southwest, North America: Quaternary Research, v. 25, p. 121-127.

Mead, J.I. and Swift, S.L., 2012, Late Pleistocene (Rancholabrean) dung deposits of the Colorado Plateau, western North America: New Mexico Museum of Natural History and Science, Bulletin 57, this volume.

Milán, 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, this volume.

Murie, O.J., 1974, Animals tracks [second edition]: Peterson Field Guild Series, Boston, Houghton Mifflin, 375 p.

Neumayer, L., 1904, Die Koprolithen des Perm von Texas: Palaeontographica, v. 51, p. 121-128.

Owen, R., 1866, On the anatomy of vertebrates. Volume I, fishes and reptiles: London, Green and Co., 650 p.

Parker, T.J., 1885, On the intestinal spiral valve in the genus *Raia*: Transactions of the Zoological Society of London, v. 11, p. 49-61.

Retallack, G.J. and Krull, E.S., 1999, Permian coprolites from Graphite Peak, Antarctica: U.S. Antarctic Journal, v. 30, p. 7-9.

Stewart, J.D., 1978, Enterospirae (fossil intestines) from the Upper Cretaceous Niobrara Formation of western Kansas; *in* Chorn, J., Reavis, E.A., Stewart, J.D. and Whetstone, K.N., eds., Fossil fish studies: The University of Kansas Paleontological Contributions, Paper 89, p. 9-16.

Stringer, G.L. and King, L., 2012, Late Eocene shark coprolites from the Yazoo Clay in northeastern Louisiana: New Mexico Museum of Natural History, Bulletin 57, this volume

Stuart, C. and Stuart, T., 2000, A field guide to the tracks and signs of Southern and East African wildlife: Cape Town, Struick Nature (Random House Struick), 310 p.

Stringer, G.L. and King, L., 2012, Late Eocene shark coprolites from the Yazoo Clay in northeastern Louisiana: New Mexico Museum of Natural History and Science, Bulletin 57, this volume.

Suazo, T.L., Cantrell, A.K., Lucas, S.G., Spielmann, J.A. and Hunt, A.P., 2012, Coprolites across the Cretaceous/Tertiary boundary, San Juan Basin, New Mexico: New Mexico Museum of Natural History and Science, Bulletin 57, this volume.

Sumner, D., 1993, Coprolites from the Viséan of East Kirkton, West Lothian, Scotland: Transactions of the Royal Society of Scotland, Earth Sciences, v. 84, p. 413-416.

Thulborn, R.A., 1991, Morphology, preservation and palaeobiological significance of dinosaur coprolites: Palaeogeography, Palaeoclimatolology, Palaeoecology, v. 83, p. 341-366.

Waterson, C.D., Oelofsen, B.N. and Oosthuizen, R.D.F., 1985, *Cyrtoctenus wittbergensis* sp. nov. (Chelicerata: Eurypterida) a large sweep-feeder from the Carbonifeous of South Africa: Transactions of the Royal Society of Scotland, Earth Sciences, v. 76, p. 339-358.

Williams, M.E., 1972, The origin of "spiral coprolites:" University of Kansas Palaeontological Contributions, v. 59, p. 1-19.

Zidek, J., 1980, *Acanthodes lundi*, new species (Acanthodii) and associated coprolites from uppermost Mississippian Heath Formation of Central Montana: Annals of Carnegie Museum, v. 49, p. 49-78.

APPENDIX

SYSTEMATIC ICHNOLOGY

Eucoprus, ichnogen. nov.

Type ichnospecies: *Eucoprus cylindratus* Hunt and Lucas, 2012.

Included ichnospecies: Known only from the type ichnospecies.

Etymology: From the Greek *eu* (perfect) and *kopros* (dung).

Distribution: Permian-Recent.

Diagnosis: Coprolite that differs from other ichnogenera in being cylindrical in shape with rounded ends and containing no osseous inclusions.

Discussion: This ichnogenus seems to be particularly common in terrestrial ichnofaunas from the Triassic-Pliocene.

Eucoprus cylindratus, ichnosp. nov.

Figure 4

Holotype: NMMNH P-66582, coprolite (Fig. 3).

Etymology: From the Latin *cylindratus* (in the form of a cylinder), alluding to its shape.

Type locality: Gregory Quarry (NMMNH locality L-485), Quay County, New Mexico, USA.

Type horizon: Redonda Formation (Apachean: late Norian).

Distribution: As for ichnogenus.

Referred specimens: None

Diagnosis: As for ichnogenus.

Description: The holotype specimen (NMMNH P-66582) is a complete coprolite that is 32.96 mm long. It has a subrounded cross section with maximum diameters of 13.45 and 11.4 mm. There are no inclusions.

Discussion: This ichnogenus seems to be particularly common in Late Cretaceous-Early Tertiary nonmarine ichnofaunas (Suazo et al., 2012).