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VERTEBRATE COPROLITE STUDIES: STATUS AND PROSPECTUS

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Abstract—The history of study of vertebrate coprolites can be divided into four phases: (1) 1800-1890 – initial studies; (2) 1890-1910 – first bloom; (3) 1910-1950 – intermittent work; (4) 1950-1990 – maturing science (in archeology and Pleistocene coprolite studies); and (5) 1990 to present – maturing science (study of pre-Pleistocene coprolites). The oldest putative vertebrate coprolites are Ordovician in age. Few Silurian coprolites have been described, and some large coprolites of this age have been ascribed to eurypterids. Devonian coprolites are common, but poorly described. Mississippian vertebrate coprolites have been minimally studied, but they probably represent the first relatively abundant coprofaunas. Several Pennsylvanian coprofaunas have been described. The Permo-Triassic seems to be an acme zone for coprolites as a result of their abundance in redbeds. Jurassic coprolites are locally common, but few have been described, with the notable exception of those from the Lias of England. Cretaceous coprolites and Tertiary coprolites are common. Many nonmarine Pleistocene coprolites derive from caves. Prominent misconceptions about coprolites include: (1) they are rare; (2) their morphology is too variable to allow a parataxonomy; (3) they have poor preservation potential; (4) they cannot be reworked; (5) all feces have equal chances of preservation; and (6) bromalites are of little scientific importance. Seven strategies for advancing the study of vertebrate coprolites are: (1) communicate that coprolites are common and useful; (2) describe more coproassemblages; (3) conduct more actualistic studies; (4) name additional valid ichnotaxa; (5) expand the breadth of study to include non-coprolite bromalites; (6) document coprolites in time and space; (7) conduct interdisciplinary studies involving Pleistocene, pre-Pleistocene and human coprolites; and (8) incorporate coprolites into ichnofaunal studies.

DEVELOPMENT OF COPROLITE STUDIES

Introduction

Although vertebrate coprolites were recognized very early in the study of vertebrate fossils (e.g., in the 1820s by William Buckland), they have received sporadic and uneven study for nearly two centuries. Indeed, most studies of vertebrate coprolites have been isolated efforts that describe a particular assemblage or represent attempts to gain insights into some aspects of a coprolite or coprolites, particularly with the goal of inferring the diet of the producer. Most vertebrate paleontologists regard coprolites as curiosities, not capable of providing a basis for broader interpretation of the kinds of questions usually asked of the vertebrate fossil record. In part, this view finds justification in the notorious difficulty in identifying the producers of specific coprolites. For, without knowledge of the producer, interpretations of coprolites have been and will always be somewhat limited.

Nevertheless, coprolites are trace fossils, so they are keys to understanding some aspects of vertebrate behavior, particularly all aspects of food processing, from consumption to digestion to excretion (Fig. 1). Given the well known differences in these behaviors among diverse vertebrates, coprolites should preserve distinctive morphologies that reflect the food processing behavior and anatomy of their producers, provided that the extramorphological (particularly taphonomic) features of the coprolites can be established. Thus, like other trace fossils, particular coprolite morphologies must have discrete distributions in time and space that reflect the distributions of their producers. They should be able to tell us about evolutionary breakthroughs in food processing behavior, and also inform us about the taphonomic and sedimentological contexts in which they are preserved. Furthermore, coprolites are, in a sense, micro-environments that preserve biological material not always fossilized elsewhere, including bacteria, parasites and commensals of the producer and undigested food products, from plant matter to bone phosphate. Thus, coprolites merit serious and systematic study, including the development of a parataxonomy by which to classify and discuss them.

To those ends, this volume presents 40 articles that report the results of research on vertebrate coprolites (or, more broadly, on vertebrate bromalites). These articles are arranged around the topics of: history of study of vertebrate coprolites, actualistic studies, classification and terminology, notable museum collections of coprolites and case-specific studies of Paleozoic, Mesozoic and Cenozoic coprolites. We believe the volume thus presents a substantial advance in our knowledge of the vertebrate coprolite record, one that hopefully encourages and focuses future research.

History of Study of Vertebrate Coprolites

The study of coprolites has always been on the fringes of its science (paleontology or archeology) and has been disproportionately influenced by a small number of individuals.

Buckland and the earliest studies (1800-1890)

Vertebrate coprolites were, like many other groups of fossils (e.g., Sarjeant, 1997; Delair and Sarjeant, 2002), collected and described before they were correctly identified (Duffin, 2012b). Buckland's recognition of fossil feces seemed to touch a nerve, and it inspired what Duffin (2012a) terms "copromania," particularly in Victorian England, but also in Europe and the United States (DeKay, 1830; Buckland, 1835; Geinitz, 1842; Hitchcock, 1844; Dana, 1845; Fischer, 1856; Henslow, 1845; Quadrat, 1845; Reuss, 1856; Pemberton and Fry, 1991; Duffin, 2009, 2012a, b; Pemberton, 2012). There was interest, excitement (and some ridicule), but not a large volume of publications after the 1860s (Fig. 2). Following Buckland's early work on terminology, preservation and description of large coprofaunas, his disciples were content to record occurrences or
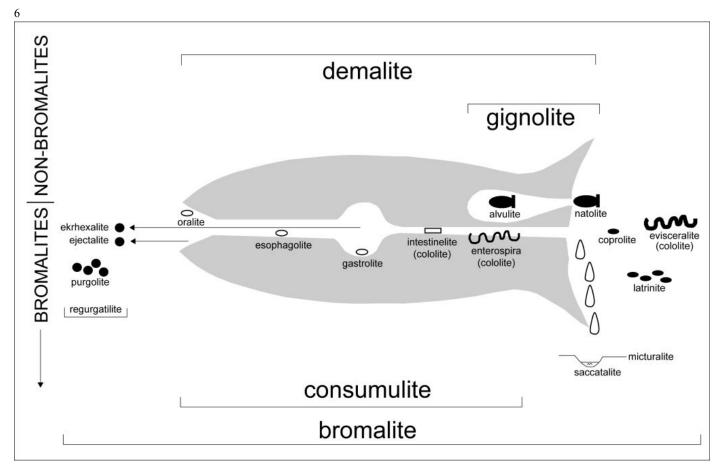
FIGURE 1. Selected classification terms for bromalites (related to food processing), gignolites (related to reproduction) and associated trace fossils (from Hunt and Lucas, 2012a).

conduct limited chemical analyses. During this time, from the 1840s onwards, there was a period of intensive "coprolite mining" for fertilizer that involved the extraction of both coprolites *sensu stricto* and phosphate nodules, initially in the United Kingdom but also elsewhere in Europe (O'Connor and Ford, 2001; Ford and O'Connor, 2009; Le Loeuff, 2012).

First bloom (1890-1910)

Around the beginning of the 20th century, several workers explicitly addressed the classification of coprolites and other bromalites. Neumayer (1904) studied a sample of coprolites from the Early Permian of Texas and applied the terms amphipolar and heteropolar to different types of spiral coprolites, and these names are still in use. Hoernes (1904) reviewed the older literature on coprolites and proposed restricting the term coprolite to fossil feces *sensu stricto*. He introduced the name enterolite for traces, previously considered to be coprolites, which he interpreted to represent infilled spiral-valved intestines. Fritsch (1907), in turn, suggested the name enterospirae for the same trace fossils. During this time there were a few significant descriptions of larger coprofaunas, the first since Buckland (e.g., Bertrand, 1903; Neumayer, 1904). Also, Harshberger (1896) called attention to the potential importance of human coprolites at this time.

The quiet years (1910-1950)

For a period of 40 years papers were published intermittently on coprolites but none that were conceptually substantial or that described large samples. Two important papers on human coprolites were published during this time period. Loud and Harrington (1929) published the first analysis of human coprolites, and Wakefield and Dellinger (1936) used chemical and microscopic techniques to address issues of prehistoric health.

Callen and Martin: A maturing science (1950-1990)

Eric O. Callen first became interested in human coprolites (Callen and Cameron, 1955) by accident and he subsequently worked for several decades "with missionary zeal to convince archaeologists and others about the importance of coprolite research" (Bryant and Reinhard, 2012). Notable among those inspired by him were Vaughn M. Bryant, Jr. and Karl J. Reinhard (Fig. 3). One of Callen's earlier collaborators was Paul S. Martin (Callen and Martin, 1969). Martin was interested in Pleistocene animal coprolites (e.g., Martin et al., 1961) and he began to develop a large comparative collection of modern dung and to mentor students, one of whom, Jim I. Mead, became the driving force behind the study of the desiccated coprolites from the American Southwest (Mead and Swift, 2012). The study of both human coprolites and Pleistocene coprolites blossomed during this time, and the "Golden Age of [human] Coprolite Analysis" lasted for just over 30 years, ending in the early 1990s (Reinhard, 2006). Both human and Pleistocene studies addressed sophisticated research questions, notably with reference to diet, climate and parasites (e.g., Bryant and Dean, 1975; 2006; Wilke and Hall, 1975; Bryant and Reinhard, 2012; Mead and Swift, 2012).

The pre-Pleistocene catches up (1990-Present)

While researchers in Quaternary studies and archeology were using coprolites as important research tools, most other paleontologists still treated them as not usually worthy of collection, let alone study, with the exception of some Paleozoic fish workers (e.g., Zangerl and Richardson, 1963; Williams, 1972). This began to change in 1990s as there was a renewed interest in pre-Pleistocene coprolites. Karen Chin did much to popularize the study of coprolites within paleontology as she and co-workers studied the coprolites of the most glamorous of fossil animals – dinosaurs (e.g., Chin and Gill, 1996; Chin et al., 1998,

FIGURE 2. A caricature by De la Beche (ca. 1829) entitled *A Coprolitic Vision*, showing William Buckland lecturing to a group of defecating animals (from Pemberton, 2012).

2003, 2008; Chin and Kirkland, 1998; Chin, 2007). In a similar timeframe, two of us (APH and SGL) began to collect large samples of coprolites, especially of Triassic age, and to analyze them (e.g., Lucas et al., 1985; Hunt, 1992; Hunt et al., 1994a, 1998). Ironically, as the study of human coprolites has declined (Bryant and Reinhard, 2012), work on pre-Pleistocene coprolites has intensified and become more sophisticated, as is indicated by the number and scope of the articles in this volume.

VERTEBRATE COPROLITES IN TIME AND SPACE

Fossil Record of Vertebrate Coprolites

The earliest known vertebrate body fossils are from the Lower Cambrian of China (e.g., Shu et al., 1999, 2003). Cambrian coprolites occur at a number of localities, but all have been attributed to invertebrates (e.g., Chen et al., 2007), although some larger forms could have arguably been produced by vertebrates (e.g., Conway Morris and Robison, 1988). The Chengjiang Lagerstätte has yielded hundreds of finely preserved examples of the vertebrate *Haikouichthys* (Shu, 2008), which is a possible source of vertebrate coprolites.

Aldridge et al. (2006) described five morphotypes of bromalites, including both coprolites (including a spiral form) and regurgitalites, from the Soom Shale Lagerstätte of Late Ordovician age in South Africa. The Soom Shale fauna includes vertebrates that could have produced some of the bromalites (Aldridge et al., 2006).

Scroll coprolites attributed to vertebrates occur in Late Silurian fish-bearing strata of Ireland and Scotland (Gilmore, 1992). These coprolites are argillaceous rather than phosphatic. The Ludlow bone bed (Ludlow Bone Bed Member of Downton Castle Sandstone Formation) is a Late Silurian source of vertebrates in the area along the border between England and Wales. Coprolites have long been known to be locally common in the Ludlow bone bed but have not been described in detail (e.g., Strickland and Hooker, 1853), although some have been illustrated

(e.g., Murchison, 1867). Buckland (1835, pl. 30, figs. 31-41) described coprolites from a bone bed in the "Mountain Limestone" near Clifton, which we take to be the Silurian locality at Tites Point. There are Early Silurian coprolites from Scotland and Nova Scotia of a size that could have been produced by vertebrates (e.g., Rolfe, 1973), but they have been attributed to large predatory eurypterids such as *Lanarkopterus* (Selden, 1984; Turner, 1999).

Few specimens of coprolites have been described from the Devonian "Age of fishes." McAllister (1996) published a detailed study of coprolites and some regurgitalites from the Upper Devonian Escuminac Formation of Quebec, Canada, and Williams (1990) discussed bromalites from the Upper Devonian Cleveland Shale Member of the Ohio Shale. The classic "Old Red Sandstone" of the United Kingdom contains vertebrate coprolites, but they have only been described from a few localities (e.g., Lower Devonian of Scotland: Trewin and Davidson, 1995). Hunt et al. (2012b) describe Lower Devonian coprolites from Latvia/Estonia. Devonian coprolites are locally common in the German Hunsück Slate (e.g., Bartels et al., 1998; Wagner and Boyce, 2006), but they await full description. Devonian coprolites have been reported from other areas including Brazil (Maisey and Melo, 2005) and the United States (e.g., Branson, 1914).

Mississippian (Early Carboniferous) coprolites have been documented from localities in Europe and North America, and they represent the first abundant samples of vertebrate coprolites (Turner, 1999). Mansky et al. (2012) describe coprolites and cololites from the Early Mississippian (Tournaisian) Horton Bluff Formation of Nova Scotia. Coprolites are known from a number of Mississippian localities in Scotland and include ichnofaunas from the Early (Dinantian) and Middle (Viséan) Mississippian of the southeastern part of the country (Buckland, 1836; Pollard, 1985; Sumner, 1991). Buckland collected concretions containing coprolites from the Wardie Shale near Edinburgh and incorporated some of them in the top of a table that is preserved at the Lyme
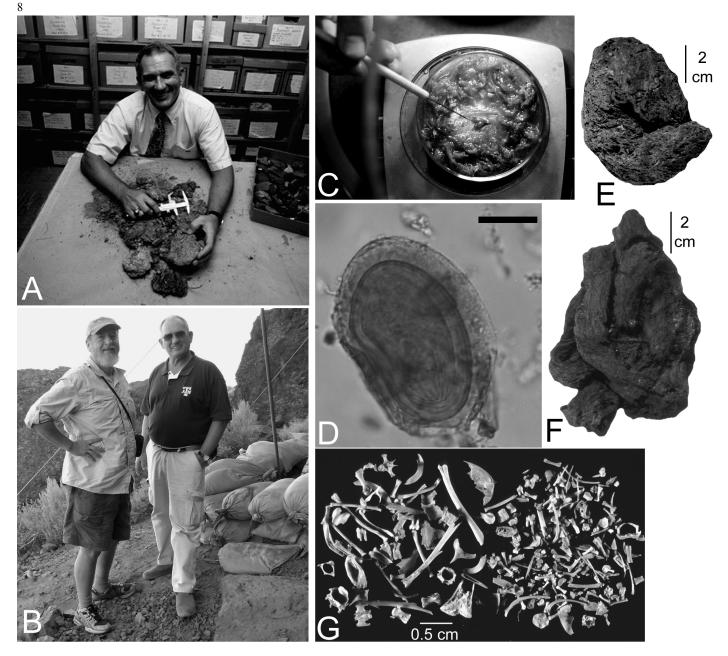
FIGURE 3. Human coprolite researchers and specimens. **A**, Vaughn Bryant examining some of the 2,000+ human coprolites (Lower to Upper Archaic Period) recovered from Hinds Cave, southwest Texas. **B**, Karl Reinhard (left) and Vaughn Bryant (right) at Paisley Cave, south-central Oregon, where pre-Clovis human DNA (over 12,000 years old) was recovered from human coprolites. **C**, Coprolite (Upper Archaic Period) from Conejo Shelter, Lower Pecos region of Texas. The probe is pointing to a wild onion (*Allium*) bulb, one of many found in these coprolites that contained high amounts of plant fiber. **D**, An acanthocephalan (thorny-headed worm) from a human coprolite, Antelope Cave, Arizona, dating to about 1100 years old. This discovery, and others from the Great Basin, show that ancient people have been parasitized with this type of worm for 10,000 years due to the dietary habit of eating insects. Scale bar is 10 micrometers. **E-F**, Two of the many coprolites found at Hinds Cave. Most of the recovered coprolites were amorphous and flattened, caused by loose stools from eating excessive amounts of fiber. **E-F** represent two of only a few coprolites that demonstrate a more typical morphology of human coprolite. **G**, Small mammal, reptile, bird, and fish bones recovered from coprolites (Middle Archaic Period) from Hinds Cave. Photographs courtesy of Vaughn Bryant and Karl Reinhard.

Regis Museum (Buckland, 1836; Duffin, 2009, unnumbered fig. on p. 7; Pemberton, 2012, fig. 7). The Bear Gulch Lagerstätte of Montana, USA, has yielded a small sample of coprolites (Zidek, 1980; Hunt et al., 2012e).

Coprolites occur in marine shales in many localities in the Pennsylvanian (Late Carboniferous) as well as in some nonmarine coal successions. Zangerl and Richardson (1963) conducted a classic and extensive study of the paleoecology of the Middle Pennsylvanian (Desmoinesian) Mecca Quarry Shale Member and Logan Quarry Member of the Carbondale Formation in western Indiana, USA, and described

multiple bromalites (coprolites and regurgitalites). Farther east, the Francis Creek Shale Member of the Carbondale Formation (Desmoinesian) in Illinois yields the classic nodular Mazon Creek fauna. Vertebrate coprolites are present, but not extensively studied (Johnson and Richardson, 1966).

Konservat Lagerstätten of Late Pennsylvanian age in central New Mexico in the southwestern United States yield extensive coprofaunas from lagoonal and estuarine shales. The Tinajas Lagerstätte of late Missourian age includes more than 10 morphotypes/ichnotaxa (Lerner et al.,

2009; Hunt et al., 2012h), whereas the Kinney Brick Quarry Lagerstätte is of middle Missourian age and has produced more than 50 specimens of bromalites (Hunt, 1992; Hunt et al., 2012g). Farther south in New Mexico, a Late Pennsylvanian coprofauna consisting of diverse spiral coprolites is present in marine offshore shale of the Beeman Formation of late Missourian age (Hunt et al., 2012f).

McAllister (1988) described Late Pennsylvanian coprolites and regurgitalites from Hamilton Quarry in Kansas, USA. There are examples in both Colorado and West Virginia, USA, of Pennsylvanian coprolites that are widespread in narrow stratigraphic intervals (Price, 1927; Johnson, 1934). Hunt et al. (2012b) illustrate some other specimens from that state. Pennsylvanian coprolites occur in Europe, for example in England, Scotland, Belgium and Germany (e.g., Bayer, 1934; Hunt et al., 2012b-c), but they have received little study.

There is an acme for vertebrate coprolites in the Permo-Triassic, and they are common in various Permian strata (Hunt and Lucas, 2005b). Coprofaunas with an abundance of spiral forms characterize redbeds of Early Permian age in northern (Hunt et al., 2005b) and central New Mexico (Cantrell et al., 2012), West Texas (Neumayer, 1904; Hunt and Lucas, 2005a, c, Hunt et al., 2005a) and Oklahoma (Williams, 1972; McAllister, 1985; Hunt et al., 2012b) in the United States. In Europe, coprolites occur in Permian marine deposits in France (Hunt et al., 2012b) and the classic Rotliegend redbeds of central Europe (e.g., Augusta, 1936; Eichler and Werneburg, 2010) and the Late Permian Kupferschiefer (e.g., Germer, 1840; Diedrich, 2009). The European Permian coprolites are in need of comprehensive and detailed study. Permian coprolites also occur in other areas, including South Africa (Smith and Botha-Brink, 2011), Russia (A. Sennikov, person commun., 2010) and Brazil (Ragonha, 1987).

Triassic coprolites are abundant, widely dispersed and relatively well studied (Hunt et al., 2007). Early Triassic coprolites occur in Australia (Northwood, 2005) and Arizona, USA (Benz, 1980), and Middle Triassic specimens are known from Russia, Kazakstan (Ochev, 1974), Argentina (Rusconi, 1947, 1949; Mancuso et al., 2004), Brazil (Souto, 2001), India (Jain, 1983) and the southwestern United States (Benz, 1980). Coprolites also occur in the Middle Triassic Muschelkalk of Germany but they have not been studied in detail (e.g., Geinitz, 1842; Fraas, 1891; Hunt and Lucas, 2010, fig. 2). Vertebrate coprolites of Late Triassic age have been studied in the southwestern United States (e.g., Ash, 1978; Hunt et al., 1998), Argentina (Contreras, 1995), Greenland (Milàn et al., 2012c), England (e.g., Buckland, 1835), Thailand (Laojumpon et al., 2012) and India (Jain, 1983). Coprolites are common in Rhaetic bone beds in England and Western Europe (e.g., Fluckiger, 1861; Duffin, 1979; Swift and Duffin, 1999). Two areas that have abundant Late Triassic coprolites that are in need of study are the eastern United States (Newark Supergroup) and Europe ("Keuper").

In general, Jurassic coprolites have not been well studied, with the notable exception of those from the marine Lias of England (Buckland, 1835; Hunt et al., 2007, 2012a; Duffin, 2010). Other Early Jurassic units in Europe yield relatively few coprolites, for example the Posidonienschiefer of Germany (e.g., Hauff, 1921). The Early Jurassic portion of the Newark Supergroup in eastern North America contains coprolites that are poorly studied (Hitchcock, 1844; Dana, 1845).

Late Jurassic (and Cretaceous) lithographic limestones in Europe contain coprolites (e.g., Hunt et al., 2012a, fig. 1F; Hunt et al., 2012c, fig. 2Q), but the only detailed study is by Schweigert and Dietl (2012). Chin and Kirkland (1998) described putative herbivore coprolites from the Upper Jurassic Morrison Formation of Colorado, USA. The Natural History Museum in London has coprolite collections from the Purbeck Limestone Formation and Oxford Clay Formation of England, which are largely unstudied (Hunt et al., 2007, 2012c). The Oxford Clay is notable for yielding many vertebrate coprolites (Martill, 1985).

Both marine and nonmarine coprolites of Cretaceous age have been collected, and studied in many cases, from localities around the world. In general, the majority of the research has focused on nonmarine coprolites from the Late Cretaceous. Chin and co-workers have under-taken detailed studies of selected dinosaur coprolites, in particular the United States and Canada (e.g., Chin and Gill, 1996; Chin et al., 1998, 2003, 2008; Chin, 2007), while others have described Cretaceous coprolite ichnofaunas (e.g., Sullivan and Jasinski, 2012; Suazo et al., 2012). There are also numerous reports of isolated specimens or generally small samples (but see Friedman, 2012) from marine and nonmarine strata in the western and eastern USA and Canada (e.g., DeKay, 1830; Stewart, 1978; Coy, 1995; Shimada, 1997; Everhart, 2007; Harrell and Schwimmer, 2010; Hunt et al., 2012b). Late Cretaceous coprolites in the Western Hemisphere also occur in Mexico (Rodriquez de la Rosa et al., 1998) and various localities in Brazil (Nobre et al., 2008; Souto, 2010; Souto and Medeiros, 2012). There are a smaller number of reports from the Late Cretaceous of Europe (e.g., Quadrat, 1845; Fischer, 1856; Longbottom and Patterson, 2002; Milàn et al., 2012a). There has been a considerable amount of research on the coprolites from the nonmarine Upper Cretaceous of India (e.g., Matley, 1939; Ghosh et al., 2003; Prasad et al., 2005; Hunt et al., 2007). There is a lesser literature on Lower Cretaceous coprolites, but it includes records from North and South America, Africa, Australasia and Europe (e.g., Bertrand, 1903; Etheridge, 1904; Benton et al., 2000; Martill and Naish, 2001; Goldring et al., 2005; Vega et al., 2006; Souto and Schwanke, 2010; Hunt et al., 2012b).

North America has the best described record of Tertiary vertebrate coprolites, with nonmarine specimens from almost every epoch and notably large samples in the Eocene Green River Formation and Eocene/Oligocene White River Group (Hunt and Lucas, 2007). Tertiary coprolites are present in several localities in South America, including the Paleocene of Brazil (Souto, 2007), Oligocene of Brazil (Castro et al., 1988) and Miocene of Argentina (Tauber et al., 2007) and Venezuela (Royo and Gomez, 1960). Other localities include China (Young, 1964), the Czech Republic (Mikuláš, R. and Dvorák, 2010), Denmark (Milàn, 2010; Milàn et al., 2012b), Germany (Fikentscher, 1933; Richter and Baszio, 2001), Kazakstan (Lucas et al., 2012b) and the United Kingdom (Rayner et al., 2009). The Late Pliocene-Pleistocene Red Crag Formation of southeastern England is notable as a source of phosphatic nodules (and a lesser number of true coprolites; Ford and O'Connor, 2009, fig. 1) that fueled "coprolite" mining in the 19th Century (Henslow, 1845; O'Connor and Ford, 2001). There is a need for further study to determine how many of the numerous formations that yielded "coprolites" during this period (e.g., Ford and O'Connor, 2009) actually contain trace fossils as opposed to inorganic phosphatic nodules.

There are numerous Quaternary coprolites in paleontological and archeological sites worldwide. The largest known Quaternary coprolite fossil record is arguably in North America, where the caves of the arid Southwest have yielded large latrines of megaherbivore coprolites such as mammoth (e.g., Bechan Cave: Mead et al., 1986) and ground sloth (e.g., Rampart Cave: Martin et al., 1961) as well as individual coprolites of other animals, including humans (Fig. 3: Bryant and Reinhard, 2012; Mead and Swift, 2012). The Quaternary of Europe, the Middle East, Africa and Asia is characterized by caves with hyena coprolites and latrines (e.g., Buckland, 1822, 1824, 1827; Chow, 1955; Kao, 1962; Musil, 1962; Mitzopoulos, and Zapfe, 1963; Mohr, 1964; Scott, 1987; Fernandéz-Rodrìguez et al., 1995; Tournepiche and Couture, 1999; Diedrich, 2012b). Many Pacific islands yield abundant and important records of Quaternary bird coprolites (e.g., James and Burney, 1997; Horrocks et al., 2004; Wood et al., 2008, 2012a, b; Worthy and Cooper, 2008). Other areas such as South America also yield significant specimens (e.g., Spillmann, 1929; Verde and Ubilla, 2002; Kerber and Oliveira, 2008).

In summary, the earliest putative vertebrate coprolites are currently Ordovician in age. Few Silurian or Devonian coprolites are described, although they are known to be locally common. Mississippian coprofaunas represent the first widespread occurrence of vertebrate coprolites. Mississippian coprolites have been little studied, but several Pennsylvanian coprofaunas have been described. The Permo-Triassic seems to be an acme zone for coprolites as a result of their abundance in

redbeds, and the literature is relatively diverse. Jurassic coprolites are locally common, but few have been described, with the notable exception of those from the Lias of England. Cretaceous and Tertiary coprolites are common, but have been relatively poorly studied. Many nonmarine Pleistocene coprolites derive from caves.

Biostratigraphy and Biochronology

Like other vertebrate trace fossils (e.g., Lucas, 2007), coprolites have limitations to their utility in biostratigraphy and biochronology imposed by: (1) small sample size; (2) homeomorphy – pre-Pleistocene coprolites can only be ascribed to a producer at a high taxonomic level (family or above); (3) extramorphological variation is probably not such an issue as in tracks, but the substrate may affect the shape of coprolites; (4) facies control – many feces are physically and chemically delicate, and their preservation is controlled at least in part by facies; (5) most (terrestrial) vertebrates are herbivores, yet most coprolites represent carnivores, so the subset of body fossil taxa represented by coprolites is small; and (6) coprolites can, and are, reworked, if only within formations. However, coprolites are abundant, exhibit morphological changes through time, and are often preserved in the absence of body fossils. Thus, coprolites have potential for use in biostratigraphy and biochronology.

The establishment of an ichnotaxonomy is a necessary precursor to the development of a useful biostratigraphy or biochronology utilizing coprolites. There is currently only a critical mass of named coprolite ichnotaxa in the Permian and Triassic (Table 1). Hunt et al. (1998, 2005a, 2007) have demonstrated the utility of Permo-Triassic coprolites in this regard, and we anticipate that coprolites will prove of greater value to biostratigraphy and biochronology in the future.

Ichnofacies

The database of described coprolites is still relatively small. However, some facies and geographic associations are clear. An obvious example is the contrast between the Pleistocene cave ichnofaunas of the Americas, which are dominated by sloth coprolites, and those of the Old World, which are characterized by hyena coprolites (Hunt and Lucas, 2007). In another example, Hunt et al. (1994a, 1998) were able to identify three coprofacies in the Late Triassic redbeds of the American Southwest (swamp, fluvial, pond). More description of coprofaunas will undoubtedly allow the recognition of other distributional patterns. It will also enable the testing of ichnofacies hypotheses, for example those of Diedrich and Felker (2012) regarding the ichnofacies of Eocene marine coprolites.

PROMINENT MISCONCEPTIONS ABOUT COPROLITES

Probably nothing has hindered the study of coprolites more than simple misconceptions about these important trace fossils.

1. Coprolites (and other bromalites) are rare.

Coprolites are very common fossils in some rock units, especially some marine anoxic shales and siliciclastic red beds. Indeed, at some localities they are as common as or more common than bone. Examples of coprolite-rich facies include: (1) marine bone beds (e.g., Rhaetic bone bed, Ludlow bone bed); (2) nonmarine intraformational conglomerates, particularly of Permian-Eocene age; (3) beds with articulated fish; (4) Pleistocene and Holocene cave deposits, particularly in arid environments (Andrews, 1990; Mead and Swift, 2012); (5) nonmarine microvertebrate sites (Mellett, 1974); and (6) Lagerstätten that include vertebrate fossils. Consumulites occur in most deposits that contain multiple articulated fish.

2. The morphology of feces is very variable.

The idea that the morphology of coprolites is very variable and defies parataxonomic classification is widespread. In part, this attitude stems from the fact that primates (such as us) produce unusually variable morphologies of feces. Omnivores produce different, but consistent, fecal types based on diet (e.g., bear eating salmon versus eating berries). However, the majority of vertebrates—carnivores and herbivores—produce a consistent morphology of feces, which is apparent from studies of Recent animal traces (e.g., Murie, 1974; Stuart and Stuart, 2000; Chame, 2003).

3. Feces have a poor preservational potential.

The phosphatic content of many carnivore feces makes them durable objects prone to fossilization. Some coprolites, notably those of carnivores, can be fossilized rapidly (e.g., Hollocher and Hollocher, 2012).

4. Coprolites cannot be reworked.

The most prominent vertebrate trace fossils – footprints – are very rarely reworked, which limits the breadth of facies in which they are fossilized. However, the common occurrence of coprolites in bone beds/intraformational conglomerates indicates that they can be reworked.

5. All feces have equal preservational potential.

Certain coprolites have much higher potential for preservation than others. Carnivore coprolites are much more commonly preserved than those produced by herbivores (Fig. 4). Heteropolar coprolites (mainly chondricthyan?) are preferentially preserved in many environments (e.g., Diedrich and Felker, 2012; Stringer and King, 2012). There is some indication that crocodile coprolites may be overrepresented among carnivore coprolites of the late Mesozoic and early Tertiary (e.g., Suazo et al., 2012; Lucas et al., 2012b).

6. Bromalites are of no scientific significance.

Vertebrate coprolites have demonstrated potential in diverse areas of geology and paleontology, from reconstructing ancient diet to biochronology and ichnofacies analysis, and from parasitology to the evolution of modern medical conditions (e.g., Hansen, 1978; Hunt, 1992; Hunt et al., 2005a; Bryant and Reinhard, 2012; Mead and Swift, 2012).

VERTEBRATE COPROLITES (AND ASSOCIATED TRACE FOSSILS): AN OVERVIEW

This volume consists of 40 articles devoted to various aspects of coprolites. Here, we provide an overview of these articles and place them in a broader context.

Early History of Study

Coprolites were first recognized in the United Kingdom (Buckland, 1822), and for a period of time there was intense interest in these trace fossils in Victorian Britain. Three articles discuss this early history of the study of coprolites (Duffin, 2012a, b; Pemberton, 2012).

Duffin (2012b) documents the earliest published records of coprolites, which appear to date from the late 17th and the early 18th centuries. Thus, Edward Lhwyd, Keeper of the Ashmolean Museum in Oxford, illustrated an apparent spiral coprolite, probably from the Jurassic Corallian Group (Oxfordian), in his 1699 volume, the *Lithophylacii Britannici Ichnographia.* Gottlieb Friedrich Mylius illustrated another coprolite from the Permian Kupferschiefer of Eisleben in Saxony in his 1709 *Memorabilium Saxoniae Subterraeae.* Even though these are the earliest known published records of coprolites, William Buckland, who subsequently recognized the fecal origin of coprolites, was apparently unaware of them (e.g., Buckland, 1829a-b, 1835, 1836).

William Buckland first recognized the fecal origin of some trace fossils (Buckland, 1822) and subsequently introduced the term coprolite. In this volume, Pemberton (2012) discusses the scientific achievements and influence of Buckland, who possessed one of the most innovative and fertile minds in geology and truly was one of its most interesting and eccentric characters. Buckland's accomplishments included the

first scientific study of dinosaur footprints, the first study of coprolites, the first mention of preserved raindrop impressions, and (by injecting Recent shark and ray intestines) the first study to utilize modern analogs to interpret ancient anatomical structures. He also pioneered the study of cave paleontology, was an early leading advocate of economic geology, was one of the first naturalists to accept the glacial theory of Agassiz, and was one of the first to recognize the importance of functional morphological studies. Buckland also identified the beneficial effects of coprolites on agriculture and was thereby instrumental in establishing the "coprolite" mining industry. Buckland's works on footprints and coprolites were the first attempts at neo-ichnology and taphonomy, and his work on coprolites led directly to the creation of the engraving *Duria Antiquior* by Sir Henry De la Beche, which represented the first attempt at a paleoecological reconstruction. De la Beche also produced the famous caricature lithographs, including *A Coprolitic Vision*, which showed Buckland in academic regalia in a cave with an audience/congregation of defecating animals (Fig. 2)

Duffin (2012a) provides background information not only on Buckland but also on some of the leading characters and personalities, mostly from Victorian Britain, who contributed to what might he terms "copromania." Duffin thus uses the collections at the Oxford Museum of Natural History and the Natural History Museum as foci, many specimens from which have not been described. Mary Anning may have stimulated William Buckland's thoughts about coprolites as early as 1824, given that the Lower Jurassic succession of the Dorset Coast proved to be a focus of much early coprolite collecting. Anning and the Philpot sisters of Lyme Regis collected there, as did Buckland, who also purchased specimens from local and metropolitan dealers. Following Buckland's (1829a-b, 1835) first descriptions of coprolites, a number of colleagues repeated his experiments on filling the intestines of modern sharks with Roman cement in order to produce analogues of spiral coprolites. Buckland's students, Sir Philip de Malpas Grey Egerton and Lord Enniskillen, collected from the Lyme Regis coast, as did Buckland's Oxford colleague, Charles Daubeny. Daubeny also saved some of Buckland's original material for Oxford at the sale of his collection in 1857. The largest collection of Lyme Regis coprolites was made by Thomas Hawkins. Later Victorian coprolite collectors included Toulmin Smith and Samuel Beckles.

Actualistic Studies

Buckland (1824, 1824, 1835) conducted actualistic studies, for example, feeding bones to a hyena and injecting shark intestines, but this aspect of the study of coprolites was largely neglected until the late 20th Century. At that point, Williams (1972) and several other authors studied modern feces and intestinal structures to determine the origin of spiral coprolites (Jain 1983; McAllister, 1985).

Antunes et al. (2006) described a very unusual occurrence of Miocene mammalian footprints preserved in coprolites, but otherwise there is no other evidence of the co-occurrence of these two kinds of vertebrate trace fossils. Here, Lockley (2012) notes that tracks in feces are ubiquitous in modern environments. He describes a case study in which Canada Geese transferred feces to hard substrates, as "dirty" footprints, where they may be preserved for several weeks without being weathered or eroded away. In such cases their preservation potential may be equal to or greater than tracks made on soft substrates. Therefore, there is some potential for finding such footprints made on hard substrates in the fossil record.

Buckland (1824) invoked comparison with modern hyena feces to identify fossil specimens (now assigned to *Hyaenacoprus* by Hunt et al., 2012a), and similar work has also been useful in identifying the producers of Pleistocene herbivore coprolites from caves of the Southwestern United States (e.g., Mead et al., 1986). In this volume, Milàn (2012) presents the first detailed study of the morphology (internal and external), inter- and intraspecific variation and inclusions in the feces of extant crocodylians. To do so, he examined 17 specimens of feces of 10 species of crocodylians living in the CrocodileZoo in Denmark. The crocodylian feces are typically cylindrical to tapering, with rounded terminations, and longitudinal striations were observed in one specimen. Internally, they consist of concentric layers of darker, clay-like material and a lighter mass containing undigested prey remains. The prey remains (of piglets, rats and chickens) comprise relatively well-preserved hair, and partly dissolved feathers with only the rachis left. Even when sieved to a mesh size of 0.122 mm, no remains of bones could be found. Scats from a gharial that ate only fish contained no remains of bones or scales. Milàn's study shows that the diameter of the feces correlates well with the total body length of the animal, and this provides a means by which to estimate the size of the producers of coprolites. Nevertheless, the intraspecific variation in morphology among crocodylian feces reflects the full spectrum of observed interspecific variations, making it impossible to distinguish feces of different species from each other.

In this volume, Wings (2012) examines Recent ostrich feces to investigate the potential of the preservation of gastroliths in coprolites. He argues that knowledge about gastroliths in coprolites is important because such finds can provide information about the retention and utilization of stomach stones in certain taxa, the size of excreted sediment particles, and special surface features of gastroliths. Gastroliths could thus help to link coprolites with their producer. A review of published reports reveals that direct evidence of gastroliths within coprolites is very rare and can be almost exclusively attributed to crocodylians or birds. Preliminary data from Recent ostrich feces show that 12.3% of the fecal mass is composed of sediment. A separation into grain sizes demonstrated that the vast majority (94.3%) of sediment particles excreted by ostriches are sand-sized (<2 mm in diameter), while the largest excreted ostrich gastroliths are <8 mm in diameter. This suggests that the rarity of gastroliths in coprolites may be partly attributed to collection bias or a lack of research interest. Wings (2012) believes that an elevated awareness of the possible presence of gastroliths in coprolites will not only help to assess their true frequency, but might help resolve some paleobiological isues.

Gechemistry, Analysis and Preservation

Buckland (1835, pl. 28, figs.12, 12'; 1836, pl.15, figs. 4, 6) prepared polished sections of coprolites to study their structure and solicited chemical analyses of Jurassic and Cretaceous specimens. In the last decade, sophisticated methodologies have been applied to study coprolites, such as the techniques explored by Milàn et al. (2012b) and Gill and Bull (2012). Hollocher and Hollocher (2012) examine the reasons for the counterintuitive notion that feces can be preserved, let alone reworked, soon after their formation.

Here, Hollocher and Hollocher (2012) examine early processes in the fossilization of terrestrial feces and the preservation of microstructure. They note that carnivorous and herbivorous feces are so chemically labile and, in general, physically fragile, that they usually decay rapidly. Thus, the existence of coprolites indicates that in some cases preservation processes must occur very early, perhaps on a scale of days to a few years. Early mineralization is critical and likely is commonly aided by burial and the onset of long-term anaerobic conditions. This slows decay and physical disruption, and places the material in contact with groundwater, which can be a source of chemical components for mineralization. Hollocher and Hollocher (2012) note that in addition to anaerobic stabilization, work during the past 20 years has established that the very bacteria active in tissue and feces decay can, under the appropriate conditions, facilitate their mineralization. This process likely contributes to the preservation of feces, and Hollocher and Hollocher (2012) discuss an example of this process in the preservation of dinosaur feces. An additional important factor in the scat of carnivorous animals is the dietary load of calcium and phosphate acquired chiefly from ingested bone. Some or most of these chemical components appear in scat as a microcrystalline apatite slurry that, with further crystallization, lends structural strength soon after the deposition of the feces. The partially premineralized state of the feces of carnivores gives them a preservational advantage, which helps explains why phosphatic carnivore coprolites

TABLE 1. Named vertebrate bromalite ichnotaxa.

Ichnotaxon	Type locality	Type horizon	Stratigraphic range	Coprolite (C), regurgitalite (R) or evisceralite (E)	Producer	Original reference	Other references	Notes
Alococoprus indicus	Kadubana, India	Lameta Formation (Upper Cretaceous: Maastrichtian)	Late Cretaceous	C	Archosaur	Hunt et al. (2007)		
Alococoprus triassicus	Crosby County, Texas, USA	Tecovas Formation of Chinle Group (Upper Triassic:	Early Permian-Late Eocene	C	Archosaur	Hunt et al. (2007)	Lucas et al. (2012b); Cantrell et al. (2012); Suazo et al. (2012)	*A.triassicus* is the type ichnospecies
Bibliocoprus beemanensis	Sacramento Mountains, New Mexico, USA	Beeman Formation (Upper Pennsylvanian)	Late Pennsylvanian	C	Chondrichthyan	Hunt et al. (2012f)		
Conchobromus kinneyensis	Kinney Brick Quarry Lagerstätte, New Mexico, USA	Tinajas Member of Atrasado Formation (Upper Pennsylvanian)	Late Pennsylvanian	R?	Acanthodian, platysomid	Hunt et al. (2012g)	Hunt et al. (2012h)	Also occurs at Tinajas Lagerstätte
Costacoprus chinae	Cambridge, England	Cambridge Greensand (Lower Cretaceous: Albian)	Early Cretaceous	C	Fish	Hunt et al. (2012c)		
Crassocoprus mcallisteri	Tinajas Lagerstätte, New Mexico, USA	Tinajas Member of Atrasado Formation (Upper Pennsylvanian)	Late Pennsylvanian-Eocene	C	Chondrichthyan	Hunt et al. (2012h)		
Crustacopus tinajaensis	Tinajas Lagerstätte, New Mexico, USA	Tinajas Member of Atrasado Formation (Upper Pennsylvanian)	Late Pennsylvanian	**C**	Acanthodian, platysomid	Hunt et al. (2012h)		
Dakyronocoprus arroyoensis	Taylor County, Texas, USA	Arroyo Formation (Lower Permian: middle Leonardian)	Early Permian (Late Wolfcampian-Middle Leonardian)	C	Fish or tetrapod	Hunt and Lucas (2005a)	Cantrell et al., 2012)	
Dicynodontocoprus maximus	Crosby County, Texas, USA	Tecovas Formation of Chinle Group (Upper Triassic: late Carnian)	Late Triassic	C	Dicynodont	Hunt et al. (1998)		
Elacocoprus williamsi	Tinajas Lagerstätte, New Mexico, USA	Tinajas Member of Atrasado Formation (Upper Pennsylvanian)	Late Pennsylvanian	C	Chondrichthyan or sarcopterygian	Hunt et al. (2012h)		
Elongatocoprus amadoensis	Tinajas Lagerstätte, New Mexico, USA	Tinajas Member of Atrasado Formation (Upper Pennsylvanian)	Late Pennsylvanian	C	Chondrichthyan or sarcopterygian	Hunt et al. (2012h)		
Eucoprus cylindratus	Gregory Quarry, New Mexico, USA	Redonda Formation (Upper Triassic: Norian)	Late Triassic (?)-Recent	C	Fish, amphibians, tortoises, iguanas, crocodylians, theropods, birds, mammalian carnivores	Hunt and Lucas (2012b)	Lucas et al. (2012b)	
Falcatocoprus oxfordiensis	Peterborough, England	Oxford Clay (Upper Jurassic: Oxfordian)	Late Triassic-Late Jurassic	C	Vertebrate	Hunt et al. (2007)	Duffin (2010); Hunt et al., 2012d	
Heteropolacoprus texaniensis	Crosby County, Texas, USA	Tecovas Formation of Chinle Group (Upper Triassic: late Carnian)	Early Permian-Late Triassic-	C	Chondrichthyan	Hunt et al. (2007)	Cantrell et al. (2012); Hunt et al. (2012f)	

TABLE 1. Continued.

Hirabromus seilacheri	Rhame, North Dakota, USA	Golden Valley Formation (Paleocene)	Late Permian-Late Miocene	E	Vertebrate	Hunt et al. (2012b)		
Hyaenacoprus bucklandi	Kirkdale Cave, England	Unnamed cave fill (Upper Pleistocene)	Pliocene-Recent	C	Hyena	Hunt et al. (2012a)		
Hyronocoprus amphipola	VanderHoof Quarry, New Mexico, USA	El Cobre Canyon Formation (Lower Permian: Wolfcampian)	Late Pennsylvanian-Early Permian	C	Sarcopterygian or chondrichthyan	Hunt et al. (2005b)	Hunt et al. (2012f)	
Ichthyosaurolites duffini	Lyme Regis, England	Lias (Lower Jurassic)	Early Jurassic	C	Plesiosaur or ichthyosaur	Hunt et al. (2012a)		
Iuloeidocoprus mantelli	Huntsboro, Alabama, USA	Selma Chalk (Upper Cretaceous)	Late Craterous	C	Fish	Hunt et al. (2012b)		Occurs in Upper Cretaceous chalk in USA and Europe
Kalocoprus oteroensis	Sacramento Mountains, New Mexico, USA	Beeman Formation (Upper Pennsylvanian)	Late Pennsylvanian	C	Chondrichthyan	Hunt et al. (2012f)		
Liassocoprus hawkinsi	Lyme Regis, England	Lias (Lower Jurassic)	Late Pennsylvanian-Late Cretaceous	C	Chondrichthyan	Hunt et al. (2007); Hunt et al. (2012b)	Duffin (2010); Hunt et al. (2012b, c, f); Laojumpon et al. (2012)	
Malericoprus matleyi	Maleri, India	Maleri Formation (Upper Triassic; late Carnian)	Permian-Late Triassic	C	Chondrichthyan	Hunt et al. (2007)	Hunt et al. (2012b)	
Megaheteropoalacoprus sidmacadami	Sid McAdams locality, Texas, USA	Vale Formation (Lower Permian: middle Leonardian)	Early Permian	C	Fish	Hunt et al. (2005a)		
Ostracocoprus snowyensis	Bear Gulch Lagerstätte, Montana, USA	Bear Gulch Limestone Member of Tyler Formation (Upper Mississippian: Chesterian)	Late Mississippian	C	Fish	Hunt et al. (2012e)		
Plektecoprus whitbyensis	Whitby, England	Lias (Lower Jurassic)	Early Jurassic	C	Ichthyosaur or plesiosaur	Hunt et al. (2012a)		
Saurocoprus bucklandi	Lyme Regis, England	Lias (Lower Jurassic)	Late Triassic-Early Jurassic	C	Chondrichthyan	Hunt et al. (2007)	Duffin (2010); Laojumpon et al. (2012)	
Speiracoprus socorroensis	Tinajas Lagerstätte, New Mexico, USA	Tinajas Member of Atrasado Formation (Upper Pennsylvanian)	Late Pennsylvanian	C	Chondrichthyan or sarcopterygian	Hunt et al. (2012h)		
Strabelocoprus pollardi	Watchet, England	?Penarth Group (Upper Triassic: Rhaetian)	Late Triassic	C	Chondrichthyan or sarcopterygian	Hunt et al. (2012a)		
Strophocopros valensis	Sid McAdams locality, Texas, USA	Vale Formation (Lower Permian: middle Leonardian)	Early Permian	C	Chondrichthyan	Hunt and Lucas (2005c)		

greatly outnumber those derived from herbivores. Hollocher and Hollocher (2012) discuss two studies of phosphatic coprolites in which early apatite precipitation was important for their preservation. In one, later permineralization was complete, and, in the other, mineralization apparently ceased at an intermediate state, after complete precipitation of autochthonous apatite, but before subsequent permineralization or recrystallization. Rapid mineralization can preserve coprolites and some microstructure in fine detail. Thus, because of their high-fidelity preservation, coprolites can provide an important window into the diets and digestive system characteristics of the producing animals.

Lipid analysis is a relatively new approach to obtaining paleobiological and paleoecological information from coprolites. In this volume, Gill and Bull (2012) describe how lipids in feces are derived from multiple sources, including diet, digestive processes and digestive tract micro-organisms. The feces of herbivorous animals contain a much wider range of lipids than do those of carnivores because of the greater diversity of lipids in dietary plants, compared to prey animals, and the more complex digestive systems of herbivores. Further, depending on their structure and their preservation in fossilized material, fecal lipids can provide general or very specific biological and ecological information. Gill and Bull (2012) note that research using lipid analysis of coprolites has been infrequent, but this approach has the potential to reveal unique information about ancient animals and environments, so it should be considered a valuable tool for analysis given suitable specimens.

The MDCT (Multi-Detector Computed Tomography) scanner has proven useful in facilitating elaborate three-dimensional anatomical reconstructions (e.g., Mueller-Töwe et al., 2008; Farlow et al., 2010). Here, Milàn et al. (2012b) explore the possibilities of using MDCT scans to study the content and internal architecture of a well-preserved vertebrate coprolite from the lower Paleocene (Danian) limestone of Faxe Quarry, Denmark. The oval/sub-cylindrical coprolite is 34 mm long and 16 mm in diameter, and at one end, a small vertebra, 3.8 mm long and
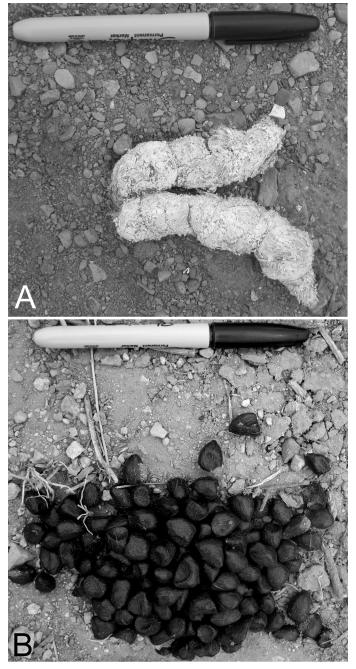
FIGURE 4. Modern carnivore and herbivore feces from southern New Mexico, USA. **A**, Scat of Coyote (*Canis latrans*). **B**, Dung of Gemsbock Oryx (*Oryx gazella*). For scale, the marking pen is 13.5 cm long.

approximately 2.7 mm in diameter, is partly exposed. The scanning data show that the coprolite is composed of several concentric layers, each approximately 2 mm thick. This reflects the original way the fecal mass was deposited in the intestines of the producer. Furthermore, the scanning shows that the embedded vertebra is complete and three-dimensionally preserved, and it is possible to identify the vertebra as that of a bony fish. In addition, numerous other, smaller, elongate bone fragments were revealed inside the coprolite. The high quality and resolution of the scanning images demonstrate that MDCT scanning is a useful, non-destructive way to examine the internal architecture and dietary remains of well-preserved, non-recrystallized coprolites. Advances in Micro CT scanners and their increased accessibility will produce images of much higher resolution and will enable more detailed non-destructive mapping and analysis of inclusions and of the internal structures of coprolites.

Museum Collections

William Buckland was the first to amass a collection of coprolites, and a portion of his collection is preserved at the University of Oxford Museum of Natural History (Duffin, 2012b; Pemberton, 2012). Subsequently, only a small number of museums have acquired significant coprolite collections, of which the most extensive are at the National Museum of Natural History (Smithsonian Institution), The Natural History Museum (London) and the New Mexico Museum of Natural History and Science (Albuquerque).

The largest collection of coprolites is at the National Museum of Natural History (Smithsonian Institution), USA. In this volume, Hunt et al. (2012b) provide an overview of the collection, which includes specimens from the middle-upper Paleozoic (Devonian, Carboniferous, Permian), Mesozoic (Triassic, Jurassic, Cretaceous), Tertiary (Paleocene, Eocene, Miocene, Oligocene) and Quaternary (Pleistocene). They describe two new ichnotaxa from the collection: *Iuloeidocoprus mantelli*, ichnogen et ichnosp. nov., is a widespread Late Cretaceous coprolite, and *Hirabromus seilacheri*, ichnogen et ichnosp. nov., is a cololite known from the Mesozoic and Cenozoic. Hunt et al. (2012b) also discuss the importance of the coprolite collections at: (1) the New Mexico Museum of Natural History and Science, which has an extensive vertebrate trace fossil collection (including bromalites) that is large, diverse and rapidly growing; (2) the Buckland collection at the University of Oxford Museum of Natural History, the oldest collection of coprolites in the world; and (3) The Natural History Museum, a modest-sized but diverse collection.

In this volume, Hunt et al. (2012a) describe a number of new ichnotaxa from the Buckland Collection at the Oxford University Museum of Natural History in England. The collection comprises Mesozoic and Cenozoic coprolites and other bromalites. It includes the most comprehensive samples of two important British coprofaunas – the Lower Liassic of Lyme Regis and the Rhaetic bone bed. Hunt et al (2012a) describe four new coprolite ichnotaxa from this collection: *Ichthyosaurolites duffini* ichnogen. et ichnosp. nov., *Strabelocoprus pollardi* ichnogen. et ichnosp. nov. and *Plektecoprus whitbyensis* ichnogen. et ichnosp. nov. from the Upper Triassic-Lower Liassic, and *Hyaenacoprus bucklandi* ichnogen. et ichnosp. nov. from the Late Pleistocene.

The Natural History Museum (London, England) has a diverse collection of coprolites that represents the second oldest coprolite collection, after the Oxford University Museum of Natural History (Hunt et al., 2012c). The Paleozoic collection includes Carboniferous coprolites from Europe and the Lower Permian of the USA. Early-middle Mesozoic specimens are represented by Rhaetian coprolites from England, a diverse collection from the Lower Jurassic of England and Late Jurassic coprolites from Germany and England. There are coprolites from the Lower Cretaceous of England, including *Costacoprus chinae* ichnogen. et ichnosp. nov., and six coprolites from the Upper Cretaceous of India. There is also a single Cenozoic coprolite from Nigeria. There is need for further study of the collection, notably a description of the large samples from the Oxford Clay Formation and Purbeck Limestone Formation.

Classification and Terminology

Shortly after bromalites were first recognized, Buckland (1829b) and Agassiz (1833) introduced the first terms for them, coprolite and cololite, respectively. Since that time various workers have introduced new terms, but there has been no consensus as to usage. In this volume, Le Loeuff (2012) discusses a forgotten classification scheme, and Vallon (2012) and Hunt and Lucas (2012a-b) review older terminology and introduce new nomenclature.

Vallon (2012) proposes the new ethological class Digestichnia to encompass all trace fossils (and their recent counterparts) originating from the digestive process of animals, including coprolites, regurgitalites and gastroliths (geo- and pathogastroliths *sensu* Wings, 2004, 2007). The class is based upon a classification system for trace fossils originally

proposed by Vialov (1972). Any material of non-caloric value leaving the digestive tract of the tracemaker is regarded as a digestion trace and is included within Digestichnia. However, in the fossil record, individual bones or other hard body parts preserved within Digestichnia may be regarded as body fossils. Vallon (2012) discusses ichnotaxobases at the ichnogeneric level.

Hunt and Lucas (2012a) review all terminology that has been applied to vertebrate bromalites. They argue that more clarity and consistency is needed in the use of terminology for vertebrate trace fossils. Several principles are deemed important in assessing the nomenclature of vertebrate trace fossils: (1) ichnofossils should have a terminology distinct from that applied to Recent traces; (2) priority of terminology is important; (3) stability of nomenclature should be maintained; (4) universality of usage should be considered in the choice of terms; (5) when possible, there should be consistency in etymology and usage; and (6) the terminology should have practical utility. Hunt and Lucas (2012a) propose a comprehensive and internally consistent hierarchical terminology for bromalites and related ichnofossils. Some of the most important terms are "coprolite" (all trace fossils that represent food items that have entered the oral cavity or gastrointestinal tract and have been expelled or retained within them), "consumulite" (fossilized food material preserved in, or partially in, the body cavity), "demalite" (skeletal material preserved with the body cavity of an animal that does not pertain to it), "cumulite" (fossil accumulation of organic or inorganic material concentrated by an organism), "gignolite" (trace fossils related to reproduction) and "gastrolith" (a hard object of no caloric value that is, or was, retained in the digestive tract of an animal) (Fig. 1).

Ferdinand Panescorse was an amateur geologist in the 19th Century who prospected for phosphatic nodules in the Var region in Provence, France (Le Loeuff, 2012). There was a "coprolite mining rush" in the early part of the second half of the nineteenth century in France, as well as in the UK. Le Loeuff (2012) describes how, in 1872, Panescorse published a catalogue of his finds that were interpreted as coprolites. Panescorse recognized 70 morphotypes distributed among 19 groups. However, Le Loeuff (2012) demonstrates that most if not all of Panescorse's "coprolites" are sedimentary nodules of inorganic origin.

Hunt and Lucas (2012b) review the morphological terms applied to coprolites and provide a morphotype scheme to encompass all coprolites and recent feces of vertebrates. Spiral coprolites externally have the appearance of a ribbon coiled around a long axis, but internally they consist of stacked, and spiraling, cones, whereas scroll coprolites are more analogous in structure to a rolled sheet of paper. These two morphologies reflect two architectures of valvular intestines of which Type D (mucosa forming spiraling cones, pointed anteriorly) is the most common, and these form coprolites of spiral morphology. The oldest possible spiral coprolites are from the Late Ordovician of South Africa, but it is possible that some putative spiral vertebrate coprolites from the Ordovician-Permian might have been made by eurypterids. Spiral coprolites are considered 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 proposed for cylindrical coprolites with no inclusions. Hunt and Lucas (2012b) recognize 27 morphotypes of coprolites and Recent vertebrate feces in 11 main categories.

Paleozoic Bromalites

The study of Paleozoic coprolites has stimulated much research on spiral coprolites (e.g., Williams, 1973; McAllister, 1985) but there have been relatively few descriptions of entire coprofaunas (e.g., McAllister, 1996). This volume includes six reviews of coprofaunas ranging in age from the Early Mississippian to the Early Permian.

One of the most significant Missisippian vertebrate bone and tracksites is Blue Beach (Horton Bluff) in Nova Scotia, Canada. Mansky et al. (2012) describe bromalites from the Lower Mississippian Horton Bluff Formation there that are associated with a significant record of plant, vertebrate and invertebrate body fossils and invertebrate and vertebrate trace fossils. The cololites from this locality are comparatively large for the Mississippian, and the rhizodont *Letognathus* is interpreted as the tracemaker. Mansky et al. (2012) recognize six coprolite morphotypes: (1) ovoid pellets, some spiraled; (2) elongate pellets, some spiraled; (3) twisted pellets, known from a single example; (4) a flattened regular mass; (5) an irregular flattened mass; and (6) an irregular coprolitic mass. The Horton Bluff coprolite ichnofauna is similar to other Mississippian coprolite assemblages, including the Visean of East Kirkton and, to a lesser extent, the Dinantian site of Foulden, which is the nearest equivalent in both age and fauna to the Nova Scotian locality.

The Mississippian Bear Gulch Lagerstätte of central Montana, USA, is one of the most significant sources of Paleozoic fish body fossils, notably of chondrichthyans (e.g., Horner and Lund, 1985; Lund et al., 1993, 2012; Grogan and Lund, 2002). Hunt et al. (2012e) describe the vertebrate coprofauna, which includes six morphotypes/ichnotaxa of bromalites: (1) morphotype A coprolites are large and ovoid to pear shaped; (2) morphotype B coprolites are elongate and triangular in shape; (3) morphotype C coprolites are elongate and rounded; (4) morphotype D coprolites are small, ovoid and composed of dense groundmass; (5) spiral coprolites; and (5) *Ostracobromus snowyensis* ichnogen. et ichnosp. nov, is ovoid, characterized by inclusions of multiple valves of ostracods set in a groundmass and is possibly a regurgitalite.

The Tinajas Lagerstätte is located in Socorro County, New Mexico, USA, and it was only recognized recently (Lerner et al., 2009). In this volume, Hunt et al. (2012h) describe the diverse bromalite ichnofauna collected there from the Upper Pennsylvanian Tinajas Member of the Atrasado Formation, which is of late Missourian age based on conodont biostratigraphy. The diverse bromalites (11 coprolites, 1 regurgitalite) from this Lagerstätte include seven morphotypes (morphotype A are amphipolar, morphotype B are rounded cylinders, morphotype C are longitudinally-striated, morphotype D are small, flattened ovoids, morphotype E are spindle shaped, morphotype F are ovoid with nodular texture, and morphotype G are flattened ovoid with acanthodian scales), one existing ichnotaxon (*Conchobromus kinneyensis*) and five new ichnotaxa (*Crassocoprus mcallesteri*, *Spierocoprus socorroensis*, *Elongatocoprus amadoensis*, *Elacacoprus williamsi* and *Crustacoprus tinajaensis*).

The Kinney Brick Quarry is a Late Pennsylvanian (middle Missourian) Konservat Lagerstätte in central New Mexico that yields a diverse paleofauna and paleoflora (Lucas et al., 2011). The fossils derive from lagoonal shales in the Tinajas Member of the Atrasado Formation. Hunt (1992) initially described bromalites from the Kinney Brick Quarry Lagerstätte. Subsequently, a large collection has been amassed, and in this volume Hunt et al. (2012g) provide a re-evaluation of the Kinney coprofauna. Thus, a diverse bromalite assemblage preserves seven morphotypes, including *Conchobromus kinneyensis* ichnogen. et ichnosp. nov., morphotype A (large, flat ovoid with little groundmass and abundant fish debris), morphotype B (no groundmass, scattered fish debris), morphotype C (medium-sized, ovoid with compact bone and some groundmass), morphotype D (elongate, thick), morphotype E (small, ovoid with macerated fish debris and groundmass), morphotype F (small, linear) and morphotype G (ovoid and within digestive tract). The bromalites probably represent sharks (morphotype A, B, D, G), palaeoniscoids (morphotype C, E?, F?) and/or acanthodians (morphotypes E?, F?). *Conchobromus kinneyensis* could represent an acanthodian or possibly a platysomid. A variety of bromalites (one morphotype of regurgitalite, one of an incorporeal pelletite and two of coprolites) were produced by the relatively uncommon large sharks at Kinney.

Hunt et al. (2012f) here describe a new Late Pennsylvanian coprofauna from the Beeman Formation in the Sacramento Mountains of southeastern New Mexico, USA. The Beeman Formation is middle to upper Missourian in age based on fusulinids. The coprolite locality

occurs in a road cut on the north side of NM Highway 82 where the Beeman is represented by a basinal marine facies. The Beeman coprofauna differs from the Kinney and Tinajas Lagerstätten coprofaunas from elsewhere in New Mexico in: (1) representing a basinal marine facies rather than a lagoonal facies; (2) the majority of Beeman coprolites are spiral in form, representing chondrichthyans or sarcopterygians, whereas the Kinney and Tinajas assemblages are more diverse; (3) Beeman coprolites are preserved three-dimensionally, are relatively undeformed and are readily separable from the matrix, whereas those from Kinney and Tinajas are compressed and occur in finely-laminated shale; and (4) there is currently no fish fauna known from the Beeman Formation, whereas Kinney, and to a lesser extent Tinajas, have yielded diverse ichthyofaunas. The Beeman coprolites may provide a baseline for comparison of marine basinal coprofaunas with those of lagoonal environments, both in taphonomy and taxonomy, and may indicate distinct differences in the ichthyofaunas that produced them.

The area near the Tinajas Lagerstätte in central New Mexico, USA, includes fossiliferous red beds of Early Permian age. Cantrell et al. (2012) describe vertebrate coprolites from these beds at the Lower Permian (middle Wolfcampian) Gallina Well locality. This ichnoassemblage includes *Heteropolacopros texaniensis* and amorphous coprolites as well as the first occurrence of *Dakyronocopros arroyoensis* in New Mexico and the oldest record of *Alococopros triassicus*. The age and faunal associations of *Alococopros triassicus* from the Gallina Well locality refute earlier assertions that longitudinally-striated coprolites were produced by stem archosauromorphs and are restricted to the Mesozoic and Cenozoic.

Mesozoic

There have been a relatively large number of publications on Mesozoic coprolites in the past two decades, with an emphasis on dinosaur coprolites (e.g., Thulborn, 1991, Chin and Gill, 1996; Chin and Kirkland, 1998; Chin et al., 1998, 2008; Ghosh et al., 2004; Chin, 2007). However, a diverse literature also exists on coprolites from Triassic nonmarine red beds, which have an extensive global record (Hunt et al., 2007 and references cited therein). In this volume, nine articles describe a diversity of Mesozoic coprolites and other bromalites, only a few of which pertain to dinosaurs.

Milàn et al. (2012c) and Laojumpon et al. (2012) document important samples of Late Triassic coprolites from geographically disparate occurrences in Greenland and Thailand. Schweigert and Dietl (2012) and Friedman (2012) describe marine coprolites from the Jurassic and Cretaceous, respectively, whereas Milàn et al. (2012a), Souto and Medeiros (2012) and Sullivan and Jasinski (2012) report on Cretaceous nonmarine forms. Diedrich's (2012a) contribution focuses on material preserved within the gastro-intestinal tract (consumulites *sensu* Hunt and Lucas, 2012a) of Cretaceous fish. Suazo et al. (2012) present data on nonmarine coprolites across the K/T boundary.

Milàn et al. (2012c) provide a preliminary report on coprolites from the basal, Late Triassic part of the Triassic-Jurassic (Rhaetian-Sinemurian) Kap Stewart Formation, exposed at Jameson Land, East Greenland. The locality yields an extensive coprolite collection from black, parallel-laminated mudstone ("paper shale"), representing an open lacustrine system. Preliminary investigations demonstrate the presence of three different types of coprolites: elongated cylindrical masses, composed of irregularly wrapped layers; elongated cylindrical masses with constriction marks; and spirally-coiled specimens.

Laojumpon et al. (2012) report on the first records of Late Triassic coprolites from Southeast Asia. A large coprofauna (169 coprolites) was found at Huai Nam Aun (Upper Triassic Huai Hin Lat Formation) in Chaiyaphum Province, Thailand. Laojumpon et al. (2012) sub-divide these coprolites into seven different morphotypes. Four groups of spiral coprolites are interpreted as being produced by fish-eating sharks and lungfish, whereas non-spiral coprolites containing numerous bone fragments and fish scales were probably produced by other carnivorous

vertebrates. *Liassocopros hawkinsi* and *Saurocopros bucklandi* are recognized for the first time in Southeast Asia. The presence of these ichnogenera supports palynological studies suggesting a Carnian-Norian age for the Huai Hin Lat Formation.

The Jurassic-Cretaceous lithographic limestones of Europe yield numerous vertebrate coprolites (e.g., Hunt et al., 2012a, fig. 1F, 2012c, fig. 1P), but no study until now has focused on the specimens from a single locality. Here, Schweigert and Dietl (2012) describe coprolites from the Nusplingen lithographic limestone (Upper Jurassic, southwestern Germany). The coprolites are phosphatic, and some contain undigested remains of prey (fish bones, fragments of crustaceans, and hooks of coleoid cephalopods). Most of the coprolites were probably produced by bony fish and sharks, but others may derive from marine crocodiles. All of these predators are represented by skeletons or isolated teeth in the strata that yield the coprolites. The diversity of coprolite morphotypes suggests a complicated food chain in the Nusplingen lagoon water column despite conditions on the sea floor.

Friedman (2012) describes a collection of vertebrate coprolites from the Turner Park Member of the lower Britton Formation (lower Eagle Ford Group) of north-central Texas, USA. Many contain inclusions and are attributed to shark and/or large fishes due to their size, morphology and the inclusions. The most abundant associated vertebrate fossils are shark as well as other fish teeth, vertebrae and other remains assigned to *Cretoxyrhina*, *Squalicorax*, *Cretolamna*, *Enchodus*, *Ptychodus*, *Carcharias*, *Cretodus*, *Protosphyraena* and saurodontids. The environment of deposition of the locality is interpreted as low-energy, offshore, and poorly oxygenated. There is an abundant pelagic ichthyofauna, rare benthic invertebrate fauna and absence of an infauna. The fossil assemblage is consistent with the oceanic anoxic event recorded worldwide during the late Cenomanian. Friedman (2012) notes that coprolite-rich horizons have been underutilized in paleoecological reconstructions and biostratigraphic correlation.

Souto and Medeiros (2012) describe approximately 80 coprolites from a Cenomanian bone bed in northeastern Brazil. The locality is named Laje do Coringa, on Cajual Island, Maranhão State, where there is a 4 km-long exposure of a bone bed in the Alcântara Formation. The bone bed was deposited in a nearshore environment, subject to tidal currents, and yields numerous bones and teeth as well as stems of conifers and ferns. Some of the coprolites were analyzed in thin section and by x-ray fluorescence. Several morphotypes were recognized, including ovoid, conical, spiral and cylindrical The ovoid and conical morphotypes have larger amounts of calcium, whereas the concentrations of phosphorus and calcium are higher in the cylindrical and spiral forms. The spiral morphotypes are considered to represent chondrichthyans, and the cylindrical forms are attributed to reptiles.

Coprophagy is presumably an extremely ancient behavior, but it has only been recently recorded in coprolites (Chin and Gill, 1996; Northwood, 2005). Milàn et al. (2012a) document coprolites with prey remains and traces from coprophagous organisms from the Lower Cretaceous (late Berriasian) Jydegaard Formation of Bornholm, Denmark. These are the first records of coprolites from continental Mesozoic deposits in Denmark. Computed tomography scanning proves to be a useful nondestructive technique to examine the coprolites (also see Milan et al., 2012b). Milàn et al. (2012a) examine two fragmentary coprolites and, based on morphology, inclusions and the potential producers represented by body fossils in the formation, they tentatively suggest that the coprolites were produced by a turtle or a piscivorous theropod. One specimen show pits and grooves in the surface, as well as two deep cylindrical burrows, made by coprophagous organisms.

Agassiz (1833) first recognized infilled intestines in fossil fish. Subsequently, many descriptions of fossil fish have mentioned the presence of consumulites (*sensu* Hunt and Lucas, 2012a), but there are virtually no individual studies devoted to them. Diedrich (2012a) describes stomach (gastrolite) and gastrointestinal tract infillings (intestinelites) from late Cenomanian teleosts from black shales of northern Germany.

Three skeletons of *Anogmius*, *Elopopsis* and *Protostomias* have preserved swallowed fish, gastrolites and intestinelites. The *Anogmius* specimen contains four small fish skeletons, and other partially digested specimens, and intestinelites; the *Elopopsis* specimen has elongate intestinelites; the *Protostomias* has a gastrolite, and other specimens from Morocco contain swallowed fish. The Cenomanian/Turonian fish faunal assemblages and their taphonomy are different in upwelling deep basin sediments (= black shale), slope facies (= marl), carbonate platform deposits (= platy limestone), and coastal sands (= greensand). Diedrich (2012a) believes that fish mortality was connected to plankton blooms. Planktonic foraminiferans indicate that mortality events first affect the oxygen minimum zone (OMZ), then drop into the upper warm water column, and larger blooms also reach the lower cold water zones.

Sullivan and Jasinski (2012) describe coprolites from the Upper Cretaceous section in the San Juan Basin of New Mexico, USA (Fruitland, Kirtland and Ojo Alamo formations). They identify seven morphotypes (A-G), at least four of which are unique (B, D, F,G), and attribute them to carnivorous vertebrates (fishes, turtles and crocodylians). Four different surface textures are recognized (smooth, slightly blistered, wrinkled and striated). Bone inclusions occur in approximately 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 (sub-adult hadrosaurid), ?vertebral centra and partially digested bone is identified as a probable tyrannosauroid coprolite.

Coprolites could potentially preserve information relevant to the study of mass extinctions. Suazo et al. (2012) provide context for one example with their description of vertebrate coprolites across the Cretaceous/Tertiary boundary in the San Juan Basin of New Mexico, USA. They document a large collection at the New Mexico Museum of Natural History of Late Cretaceous (Kirtlandian, Edmontonian) through early Cenozoic (Puercan, Torrejonian, Wasatchian) coprolites. A minimum of four morphotypes are present (spindle-shaped, elongated cylinders, cylindrical segments, conglomerated masses) that exhibit various surface textures (worn, smooth, pitted, striated) and other features (constriction marks, inclusions). One specimen assigned to *Alococopros triassicus* extends the range of this ichnotaxon into the Late Cretaceous. Most of the San Juan Basin coprolites can be confidently assigned to carnivorous producers based on morphology, composition and inclusions (such as bones or gar scales). However, there are clearly biases in the collection, notably the prevalence of small carnivore coprolites. Suazo et al. (2012) conclude that none of the coprolites are dinosaurian, or that dinosaurian coprolites are homeomorphic with those of some other vertebrates, such as crocodiles.

Tertiary

There are many scattered reports of Tertiary coprolites (e.g., references in Hunt and Lucas, 2007), but few substantial works. In this volume, two major studies of Eocene shark coprolites, by Stringer and King (2012) and Diedrich and Felker (2012), are presented, as is a detailed description of fossil owl pellets (strigilites *sensu* Hunt and Lucas, 2012a) by Lucas et al. (2012a). In addition, Lucas et al. (2012b) describe the first coprolites from the Tertiary of Kazakstan.

Stringer and King (2012) describe Late Eocene shark coprolites from the marine Yazoo Clay in northeastern Louisiana, USA, where long-term, surface collecting of two sites has resulted in the procurement of nearly 1200 shark coprolites. They describe a sample (n = 374, 30% of total) of the coprolites in detail. The majority of the specimens (~ 98%) are classified as spiral (556 coprolites) or scroll (617 coprolites). X-ray analysis show the coprolites to be composed of moderately crystalline fluorapatite with no compositional differences between the types. Extensive collections of shark teeth (> 2500) are known from this site. Stringer and King (2012) use the shark tooth data coupled with modern information on shark size, anatomy, and excretory characteristics to identify the producers of the coprolites. The most likely source animals for the spiral coprolites are considered to be the lamniform *Isurus praecursor* and the carcharhiniform *Abdounia enniskilleni*, while the scroll coprolites were most likely produced by the carcharhiniform *Carcharhinus gibbesi*, with the exception of several large specimens, which may be the products of *Galeocerdo alabamensis*.

Diedrich and Felker (2012) provide an interesting contrast to Stringer and King (2012) by describing Eocene shark coprolites from Europe. Middle Eocene transgressive marine conglomerates from two German localities (Dalum, Osteroden) in the southern pre-North Sea basin (middle Eocene) of central Europe contain a large sample of 19 different shark taxa (tooth size > 4 mm) as well as shark coprolites (n = 556). The coprolites are classified in five main morphotypes (A-E) and are predominantly heteropolar in morphology. The largest forms (A) contain medium-sized fish bones and vertebrae and belong to megatooth and white shark ancestors (*Otodus*, *Carcharocles*, *Procarcharodon*), whereas the most abundant, medium-sized forms (B) might have been produced by laminid sharks (*Isurus*, *Jaeckelotodus*, *Xiphodolamia*, *Brachycarcharias*, *Hypotodus*, *Sylvestrilamia*), but the abundant sand shark ancestor *Striatolamia* is probably the main producer. Morphotype C is a rare, thin, elongate morphotype with zigzag-heteropolar external structure (producers: ?rays/small sized carchariniform sharks such as *Galeocerdo*, *Pachygaleus*). The smaller, including the smallest (only 3 mm), oval-round pellets, and also the unclearly heteropolar morphotype D oval- to round-shaped pellets, have only poorly-developed surface coil structures, and are preliminarily referred to sharks or rays. Rare, irregularly-formed coprolites may be referred to a crocodile producer, which supports the distal deltaic environmental interpretation of the Dalum site. The Osteroden site yields more abundant coprolites (morphotype A) of large sharks, indicating more shallow marine environments.

Lucas et al. (2012b) describe putative crocodylian coprolites from the Eocene of the Zaysan Basin of northeastern Kazakstan. Approximately 50 coprolites were collected from a single horizon stratigraphically low in the Aksyir svita. Lucas et al. (2012b) recognize two morphotypes: A, relatively large coprolites (diameter and length generally > 20 mm) with rounded ends and cylindrical cross sections; and B, relatively small coprolites (length ~16-23 mm, maximum diameter 9-16 mm) that are rounded in shape. The larger coprolites are assigned to *Eucoprus*, whereas the smaller ones are assigned to *Alococopros*. The coprolites are assigned to a crocodylian producer based on: (1) occurrence in lacustrine shoreline facies; (2) co-occurrence with crocodylian body fossils; and (3) similarity to modern crocodylian feces in shape, texture and lack of bony inclusions.

Myhrvold (2011, p. 2) rightly noted that research on bromalites has largely ignored regurgitalites and that their study has the possibility to "yield similarly valuable new information about many extinct vertebrates including pterosaurs, theropod dinosaurs, ichthyosaurs, mosasaurs, early birds, mammals and thecodonts." Lucas et al. (2012a) provide an important addition to the literature on regurgitalites. They document an extensive (at least 1 x 0.3 m) purgolite (*sensu* Hunt and Lucas, 2012a) composed of strigilites (fossilized owl pellets, sensu Hunt and Lucas, 2012a) from the lower Oligocene (Orellan) Orella Member of the White River Formation near Douglas in eastern Wyoming, USA. These pellets are preserved as calcareous nodules full of fossil mammal bones that are either discrete, bordered by green claystone matrix, or coalesced flattened masses that likely represent coalesced strigilites. The locality has yielded the type specimens of the sciurid rodent *Cedromus wilsoni* and the todid bird *Palaeotodus emryi*. The owl pellet assemblage also includes the skeletons, bearing skulls, of at least three individual owls, which strongly reinforces the interpretation of these small masses of bone as owl pellets. These owls are large enough to have preyed on the mouse-sized rodents (eomyids and heteromyids) and on the mouse-sized marsupials, which together constitute the vast majority (more than 90%) of prey individuals in the owl pellet assemblage.

The strigilites in the assemblage display many of the features

deemed characteristic of recent owl pellets based on actualistic studies, including abundant and high quality bone preservation, extreme inequitability of species distribution, intact skulls, numerous mandibles and femora and good representation of all skeletal parts. Further preparation of the bones in the Orellan strigilites is needed to quantify species abundance, bone element frequencies and the statistics of element breakage and completeness, among other data. The Orellan strigilites are apparently the oldest and one of the few unambiguous published records of fossil owl pellets. Lucas et al. (2012a) note that despite repeated claims that owl pellets are important contributors to the Tertiary microvertebrate fossil record, very few fossil owl pellets have been documented. They conclude that owl pellets are not a significant component of the Tertiary fossil record despite their abundance in some Quaternary deposits.

Quaternary Coprolites

The first fossil feces to be recognized were hyena coprolites from Late Pleistocene deposits in Kirkdale Cave in Yorkshire, England (Buckland, 1822, 1824; Duffin, 2009). Such coprolites are common in caves throughout the Old World, and, in this volume, Diedrich (2012b) describes specimens from central Europe. Similar-aged caves in the western United States, many from lands administered by the National Park Service, have yielded the largest known accumulations of coprolites, including those of humans (Bryant and Reinhard, 2012; Diedrich, 2012b; Hunt et al., 2012d; Mead and Swift, 2012). Even more abundant in these areas are Packrat middens (neotomalites of Hunt and Lucas, 2012a), which are important sources of paleoecological information. Here, Tweet et al. (2012) provide a review of these trace fossils from National Park Service areas in the United States.

The largest sample of Quaternary vertebrate bromalites is from the southwestern United States. Mead and Swift (2012) provide a very useful synopsis of the literature on Late Pleistocene (Rancholabrean) coprolites of the Colorado Plateau in western North America. The Colorado Plateau covers about 337,000 km², and most of it has not been adequately prospected for Late Pleistocene-age fossil deposits. Desiccated coprolite deposits are restricted to dry caves, rock crevices, and rock shelters. The most intensively-studied and best known Late Pleistocene taxa on the Colorado Plateau are those accompanied by added data from study of their coprolites. These species include the living packrat (*Neotoma*) and the extinct mammoth (*Mammuthus*), Harrington's mountain goat (*Oreamnos harringtoni*), and Shasta ground sloth (*Nothrotheriops shastensis*). Dried coprolites identified to the species level provide superb data used to analyze detailed aspects of chronology (plus possible time of extinction/extirpation), dietary reconstruction, and molecular phylogeny of extinct taxa.

Areas managed by the National Park Service (NPS) in the United States preserve not only scenic and historical resources, but also an extremely important fossil record. Fossil resources are not limited to areas set aside specifically to preserve fossils (e.g., Dinosaur National Monument, Fossil Butte National Monument, Hagerman Fossil Beds National Monument; John Day Fossil Beds National Monument, Petrified Forest National Park) but also occur in a wide range of other properties. The majority of bromalite resources in NPS areas are of Quaternary age. Hunt et al. (2012d) review occurrences of coprolites and other bromalites at 47 National Park Service areas, principally in the western United States. The majority of the occurrences are vertebrate coprolites or paleomiddens/neotomalites (*sensu* Hunt and Lucas, 2012a), but there are also invertebrate coprolites from Big Bend National Park and fish cololites from Fossil Butte National Monument.

The three most important coprolite assemblages in the NPS system are at Petrified Forest National Park (PEFO), Badlands National Park (BADL) and Grand Canyon National Park (GRCA). These coprolite assemblages have been central to recent work on paleoecology and biochronology and represent three of the acme zones for vertebrate coprolites in North America: Late Triassic at PEFO (Chinle Group), Eocene-Oligocene at BADL (White River Group) and Pleistocene at GRCA

(cave deposits). Coprolites typically do not require any specific NPS management action, with the exception of some of the Pleistocene or Holocene coprolites that occur in caves. The partial destruction of sloth coprolite deposits by park visitors at Rampart Cave at GRCA illustrates the need for park management action and implementation of preservation strategies to protect rare and sensitive paleontological resources. Resource management needs to be sensitive to the preservation and interpretation of vertebrate coprolites (Hunt et al., 2012d).

Packrat middens are important tools for reconstructing the paleoecology and climate of the late Pleistocene and Holocene of western North America, and Tweet et al. (2012) provide a comprehensive review of packrat (*Neotoma* spp.) middens in National Park Service areas in the United States. These collections of plant material, food waste, coprolites, bones, and other biological materials can be well-preserved in arid, protected settings such as caves and rock shelters, and document the environment within the builder's foraging range. Tweet et al. (2012) note that middens have been most widely utilized to illustrate climate through the environmental requirements of the plants preserved as inclusions, but have also been used for a variety of other studies as well. These encompass the use of included pollen, arthropods, and vertebrate remains as climate proxies, the evolution and distribution of plant taxa, erosion rates, responses to grazing, megafaunal extinction and archeology. Middens from many National Park Service units have been important components of numerous midden studies. Indeed, 33 National Park Service parks, monuments, and other areas in 11 states are currently known to contain packrat middens, with all but five known to have fossil middens. Among them are some of the best-known midden series in the USA (e.g., Big Bend National Park, Chaco Culture, National Historical Park, Death Valley National Park, Grand Canyon National Park and Organ Pipe Cactus National Monument). National Park System middens are important not only at the broad level of climate change research, but also at the park or monument level as tools for resource management, and have untapped potential as educational resources.

While the caves of North America are characterized by coprolites of megaherbivores, those of the Old World (Europe, Africa, Middle East, Asia) are characterized by hyena coprolites. Diedrich (2012b) reviews Late Pleistocene spotted hyena *Crocuta crocuta spelaea* coprolites from central Europe. These coprolites were mostly found in prey deposits and dens in hyena caves and at open air sites. In two cases coprolites were found next to mammoth and straight-tusk elephant skeletons. Coprolites of *Crocuta crocuta spelaea* are identical in morphology to those of Recent African spotted hyenas (*Crocuta crocuta crocuta*). The hyaena coprolites are composed of aggregates of what Diedrich (2012b) terms pellets, that he classifies into seven morphotypes. Most of the hyaena coprolites contain small indeterminate bone fragments, but the pollen in the coprolites originates from the intestines of the consumed prey. Fecal pellets/coprolites are/were used by extant/extinct spotted hyenas to mark their dens and territories. A large number of coprolites and phosphatic layers, built of trampled coprolites, are found at den sites (caves and open air) and are often important for distinguishing human and hyena bone assemblages.

The study of human coprolites has developed in parallel with that of other vertebrate coprolites and there has been little connection between the two; a similar situation occurred in taphonomy (e.g., Hunt et al., 1994b). Similarly, there has been little interaction between invertebrate ichnologists and those who study human coprolites. Thus, Buatuois and Mánganos's (2011) excellent review of ichnology (principally invertebrate) includes a chapter on trace fossils in archeology that does not even mention coprolites. However, in the past five years there has been some consideration of utilizing ichnological methodology in archeology (e.g., Baucon et al., 2008; Rodríguez-Tovar et al., 2010).

Bryant and Reinhard (2012) provide an important review of the history of study of human coprolites and highlight some important research directions (Fig. 3). They note that the study of human coprolites is just over 100 years old, dating back to 1896. During the last 50 years

these studies have greatly advanced our understanding of the lives, economy, and health of our ancestors. Originally, the focus of coprolite studies was on the identification and significance of inclusions of bone fragments and plant macrofossils. Later research expanded into searches for pollen, phytoliths, hairs, feathers, endoparasites, starch, and other types of micro-debris in coprolites. Most recently, advances in molecular biology have enabled the search for steroids, blood typing, DNA, and microbes present in coprolites and analysis of the implications of each type of evidence to understanding the individuals who produced them. Currently, the analysis of groups of coprolites from specific regions of the American Southwest reveals ancient diets that were high in fiber, rich in food diversity, and relied on calories from plants containing insulin, not starch. Bryant and Reinhard (2012) demonstrate that these data are now being used to gain a better understanding of why certain Native American groups suffer high rates of obesity and type II diabetes when eating traditional Western diets, instead of the types of ancient diets eaten by their ancestors.

PROSPECTUS

Despite almost 200 years of work, the study of coprolites and related trace fossils is still in an early stage of development. Here, we suggest seven strategies for advancing the field:

First, we need to communicate to other geologists and paleontologists that coprolites are both common and potentially useful. We have talked to too many geologists who either didn't look for coprolites or dispose of them as useless oddities.

Second, the coprolite literature is replete with studies of a few unusual specimens (as "curiosities"). The description of complete coprolite ichnoassemblages will provide the necessary data for a broader understanding of their fossil record.

Third, the present is the key to the past, and more actualistic studies need to be conducted, from description of the morphology and preservation of feces to analyses of the comparative anatomy of digestive systems.

Fourth, more valid ichnotaxa must be named to create a useful and all-encompassing parataxonomy of coprolites (Table 1). The process of describing the ichnotaxa introduces rigor into their analysis, and the terminology provides the necessary ease of communication and comparison that will stimulate further analysis.

Fifth, the vast majority of work on bromalites is focused on coprolites and regurgitalites, whereas consumulites have been mainly overlooked and are in need of additional work.

Six, even though a relatively small number of coprolites have been described, it is clear that their distributions in time, space and paleoenvironments have proven utility in biochronology, biogeography and ichnofacies analysis. More documentation of the distribution of coprolite ichnotaxa and morphotypes will allow broader patterns to be recognized.

Seven, there are four principal strands of coprolite studies that rarely intersect – invertebrate coprolites, human coprolites, desiccated Pleistocene vertebrate coprolites of North America and pre-Pleistocene vertebrate coprolites. Currently, the bibliography of a given paper from four sub-fields virtually never includes references from one of the others. Cross-pollination can only stimulate research.

Eight, reviews of ichnofaunas routinely ignore coprolites that could provide useful taphonomic and paleoecological data and this should not be the case.

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