CLASSIFICATION OF VERTEBRATE COPROLITES AND RELATED TRACE FOSSILS

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Abstract—Buckland introduced the term coprolite for fossil excrement. During the last 50 years, an increasing number of workers have discussed the terminology of coprolites and associated trace fossils (e.g., gastro-intestinal tract infillings and regurgitated material), particularly with regard to spiral forms. More clarity and consistency is needed in the use of terminology for vertebrate trace fossils. Ichnofossils use a different terminology than modern animal traces, and several principles are 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. We 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), "consumolite" (fossilized food material preserved in, or partially in, the body cavity), "demalite" (skeletal material preserved within the body cavity of an animal that do not pertain to it), "cumulite" (fossil accumulation of organic or inorganic material concentrated by an organism), "gignolite" (trace fossils and body 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).

INTRODUCTION

William Buckland was the first to conduct scientific studies of fossil feces. He initially recognized selected trace fossils as representing fossil excrement (Buckland, 1822, 1824). Buckland subsequently coined the term coprolite for these traces (Buckland, 1829b), and he later introduced other terminology related to them (Buckland, 1835, 1836). Although his use of the term "coprolite" was somewhat inconsistent, it became widely used to refer to fossilized excreted matter. During the last 50 years, an increasing number of workers have discussed the terminology of coprolites and associated trace fossils (e.g., gastro-intestinal tract infillings and regurgitated material), particularly with regard to spiral forms (e.g., Amstutz, 1958; Zangerl and Richardson, 1963; Häntzschel et al., 1968; Williams, 1972; McAllister, 1985; Hunt, 1992; Hunt and Lucas, 2010). Indeed, this literature underscores the need for more clarity and consistency in the use of terminology for vertebrate trace fossils. That ichnofossils use a different terminology than modern animal traces is widely acknowledged (Bertling et al., 2006). The primary purpose of this paper is to review and refine the terminology applied to coprolites and related trace fossils.

ORIGINS OF CURRENT TERMINOLOGY

Coprolite and Related Terms (Urolite, Guano, Midden)

Coprolite

Descriptions and illustrations of trace fossils, now recognized as fossil feces, date back to 1699 (Duffin, 2009, 2012). William Buckland (1822, 1824) recognized trace fossils from a cave near Kirkdale, Yorkshire as representing the fossilized feces of an extinct hyena.

On February 6 and May 1, 1829, Buckland gave presentations on coprolites to the Geological Society of London. Six publications resulted from these talks. Buckland (1829a) is a three-page summary of the February 6 presentation, and Buckland (1829b-d) are nearly identical, two-page summaries of the May 1 talk. Buckland (1830) is a six-page synopsis of both talks. Buckland (1835) is explicitly a detailed exposition of the lecture of February 6, 1829.

Buckland (1829a) discussed the fossil feces of ichthyosaurs, but did not explicitly use the term "coprolite." Buckland (1829b, p. 143) later stated that "The author concludes that he has established generally the curious fact, that, in formations of all ages, from the carboniferous (sic) limestone to the diluvium, the faeces of terrestrial and aquatic carnivorous animals have been preserved; and proposes to include them all under the generic name of coprolite." Thus, Buckland (1829b) is the first published use of the term "coprolite." However, Buckland utilized the term in three different senses:

1. Evacuated fecal material—The majority of specimens that Buckland described and illustrated represent discrete fecal bodies unassociated with skeletons (e.g., Buckland, 1835, pls. 28–31).

2. Unevacuated material preserved within the gastro-intestinal tract—Buckland (1830, p. 23) noted that "in many of the entire skeletons of Ichthyosauri found in the lias [sic], compressed coprolites are seen within the ribs and near the pelvis." Further, he noted that "the certainty of the origin of these coprolites is established by their frequent presence in the abdominal region of fossil skeletons of Ichthyosauri found in the lias [sic] of Lyme Regis. One of the most remarkable of these is represented in Pl. 13" (Buckland, 1836, p. 149). Buckland (1836s, pl. 13 and 14) illustrated two skeletons of ichthyosaurs (OUM [Oxford University Museum of Natural History, Oxford, England] J.13587 and J. 13593) with dispersed, digested/partially digested material almost filling the extent of the rib cage in each case.

3. Infilled gastro-intestinal tract—Buckland (1829b, p. 142) introduced the term "Ichthyo-coprus" for coprolites preserved within the body cavity of a fish (later Ichthyocoprus: Buckland, 1835, p. 230). Subsequently, he named a variety of this form of coprolite as "Amia [sic]-coprus" (Buckland, 1830, p. 24) that clearly represents an infilled segment of a gastro-intestinal tract (see Duffin, 2009, fig. 14).

Buckland (1829a, 1830, 1835) further introduced several subcategories of coprolites:

***Album graecum*:** This is a term that was used by apothecaries to refer to dog feces that were especially rich in phosphate as a result of feeding a bone-rich diet to dogs (Duffin, 2009). Buckland (1822, 1824) applied this term to fossil hyena coprolites from Kirkdale Cave. Buckland

(1829a, p. 143) later applied "Hyaino-coprus" to "the Album Graecum of the fossil hyena" ("Hyaena-coprus" in Buckland, 1830, p. 24).

***Nigrum graecum*:** Buckland (1829a, p. 142) proposed this term for rounded, black, polished coprolites from the Rhaetic bone beds and basal Carboniferous limestone of the Bristol area. Later, he attributed the term to a Mr. Dillwyn (Buckland, 1835, p. 227).

***Ichthyo-coprus*:** Buckland (1829a, p. 142) proposed this name for "a fossil fish from the lias [sic], which has a ball of Nigrum Graecum within its body."

***Coprus iuloides*:** Buckland (1829a, p. 143) noted that "the supposed fir-cones or Iuli in the chalk and chalk marl…are also of faecal origin…for these the provisional name of Coprus iuloides is proposed." Subsequently, Buckland (1835, p. 234) used the term Iulo-eido-coprolites.

***Amia-coprus*:** Buckland (1830, p. 24) named "Amia [sic]-coprus" for a variety of Ichthyo-coprus found within the body of the bony fish *Amia lewesiensis* (Buckland, 1835, p. 234).

***Sauro-coprus*:** Buckland (1829a, p. 143) selected this name for the abundant coprolites from the Lias that he attributed to ichthyosaurs.

***Ornithocoprus*:** Buckland (1830, p. 26) noted that dung or guano of seabirds forms thick accumulations on the coast of Peru and he proposed the term "Ornitho-coprus" for these deposits.

El-Baz (1968, p. 526) suggested that the term "coprolites should be restricted to fossilized fecal remains of vertebrates (between 1 mm and 20 cm). Invertebrate fecal remains (usually smaller than 1 mm) may be called fecal pellets, and where petrified, fossil fecal pellets." Hunt and Lucas (2010) noted that pelletized, digested material may be preserved both inside and outside the body cavity. They suggested the terms "incorporeal" and "excorporeal coprolites" for these two situations (Hunt and Lucas, 2010, p. 219).

Urolite

Duvernoy (1844) introduced the term "urolite" to differentiate the fossil, nonliquid urinary secretions produced by some groups of reptiles from coprolites. Leydig (1896a,b) and Voigt (1960) identified urolites from the Triassic and Cretaceous, respectively, which were three-dimensional objects.

Fernandes et al. (2004, p. 266) utilized the term in a different context: "we think this term (compound of two Greek words, *uro* meaning 'urine' and *lithos* meaning 'stone') is the most appropriate to determine the trace fossil formed by evacuation of liquid waste of a dinosaur or any other vertebrate." In this usage, "urolite" refers to a depression in the sediment putatively created by liquid urine, but not the remains of the urine itself, as in Duvernoy's usage.

A third use of the term "urolite" (or "urolith") is for urinary calculi of Recent animals (e.g., dogs, humans). Urinary calculi are solid particles that form in the urinary tract that are principally, although not exclusively, composed of calcium oxalate.

Guano

"Guano" originates from the Quechua word "wanu" (dung) and was first used for accumulations of sea bird excrement on Peruvian islands and coastal areas that became an important source of nitrates for fertilizer and gunpowder in the 19th century. The term has also been applied to similar deposits produced by seals and bats. El Baz (1968, p. 526) suggested that the "accumulation of petrified fecal excrements of birds may be referred to as guano deposit or fossil guano."

Midden

The term "midden" is widely used in archeology for an accumulation of debris related to human activity (e.g., shell middens). In biology, "midden" has a variety of usages for accumulations of organic material. Packrats (*Neotoma* spp.) have complex living areas that include middens. A midden is the primary area where the rodent excretes, and a place where unused plant fragments accumulate (Dial and Czaplewski, 1990; Tweet et al., 2012). Other mammals in North America (e.g., porcupine [*Erethizon*], marmot [*Marmota*], ring-tailed cat [*Bassariscus*]), Africa (e.g., hyraxes [Procaviidae], dassie rat [Petromuridae]), and Australia (e.g., stick-nest rat [*Leporillus*]) also construct middens that can be distinguished on the basis of morphology, size, and content (Fall et al., 1990; Finley, 1990; Nelson et al., 1990; Scott, 1990). Packrat middens are the most common and most studied, and they can be distinguished from others by several characteristics, including the presence of rat-sized, non-woody fecal pellets; dark, heavy urine stains or deposits; an abundance of sticks and other plant materials; bones; and gnaw marks on plants and bones consistent with the dimensions of rat incisors (Finley, 1990). Most, but not all, fossil packrat middens are indurated by crystallized packrat urine (amberat), though some are unindurated (Spaulding et al., 1990). Finley (1990, p. 28) proposed the term "paleomidden" to refer to a "fossil midden that has persisted long enough to survive environmental changes, but has not necessarily been altered over time."

Cololite and Related Terms (Enterolite, Enterospira, Gastrolite)

Cololite

Agassiz (1833, p. 676) introduced the term cololite as a corollary to coprolite to refer to the fossilized "more or less stuffed intestines of fish." He used the term in relation to both infilled intestines preserved within a body cavity and also those preserved in isolation (not associated with a body cavity).

Lumbricaria is a an enigmatic ichnotaxon that has the morphology of an elongate, convoluted, cylindrical trace fossil and is one of the most common fossils in the Upper Jurassic Solnhofen Limestone of Germany (Münster, 1831; Muller, 1969; Janicke, 1970; Barthel et al., 1990). *Lumbricaria* is not found associated with fish bodies, but "M. Agassiz has ingeniously explained this fact by observing the process of decomposition of dead fishes in the lakes of Switzerland. The dead fish floats on the surface with its belly upwards, until the abdomen is so distended with putrid gas, that it bursts: through the aperture thus formed the bowels come forth into the water, still adhering together in their natural state of convolution" (Buckland, 1835, p. 156). Thus, Agassiz (1833) considered *Lumbricaria* as an example of a cololites preserved in isolation from a carcass. Note that *Lumbricaria* is now thought to probably represent the coprolites of cephalopods (Janicke, 1970). This new attribution of the trace fossil, though, in no way invalidates the concept of a cololite as introduced by Agassiz, and the term continues to be used to refer to fossilized contents of the gastro-intestinal tract (e.g., Hunt, 1992).

Enterolite

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 but that he interpreted to represent infilled, spiral-valved intestines. Hoernes (1904) considered that the majority of the spiral "coprolites" from the Lias that were featured in Buckland's early work were actually the enterolites of ichthyosaurs. Previously, Fritsch (1895) and Neumayer (1904) had concluded that some "coprolites" represented fossilized valvular intestines, but they did not create new terms for them. Thus, an enterolite is a subcategory of cololite, specifically one that originates from a spiral valve.

Enterospirae

Fritsch (1907) suggested the name "enterospirae" for trace fossils that do not represent the "excrements of fishes…But the entire spiral-valved intestines filled with fecal matter." Thus, the term "enterospirae" is a synonym of "enterolite."

Gastrolite

Northwood (2005, p. 51) introduced the term "gastrolite" for "fossilized stomach contents (a new term to distinguish stomach contents from intestinal contents)." This term should not be confused with "gastrolith," which refers to stones and other objects swallowed by vertebrates.

Usage of terms

One key idea that has been discussed at length during the last 40 years is whether a portion of the infilled digestive tract could be preserved separately from a skeleton and might be misidentified as a coprolite or a pseudofossil (Williams, 1972; Broughton et al., 1977; Broughton, 1981; Jain, 1983; McAllister, 1988, 1996, 2003; Spencer, 1993; Seilacher et al., 2001). Williams (1972) resurrected the early idea (Hoernes, 1904; Fritsch, 1907) that some spiral "coprolites," notably heteropolar ones, are fossilized intestinal fills, for which he utilized Fritsch's term "enterospirae." This concept was accepted by some researchers (Stewart, 1978; Jain, 1983). Subsequently, McAllister (1988) convincingly argued that the specimens described by Williams (1972) and Stewart (1978) were, in fact, evacuated materials and therefore coprolites.

Seilacher et al. (2001) discussed the origin of trace fossils from the Permian of China, the Cretaceous of Canada and Madagascar, and the Miocene of the United States that had often been variously been interpreted as coprolites, pseudofossils, or casts of internal organs (Amstutz, 1958; Broughton et al., 1977; Broughton, 1981; Schmitz and Benda, 1991; Spencer, 1993; Mustoe, 2000). They convincingly argued that they are both ichnofossils and cololites. Seilacher et al. (2001, p. 11) discussed the classification of these cololites: "Intuitively one would consider them body fossils; but on the other hand cololites refer to a process shared by many tetrapods (and to a particular preservational situation), rather than a distinctive and static anatomical feature." McAllister (2003) supported the trace fossil option.

The terms "enterospirae" and "cololite" have been frequently used by paleontologists studying fossil fishes during the last 40 years (e.g., Williams, 1972; Broughton et al., 1977; Broughton, 1981; Jain, 1983; McAllister, 1985, 1988, 1996, 2003; Hunt, 1992; Spencer, 1993; Seilacher et al., 2001). In contrast, the slightly older name "enterolite" was listed in several papers that discussed terminology (e.g., Amstutz, 1968; Thulborn, 1991), but was rarely, if ever, used. However, during the last decade, several paleontologists have used the term "enterolite" with regard to traces associated with fossils of sauropodomorph dinosaurs—essentially, fossilized, *in situ* stomach contents (e.g., Barrett, 2000; Salgardo et al., 2004; Prasad et al., 2005; Barrett and Upchurch, 2005; Barrett and Rayfield, 2006; Chure et al., 2010). Many authors have also used less precise descriptions or terms from Recent biology to refer to infillings of the gastro-intestinal tract, such as "gastric contents" (e. g., Lomax, 2010), "gut contents" (e.g., Kear et al., 2003; Kear, 2006), or "gastric mass" (Pollard, 1968).

Bromalite and Related Higher Level Terms (Coprolitic Matter, Digestichnia)

Bromalite

Hunt (1992, p. 221) proposed "the term bromalite from the Greek broma, food, to apply to anally or orally derived ejecta and in-situ intestinal matter. Within bromalites, there are three main subdivisions: coprolites, cololites and regurgitalites."

Coprolitic Matter and Coprolite

McAllister (1985, 1996) proposed and subsequently used the term "coprolitic matter" to include coprolites, cololites, and vomit balls (and the subcategories of ejecta and gastric residue). Vallon (2012) considered cololites to constitute a subcategory of coprolites.

Digestichnia

Vallon (2012) revised an earlier term, proposed by Vialov (1972), and introduced the "class Digestichnia….to include all trace fossils (and Recent equivalents) produced by digestive process, which are two out of three types of gastroliths (geo- and pathogastroliths *sensu* Wings, 2004, 2007), regurgitalites and coprolites/feces."

Usage of terms

"Bromalite" has proved to be a useful category, and it has been increasingly used in the last few years (e.g., Mikulás, 1995; Steiner and Fatka, 1996; Rodriguez-de la Rosa et al., 1998; Verde, 2003; McHenry et al., 2005; Northwood, 2005; Aldridge et al., 2006; Rivera-Sylva et al., 2006; Ebbestad and Stott, 2008; Zhang and Pratt, 2008; Reboulet and Rard, 2008; Liu et al., 2009; Myhrvold, 2011; Vincent, 2011).

Gastrolith and Related Terms (Exolith)

Wieland (1906) first utilized the term "gastrolith" to apply to swallowed stones in fossil and Recent vertebrates (Wings, 2007). Wings (2007, p. 2) broadened the concept to be "a hard object of no calorific value (e.g., a stone, natural or pathological concretion) which is, or was, retained in the digestive tract of an animal." He proposed three categories of gastroliths: (1) bio-gastroliths, for non-pathologic invertebrate concretions: (2) patho-gastroliths, for pathological stones formed in the stomach; and (3) geo-gastroliths, for swallowed sediment particles. He also introduced the term "exolith" for "an exotic rock in fine-grained sediments which may show a high polish and which potentially (but not necessarily) was a former gastrolith (Wings, 2007, p. 5)." Bio-gastroliths are not relevant to this paper because they relate to invertebrates and they are arguably not trace fossils (Vallon, 2012). We believe that these are all logical, useful, descriptive terms, and they will not be discussed further.

Regurgitalite and Related Terms (Ejecta, Vomit Balls, Gastric Residue, Vomite, Emetolite)

Ejecta, Vomit Balls and Gastric Residue

Götzinger and Becker (1932) first used the term Speiballen (vomit balls) with regard to paleontological specimens of regurgitations, and this term has had limited usage (e.g., Duffin, 1983). Zangerl and Richardson (1963) used a more precise terminology and distinguished between ejected prey and gastric residues depending on the degree of processing in the digestive tract. "Ejected prey" are regurgitated materials that had been subject to mastication and minor digestion. "Gastric residues" are the results of more extensive digestion. McAllister (1985) proposed a hierarchy of terms: regurgitations were termed "vomit balls," which were divided into the subcategories of ejecta, equivalent to Zangerl and Richardson's (1963) "ejected prey," and "gastric residues," used in the sense of Zangerl and Richardson (1963). Subsequently, McAllister (1996, 2003) used this classification. Duffin (1998) utilized the term "oral ejecta." There is some usage in the German literature of the term Frassreste (food remains), for example by Keller (1977).

Vomite

Wood (1980, p. 112) introduced the term "vomite," apparently facetiously, for "paleo-regurgitate, or petrified puke."

Regurgitalite

Hunt (1992, p. 223) proposed the term "regurgitalite" as "consonant with coprolite and cololite, to refer to regurgitated material."

Emetolite

Myhrvold (2011, p. 6) proposed the new term "emetolite" to

"connote a fossil of a gastric pellet egested by an animal that habitually egested such pellets" and restricted "regurgitalite" to "fossilized oral emissions." Thus, emetolites were conceived as a subset of regurgitalites that would also include "items that were ingested, chewed or otherwise orally processed but then quickly regurgitated" (i.e., "ejecta" *sensu* McAllister, 1985) (Myhrvold, 2011, p. 6).

Regurgitalith

Bertling et al. (2006) used the term "regurgitalith," but they did not intend to introduce a new term; rather, it was an orthographic lapse from "regurgitalite" (M. Bertling, written, commun., 2012).

Usage of terms

The only term of those discussed here that has been widely recognized is "regurgitalite." This term has been used with regard to invertebrates (Donovan and Pickerill, 1995) and several groups of vertebrates (e.g., Meng and Wyss, 1997), and in studies in North America (Rodríguez-de la Rosa et al., 1998), Europe (Geister, 1998), Africa (Aldridge et al., 2006), and Asia (Gong et al., 2010).

PROPOSED TERMINOLOGY OF COPROLITES AND OTHER VERTEBRATE ICHNOFOSSILS

Principles

We propose a comprehensive and hierarchical terminology for vertebrate coprolites and related trace fossils (Fig. 1, Table 1). We believe that the following principles are important in assessing the nomenclature of vertebrate trace fossils: (1) ichnofossils should have a terminology distinct from Recent traces - the International Code of Zoological Nomenclature distinguishes between fossil and Recent traces, for example, by only allowing (Article 1.2.1) new binomials to be applied to fossil traces (Bertling et al., 2006); (2) priority of terminology is important; (3) stability of nomenclature should be maintained; (4) universality of usage should be considered in the choice of usage of terms; (5) if possible there should be consistency in etymology and usage (e.g., the suffix *-lite* is preferable to *-lith*); and (6) the terminology should have practical utility. We realize that some will resist using some of the terms proposed here because of ingrained usage (e.g., new terms for fossil guano and *Neotoma* middens), but we believe that it is important to have a comprehensive and internally consistent hierarchy of terminology for ichnofossils for consistency and ease of communication.

Higher-Level Terms

Proposed terms

Bromalite (*sensu* Hunt, 1992)—All trace fossils that represent food items that have entered the oral cavity or gastrointestinal tract of an animal and have been expelled (either orally or rectally and either pre- or post-mortem) from or retained within them.

Rationale: The varieties of bromalites are often difficult to distinguish (e.g., regurgitalites and coprolites), and it is useful to have a term to encompass all of them. "Bromalite" has been relatively widely used since its proposal.

Terms of limited utility

Digestichnia encompasses bromalites plus gastroliths and is proposed as a term consistent with the higher categories of ichnofossils first proposed by Seilacher (e.g., repichnia, domichnia). These terms have not been widely used by vertebrate paleontologists, so we consider that digestichnia has limited practical application. Thus, for example, gastroliths are distinct from other bromalites, so a term to encompass all of them may have hypothetical taxonomic value but is of limited descriptive utility.

Rejected terms

"Coprolite" and "coprolitic material" are rejected as synonyms or partial synonyms of bromalite because their usages are contrary to the original intent of Buckland and are at odds with almost two centuries of usage.

Coprolites and Related Terms

Proposed terms

Coprolite (Buckland, 1829b)—Fossil fecal material that has been ejected from the posterior end of the gastrointestinal tract.

Urolite (*sensu* Duvernoy, 1844)—Fossil nonliquid urinary secretions.

Saccatalite (from the Latin *saccatum*—urine)—Fossil accumulation of dried liquid urine.

Micturalite (from the Latin *micturio*—urinate)—Trace fossil produced by interaction between liquid urine and substrate.

Latrinite (from the Latin *latrina*—toilet)—An accumulation of coprolites.

Accretionary latrinite—Latrinite that results from accumulation due to physical, rather than biological, processes.

Ethological latrinite—Latrinite that results from behavior of an organism.

Guanolite (from Quechua *wanu*—dung)—Fossil guano deposits.

Ornithoguanolite (from Greek *ornithos*—bird)—Guanolite produced by birds.

Pinnipedaguanolite—Guanolite produced by pinnipeds.

Chiropteraguanolite—Guanolite produced by bats.

Cumulite (from Latin *cumulus*—heap)—Accumulation of organic or inorganic material concentrated by an organism.

Paleomidden—Fossil mammalian midden.

Neotomalite—Fossil packrat midden.

Postilite—Fossil site used repeatedly by an organism for defecation or urination for marking territory.

Pelletite—Fossil fecal pellets preserved inside (incorporeal pelletite) or outside (excorporeal pelletite) the body cavity. An excorporeal pelletite is a coprolite.

Rationale

We propose restricting "coprolite" to Buckland's (1829b, p. 143) usage as the feces of terrestrial and aquatic animals because this has been its nearly universal usage, even though Buckland himself used the term loosely and also applied it to material preserved within the gastrointestinal tract. We restrict "urolite" to Duvernoy's (1844) original usage as fossil, nonliquid urinary secretions produced by some groups of reptiles, and introduce the term "micturalite" for trace fossils produced by the interaction between liquid urine and the substrate (e. g., "urolite" *sensu* Fernandes et al., 2004). "Saccatalite" is a new term for fossil accumulations of liquid urine, as, for example, are frequently found in the vicinity of *Neotoma* dens (e.g., Finley, 1990). We expect that most saccalites will be identified in the Pleistocene.

There is clearly a need for terms to apply to accumulations of coprolites, for which we propose "latrinite," and we recognize "accretionary latrinite" (e.g., Diedrich, 2012) for those that result from accumulation due to physical, rather than biological, processes and "ethological latrinite" (e.g., Hunt et al., 2012, fig. 2F) for those that result from behavior of an organism. Note that the term coprocoenosis was proposed by Mellet (1974) to refer to assemblages of small bones that had passed through the digestive tracts of carnivores and not to an accumulation of coprolites *per se*. "Guanolite" is proposed for fossil guano deposits; subcategories are, and can be, named for guanolites of specific groups of organisms, such as "ornithoguanolite" (avian guanolite), "pinnipedaguanolite" (pinniped guanolite) and "chiropteraguanolite" (bat

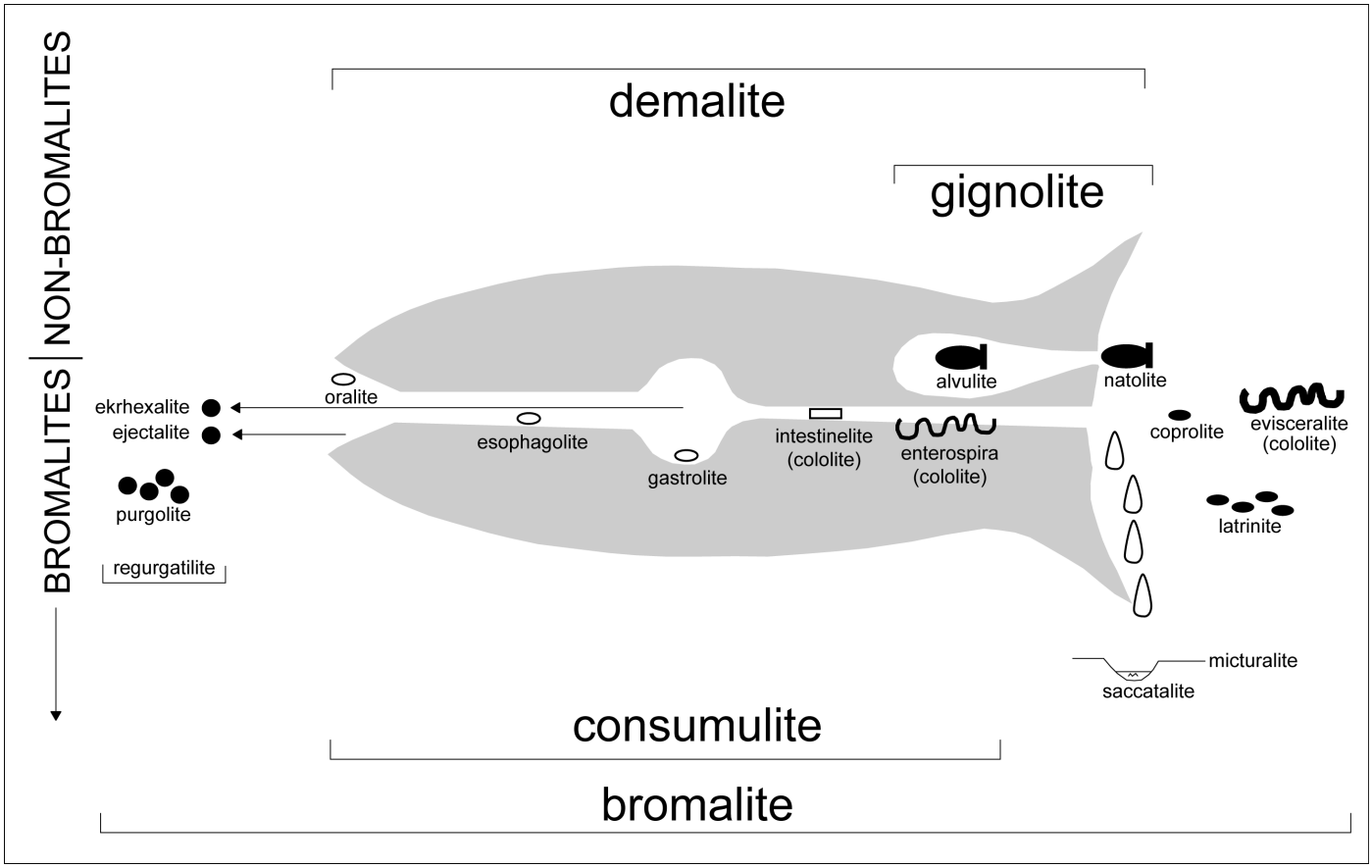

FIGURE 1. Selected classification terms for bromalites, gignolites, and associated trace fossils.

guanolite) (Table 1). Hunt et al. (2012) recognize chiropteraguanolites and an ornithoguanolite within the National Park Service properties in the USA.

"Midden" is a widely used term in archeology (and biology) to apply to concentrations of organic or/and inorganic material, regardless of the type of organism that made it. We propose the term "cumulite" as a paleontological equivalent. Use of this term should help provide clarity about accumulations of material in the geological record that may have been produced by organisms. Cumulites could include a variety of objects, from beaver dams to food caches. The term "midden" has a particular meaning with regard to small mammals (Betancourt et al., 1990), and Finley's (1990) term "paleomidden" is used in this context. The most studied paleomiddens are those produced by *Neotoma* spp., which we place in the subcategory "neotomalites." Neotomalites can be distinguished by a variety of features including "size, shape, and non-woody composition of fecal pellets; heavy urine stains or deposits (usually brown or black and hard, smooth, or glossy); presence of many sticks, bones, cactus joints, or other extraneous articles along with intermixed plant cuttings; and tooth marks or materials gnawed by teeth of the right 'rat size'" (Finley, 1990, p. 29).

Hunt and Lucas (2010) suggested that pelletized and digested food material preserved inside the body cavity should be termed "incorporeal (as opposed to "excorporeal) coprolites." We suggest the term "pelletite" for fossil fecal pellets preserved inside or outside the body cavity—incorporeal pelletites would be preserved within the body cavity, differing from intestenilites in that they represent small discrete bodies of feces rather than an infilling of a segment of the intestines. Excorporeal pelletites are coprolites. This terminology is useful because pelletites are often preserved near the anus/cloaca, some because of postmortem evacuation after death, and it can be difficult to pinpoint their exact locations as inside or outside the body (e.g., Rinehart et al., 2009).

Some authors have suggested that accumulations of coprolites represent markings at the edges of territories. We used the term "postilite" (analogous to Recent post) for a site used repeatedly by an organism for defecation or urination for marking territory (e.g., Diedrich, 2012).

Rejected terms

Hunt and Lucas's (2010) terms "incorporeal- and "excorporeal coprolites" are rejected and we propose the replacement terms incorporeal- and excorporeal pelletites. The modern term "dung" has been used in reference to many late Pleistocene coprolites in western North America (e.g., Mead and Swift, 2012).

Bromalites Preserved Within the Body Cavity

Proposed terms

Consumulite (from the Latin *consumo*—consume)—All fossilized ingested food material preserved within the body cavity.

Oralite (from the Latin *oris*—mouth)—Fossilized food material preserved wholly or partially within the oral cavity.

Gastrolite (*sensu* Northwood, 2005)—Fossilized wholly or partially digested food material preserved in the stomach.

Cololite (*sensu* Agassiz, 1833)—Fossilized digested food material preserved in the gastrointestinal tract posterior to the stomach.

Intestinelite (from the Latin *intestinum*—guts)—Cololite preserved within the body cavity.

Evisceralite (from the Latin *eviscerare*—remove internal organs)—Cololite that is a preserved segment of infilled fossilized intestines preserved independently of (exterior to) a carcass.

Esophogalite (from Greek *esophagus*—gullet)—Fossilized digested food material preserved in the gastrointestinal tract anterior to the stomach.

TABLE 1. Synoptic list of classification terms for vertebrate bromalites (coprolites and associated trace fossils).

First order term	Second order term	Third order term	Fourth order term	Definition	Trace fossil or other	Author
Bromalite				All trace fossils that represent food items that have entered the oral cavity or gastrointestinal tract and have been expelled or retained within them	Trace	Hunt (1992)
	Coprolite			Fossilized fecal material that has been ejected from the posterior end of the gastrointestinal tract	Trace	Buckland (1829b)
	Urolite			Fossilized nonliquid urinary secretions	Trace	Duvernoy (1844)
	Saccatalite			Accumulation of fossilized dried liquid urine	Trace	This paper
	Micturalite			Trace fossil produced by interaction between liquid urine and substrate.	Trace	This paper
	Pelletite			Pelletized fossilized fecal material	Trace	This paper
		Incorporeal pelletite		Pelletite preserved within the body cavity	Trace	This paper
		Excorporeal pelletite		Pelletite preserved outside the body cavity	Trace	This paper
	Latrinite			Accumulation of coprolites	Trace or other	This paper
		Accretionary latrinite		Latrinite that results from accumulation due to physical processes.	Other	This paper
		Ethological latrinite		Latrinite that results from behavior of organism	Trace	This paper
		Guanolite		Fossilized guano deposits	Trace	This paper
			Ornithoguanolite	Guanolite produced by birds	Trace	This paper
			Pinnipediteguanolite	Guanolite produced by marine mammals	Trace	This paper
			Chiropteraguanolite	Guanolite produced by bats	Trace	This paper
		Paleomidden		Fossilized mammalian midden	Trace	Finley (1990)
			Neotomalite	Fossilized packrat midden	Trace	This paper
		Postilite		Fossil site used repeatedly by an organism for defecation or urination	Trace	This paper
	Consumulite			All ingested fossilized food material preserved within the body cavity	Trace	This paper
		Oralite		Fossilized food material preserved in, or partially in, the oral cavity	Trace	This paper
		Esophagolite		Fossilized digested food material preserved in the gastrointestinal tract anterior to the stomach	Trace	This paper
		Gastrolite		Digested, or partially digested, fossilized food material preserved in the stomach	Trace	Northwood (2005)
		Cololite		Fossilized digested food material preserved in the gastrointestinal tract posterior to the stomach.	Trace	Agassiz (1833)
			Intestinelite	Cololite preserved within the body cavity	Trace	This paper
			Evisceralite	Cololite which is a preserved segment of infilled fossilized intestines preserved independently of (exterior to) a carcass	Trace	This paper
			Enterospira	Cololite preserved in a spiral valve	Trace	Fritsch (1907)
	Regurgitalite			All manipulated or digested/partially digested fossilized food material egested from the oral cavity	Trace	Hunt (1992)
		Ornithoregurgitalite		Regurgitalite produced by bird	Trace	This paper
			Strigilite	Fossilized owl pellets	Trace	This paper
		Ejectalite		Regurgitalite that has been manipulated in the mouth or undergone partial digestion (e.g., deriving from oral cavity or anterior gastrointestinal tract).	Trace	This paper
		Ekrhexalite		Regurgitalite that derives from the stomach	Trace	This paper
	Purgolite			Accumulation of regurgitalites	Trace or other	This paper
		Accretionary purgolite		Purgolite that results from accumulation due to physical processes.	Other	This paper
		Ethological purgolite		Purgolite that results from behavior of organism	Trace	This paper
Demalite				Skeletal material preserved with the body cavity of an animal that do not pertain to it		This paper
	Embryolite			Fossilized embryo	Trace	This paper
		Alvulite		Embryolite preserved within the reproductive tract	Trace	This paper
		Natolite		Embryolite preserved during the birth process	Trace	This paper
Cumulite				Fossilized accumulation of organic or inorganic material concentrated by an organism	Trace	This paper
Gignolite				Trace and body fossils related to reproduction	Trace and other	This paper
Gastrolith				A hard object of no calorific value (e.g., a stone, natural or pathological concretion) which is, or was, retained in the digestive tract of an animal	Trace	Wieland (1906)
	Patho-gastrolith			Pathological stones formed in the stomach	Trace	Wings (2007)
	Geo-gastroliths			Swallowed sediment particles	Trace	Wings (2007)

Enterospira (*sensu* Fritsch, 1907)—Cololite preserved in a spiral valve.

Incorporeal pelletite—Pelletite preserved within the body cavity.

Rationale

This is the category of ichnofossils related to coprolites with the most confused usage. The new term "consumulite" is proposed for all consumed material preserved within the body cavity, whether in the oral cavity or gastrointestinal tract (Table 1). This term has practical utility because determining exactly the location of a mass of digested material within the gastrointestinal tract can often be difficult. "Cololite" has experienced a variety of usages, but it was originally proposed by Agassiz (1833) to apply to intestinal infillings, so we restrict its use to this type of ichnofossil (e.g., Seilacher et al., 2001). "Esophagolite" is a new term for material preserved anterior to the stomach but posterior to the oral cavity, and "oralite" is a new term for material preserved within the oral cavity. We use Northwood's (2005) term "gastrolite," despite its similarity to "gastrolith," for material preserved in the stomach. The term "intestinelite" is introduced to refer to digested food material preserved in the gastrointestinal tract posterior to the stomach. An "evisceralite" is a cololite preserved in the absence of a body cavity. Hoernes' (1904) term "enterolite" has clear precedence over Fritsch's (1907) "enterospirae" for infillings of spiral valves, but, as reviewed above, the latter has been extensively used, whereas the former has only recently been resurrected as a synonym of "gastrolite" (as recognized here). Therefore, we use "enterospira" for a cololite that formed as the infilling of a spiral valve.

Rejected terms

A variety of authors have used imprecise terms, such as "gastric contents," "gut contents," or "gastric mass" for these trace fossils (e.g., Pollard, 1968; Kear, 2006; Lomax, 2010). "Consumulite" is a general term, and more specific terms can be used in cases for which there is anatomical certainty about the location in the body of the trace fossil.

Regurgitated Material

Proposed terms

Regurgitalite—Trace fossil that includes all manipulated or digested/partially digested food material egested via the oral cavity.

Ejectalite (from the Latin *ejectus*—expel)—Regurgitalite that has been manipulated in the mouth or undergone partial digestion (e.g., deriving from oral cavity or gastrointestinal tract anterior to the stomach).

Ekrhexalite (from Greek *ekrhexis*—violent discharge)—Regurgitalite that derives from the stomach.

Ornithoregurgitalite (from the Greek *ornis*—bird)—Regurgitalite produced by bird.

Strigilite (from the Greek *strix*, *strigos*—owl)—Fossil owl pellets.

Purgolite (from the Latin *purgo*—expel)—Accumulation of regurgitalites.

Accretionary purgolite—Purgolite that results from accumulation due to physical, rather than biological, processes.

Ethological purgolite—Purgolite that results from behavior of an organism.

Rationale

The term "regurgitalite" has been widely recognized and is used to include all material that is egested via the oral cavity but that may derive from the stomach or the anterior gastrointestinal tract. This includes "ejectalites" ("ejected prey"/"ejecta" of earlier authors; Zangerl and Richardson, 1963; McAllister, 1985), which have been manipulated in the mouth or undergone partial digestion (e.g., derived from the mouth or anterior gastrointestinal tract) and "ekrhexalites" that derive from the stomach (gastric residues of earlier authors; Zangerl and Richardson, 1963; McAllister, 1985) and exhibit more complete digestion.

The most common Recent regurgitations are those of birds, and we propose "ornithoregurgitalites" for regurgitalites of avian origin. As with other terms defined herein, subcategories of ornithoregurgitalites can be defined based on the fossil-making taxon. Most Recent pellets pertain to owls, and their fossil equivalents are therefore "strigilites" (e.g., Andrews, 1990). Accumulations of regurgitalites (e.g., Czaplewski, 2011) are here termed "purgolites." We recognize two kinds of purgolites: (1) "accretionary purgolites" (not trace fossils), which are accumulations of owl pellets at slope breaks that result from gravity-induced transport or hydrodynamic factors (e. g., Lucas et al., 2012); and (2) "ethological purgolites" (trace fossils), which encompass fossil examples homologous with Recent owl pellets that often accumulate directly below perches in caves or trees, because they accumulate from the behavior of an organism.

Terms of limited utility

An "emetolite" is "a gastric pellet egested by an animal that habitually egested such pellets" (Myhrvold, 2011, p. 6) and is a subset of regurgitalite. This would be an appropriate term in some cases (e.g., strigilites), but it would be unclear in most cases if a regurgitalite were a result of egestion as a result of habitual behavior or because of ingestion of inappropriate or contaminated prey.

Rejected terms

"Vomit balls," "ejecta," and "gastric residue" are not used because they are imprecise and not purely paleontological. "Regurgitalith" is rejected because of very limited usage. "Vomite" is rejected because (1) there was no usage subsequent to its proposal; (2) it was not introduced in a scientific context; and (3) its etymology is inconsistent with other terms.

Ichnofossils and Body Fossils Preserved Within the Body Cavity, Including Those Related to Reproduction

Skeletal material preserved/apparently preserved within the body cavity of a fossil animal could have several origins: (1) apparent preservation as the result of stacked carcasses with parts of one skeleton seeming to be within the body outline of a superposed specimen, as has been proposed for specimens of the Triassic dinosaur *Coelophysis* from the Whitaker Quarry at Ghost Ranch, New Mexico (Rinehart et al., 2009); (2) ingested prey; (3) an embryo; or (4) postmortem utilization of the carcass (e.g., shed carnivore teeth, refugium). There are numerous examples of juvenile ichthyosaur skeletons preserved within adult ones, and there has long been a debate as to whether they represent embryos or the results of acts of cannibalism (e.g., McGowan, 1991). We propose the term "demalite" (from the Greek *demas*—body) for skeletal material preserved within the body cavity of a vertebrate or invertebrate animal that do not pertain to it. Subsequent study may show that the demalite is an artifact, a bromalite, or a gignolite (a new term to include both trace and body fossils related to reproduction; from the Greek *gigno*—to give birth). Gignolites include fossil embryos ("embryolites"), which may be preserved within the reproductive tract ("alvulites," from the Latin *alvus*—womb) or during the birth process ("natalites," from the Latin *natus*—birth). The most well known putative natalites are associated with ichthyosaurs from Holzmaden, Germany. It is likely that these specimens represent embryos that were expelled after the death of the mother as a result of the pressure of gases associated with decay (Scott and Green, 1975; McGowan, 1991).

CONCLUSIONS

Vertebrate ichnology has generally lacked a precise and consistent terminology. We have presented a comprehensive review of the classification of bromalites and related trace fossils. However, there is a need for commensurate re-evaluations of the terminology applied to other vertebrate ichnofossils. Terms such as tracks, footprints, tooth marks and nests are regularly utilized by vertebrate ichnologists but these are imprecise and usually undefined, so we would argue that their continued use ultimately hinders the development of the study of vertebrate trace fossils.

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