Paleoecological and taphonomical aspects of the Late Miocene vertebrate coprolites (Urumaco Formation) of Venezuela

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ABSTRACT

Coprolites (fossil feces) provide important paleoecological information, such as diet of the producer, parasite infestation and gut microbiota, which cannot be accessed through body remains. The Upper Miocene Urumaco Formation, in western Venezuela, has a diverse vertebrate fauna composed of ground sloths, rodents, reptiles, fishes and amphibians, as well as coprolites. Here we describe 106 coprolites produced by a range of carnivorous and herbivorous vertebrates, classified into five different morphotypes based on their size and shape, suggesting different producers. Herbivorous morphotypes (M1, M2 and M5) are the most abundant (59%). The most common inclusions in these coprolites are Poaceae remains, although Eudicotyledoneae fragments, bacteria and cyanobacteria filaments were also found. The M1 morphotype has a bullet shape with longitudinal grooves; the M2 morphotype is rounded to oval, with at least one distinctive tapered end; and the M5 morphotype is a short cylinder with a rough surface, and rounded ends. In contrast, the morphotypes M3 and M4 are attributed by us to carnivores and have different inclusions. While M3 is a large cylinder with rounded ends and contains bacteria, nematode eggs and phytoliths, M4 is sausage-shaped and has muscle cells preserved inside. Based on the co-occurring fauna and the morphology of the coprolites, the probable producers were inferred as the following: M1, a rodent; M2, a notoungulate; M3, a crocodilian; M4, an indeterminate carnivore; and M5, a sirenian. The preservation of herbivorous and carnivorous coprolites with bacterial, parasitological and muscle remains in the same formation and even the same outcrop is rare in the geological record. This unique association and preservation suggests early lithification promoted by rapid burial, although the presence of the boring trace Gastrochaenolites in a single specimen indicates some degree of time-averaging.

1. Introduction

Since the early 19th century, when coprolites were first described by Buckland (1829), the paleoecological significance of fossil feces has been made evident. Nevertheless, throughout the intervening 150 years, coprolites have remained poorly studied. In the last few decades, however, coprolites started to attract paleontological attention due to the unique microenvironment formed inside them that enhances the fossilization potential of soft tissues, while also preserving paleoecological interactions that would otherwise go unrecognized (e.g. Qvarnström et al., 2016). Evidence of ecological phenomena, such as interactions between secondary and primary consumers (e.g. Chin et al., 2003; Eriksson et al., 2011; Nakajima and Izumi, 2014; Zatoń and Rakociński, 2014; Zatoń et al., 2015; O'goghain et al., 2016), herbivory (e.g. Scott, 1977; Chin, 2007; Hagström and Mehlqvist, 2012; Bajdek

et al., 2014), detritivory (Falcon-Lang et al., 2015), parasitism (e.g. Fugassa et al., 2006; Poinar and Boucot, 2006; Dentzien-Dias et al., 2013; Wood et al., 2013; Da Silva et al., 2014; Hugot et al., 2014; Zatoń and Rakociński, 2014; Bajdek et al., 2016) and symbiosis (e.g. Chin, 2007; Santiago-Rodriguez et al., 2013; Bajdek et al., 2016; Dentzien-Dias et al., 2017) has led ichnologists to consider coprolites as Konservat-Lagerstätten (Seilacher et al., 2001; Qvarnström et al., 2016).

However, the majority of vertebrate coprolites in the fossil record were produced by carnivores rather than herbivores (see, for example, Chin, 2002; Chin et al., 2003, Northwood, 2005; Chin, 2007; Dentzien-Dias et al., 2012; Bajdek et al., 2015; Niedźwiedzki et al., 2016; Bravo-Cuevas et al., 2017). This might happen because herbivorous feces are composed of a large quantity of undigested food attracting a wide variety of scavengers (Chin et al., 2009) and/or because the dietary composition influenced their preservation. The carnivore feces are poor

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in nutrients (attracting fewer scavengers), being decomposed mainly by microbials, and the calcium phosphate derived from bone digestion acts as a permineralizing agent (Hunt et al., 1994; Chin, 2002; Hollocher and Hollocher, 2012; Dentzien-Dias et al., 2017; Rodrigues et al., 2018), facilitating the preservation.

In some cases, the morphology of the coprolite can indicate the producer, as, for example, spiral coprolites are often attributed to non-teleost fishes (Williams, 1972; Jain, 1983; McAllister, 1985; Souto, 2008; Dentzien-Dias et al., 2012; Niedźwiedzki et al., 2016). However, feces from different groups of animals can be similar in appearance, and variations can occur within the morphology of feces among a single producer, mainly due to different food and water availability and diseases (McAllister, 1985; Thulborn, 1991; Chin, 2002, 2007; Chame, 2003; Bisceglia et al., 2007; Colares et al., 2010; Milàn, 2012; Lucas et al., 2012). Although, in some cases, the morphology is not enough to determine the animal source (Francischini et al., 2017), coprolite shape, together with inclusions, makes it possible to determine the producer.

Different interactions between vertebrates and invertebrates can be preserved in coprolites, such as surface traces, which are a clear evidence of coprophagy. Coprophagy can be indicated by biting traces, scratches or burrows on the surface of the coprolite or even in its interior (Chin and Gill, 1996; Wahl et al., 1998; Godfrey and Smith, 2010; Milàn et al., 2012; Godfrey and Palmer, 2015).

In this paper, we describe vertebrate coprolite assemblages from the Upper Miocene Urumaco Formation (Venezuela), which were collected from five vertebrate-bearing localities El Vijiadero/ Sur Llano Grande, Quebrada Bejucal, El Mamón, Corralito and Tío Gregorio). We described different coprolite morphotypes, composition and inclusions, as well as associated traces.

2. Geology

The Urumaco stratigraphic sequence is composed of seven geological units (Quiroz and Jaramillo, 2010), represented by diverse paleoenvironment facies including marine, estuarine, riverine, lacustrine and terrestrial (Díaz-de-Gamero and Linares, 1989; Quiroz and Jaramillo, 2010; Carrillo-Briceño et al., 2015). Throughout the entire section (Quiroz and Jaramillo, 2010), the lithology varies between more terrestrially influenced beds such as coal seams, and marine-influenced facies including sandstones, limestones and shales, and the associated marine, estuarine, and freshwater fauna (Tables 1 and 2; e.g. Sánchez-Villagra and Aguilera, 2006; Sánchez-Villagra et al., 2010; Aguilera et al., 2013; Scheyer et al., 2013; Carrillo-Briceño et al., 2015; Aguirre-Fernández et al., 2017) provide unequivocal evidence of a marine coastal/estuarine environment.

The Urumaco Formation (Upper Miocene) has a thickness of approximately 1700–2060 m, and the lower and upper contacts (Fig. 1) are conformable with the Socorro and Codore formations, respectively (Quiroz and Jaramillo, 2010). The unit is divided informally in to three members: the Lower Member (615 m thick), Middle Member (755 m thick) and Upper Member (330 m thick), and the unit is interpreted to

represent a variety of marine/continental environments of a prograding strandplain-deltaic complex (Quiroz and Jaramillo, 2010). Among the studied localities, El Vijiadero (Sur Llano Grande) and Quebrada Bejucal belong to the Lower Member, and El Mamón, Corralito and Tío Gregorio to the Upper Member (Table 1). The lithology and paleoenviroments of these Urumaco Formation localities are shown in Table 1.

The El Mamón, Corralito and Tío Gregorio localities were deposited in an estuarine/coastal lagoon, delta plain and floodplain environment, while Quebrada Bejucal was deposited during a transgression in an interdistributary bay and El Vijiadero (Sur Llano Grande) was formed in a floodplain.

3. Material and methods

The coprolites from the Urumaco Formation described here consist of 106 specimens, and come from five localities (Fig. 1, Tables 1–2, Supp. Table 1). Coprolites were collected *in situ* (Fig. 2) by the authors (JDCB and RS) during several expeditions beginning in 2007.

The coprolites were described and classified in five morphotypes according to their morphology, size, surface features and types of inclusion, probably reflecting different producers. Measurements of the coprolites were taken with the aid of a digital vernier caliper. Surface features (plant impressions, borings, folds and bite traces) and adhesion structures were observed and noted in the data base. Plant fragments present on the coprolite surface were identified based on size and organization of venation (Esau, 1965; Mauseth, 1988; Evert, 2006) and, posteriorly, counted in order to estimate the proportion between Poaceae and Eudicotyledoneae. The former family is characterized by leaves with parallel venation and bundles formed by cells of uniform size. In contrast, most of the eudicotyledonean leaf venation is composed of anastomosed, branching and netted bundles, with cells of varying sizes (Esau, 1965; Mauseth, 1988; Evert, 2006).

The studied material is housed in the Alcaldía Bolivariana de Urumaco (AMU-CURS), Venezuela, and in the Laboratório de Geologia e Paleontologia (LGP) of the Universidade Federal do Rio Grande (FURG), Brazil (Supp. Table 1).

Eight coprolites, of different morphotypes (from the Quebrada Bejucal, El Mamón, Corralito and Tío Gregorio localities), were transversely sectioned to expose the central portion. This portion was mounted on Al stubs, coated with Au and subjected to analysis under a JEOL JSN–6610LV Scanning Electron Microscope (SEM) at the Centro de Microscopia Eletrônica (CEME-Sul) of the FURG. Energy-dispersive X-ray spectroscopy (EDS) analyses were also conducted in six coprolites (Morphotypes M1, M2, three M3 and M4) to determine the chemical composition of the fecal matrix. Sample preparation followed standard procedures outlined by Mahaney (2002).

Another four specimens of M1, M2 and M3 (two coprolites) morphotypes and localities (Quebrada Bejucal, El Mamón, Corralito and Tío Gregorio) were sectioned to produce thin sections, for the recognition of inclusions and petrographic fabrics. In one M3 coprolite, from the

Table 1
General information of the lithology and paleoenviroments of the studied coprolite-bearing localities of the Urumaco Formation.

Locality	Formation	Member	Age	Lithology	Paleoenviroment
Tío Gregorio	Urumaco	Upper	Late Miocene	Fine-grained sandstones and organic-rich mudstones	Estuarine/Coastal lagoon, delta plain and floodplain areas
Corralito	Urumaco	Upper	Late Miocene	Interbedding layers of gray-massive mudstones and fine-grained sandstones	Estuarine/Coastal lagoon, delta plain and floodplain areas
El Mamón	Urumaco	Upper	Late Miocene	Interbedding layers of gray-massive mudstones and yellow middle/fine-grained sandstones. Abundant plant remains	Estuarine/Coastal lagoon, delta plain and floodplain areas
Quebrada Bejucal	Urumaco	Lower	Late Miocene	Coquinoid limestone with abundant invertebrate and vertebrate remains	Deposits of a transgression in a interdistributary bay
El Vijiadero (Sur Llano Grande)	Urumaco	Lower	Late Miocene	Interbedding layers of gray-massive mudstones, fine-grained sandstones and organic-rich mudstones	Floodplain areas