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Residues from the Upper Permian carnivore coprolites from Vyazniki in Russia - key questions in reconstruction of feeding habits

Piotr Bajdek [a], Krzysztof Owocki [b], Andrey G. Sennikov [c,d], Valeriy K. Golubev [c,d], Grzegorz Niedźwiedzki [e,*]

[a] Aleja Najświętszej Maryi Panny 20/20A, 42-200 Częstochowa, Poland
[b] Institute of Paleobiology, Polish Academy of Sciences, Twarda 51/55, 00-818 Warsaw, Poland
[c] Borissiak Paleontological Institute, Russian Academy of Sciences, Profsoyuznaya 123, Moscow 117997, Russia
[d] Kazan Federal University, Kremlyovskaya 18, 420008 Kazan, Russia
[e] Department of Organismal Biology, Evolutionary Biology Centre, Uppsala University, Norbyvägen 18A, 752 36 Uppsala, Sweden

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ABSTRACT

Residues of twenty-five coprolite fragments collected from the Upper Permian of Vyazniki (European Russia) were studied in detail. The phosphatic composition, general shape and size, and bone inclusions of these specimens indicate that medium to large-sized carnivores, such as therocephalian therapsids or early archosauriforms, were the most likely coprolite producers. The contents of the examined fossils (i.e. scale, bone and tooth fragments, mineral grains, and microbial structures) do not differ significantly among the samples, implying fairly comparable feeding habits of their producers. Fragments of large tooth crowns in two of the analyzed samples imply that either (1) the coprolite producer swallowed the cranial elements of its prey or (2) the coprolite producer broke and swallowed its own tooth while feeding (such tooth damage is known in archosaurs that have tooth replacement, e.g. crocodiles and dinosaurs). Indeed, the most complete tooth fragment in these fossils is serrated, most likely belonging to an early archosauriform known from skeletal records from the Late Permian of Vyazniki. Another coprolite fragment contains the etched tooth of a lungfish, while putative actinopterygian fish remains (scales and small fragments of bones) are abundant in some samples. Mineral particles (mostly quartz grains, feldspars and mica) may have been swallowed accidentally. The preserved microbial colonies (mineralized fossil fungi and bacteria or their pseudomorphs), manifested in the coprolites as Fe-rich mineral structures, seem to have developed on the expelled feces rather than on the items before they were swallowed.

1. Introduction

Coprolites (fossil feces) are of great interest and increasing importance in the study of food chains in ancient ecosystems (Thulborn, 1991; Chin et al., 2008; Wood et al., 2012; Zatoń and Rakociński, 2014; Schwimmer et al., 2015; Niedźwiedzki et al., 2016a, 2016b; Silva et al., 2017). Such study is possible due to incompletely digested food components and other inclusions which these fossils often contain (Rodríguez-de la Rosa et al., 1998; Northwood, 2005; Yates et al., 2012; Zatoń et al., 2015, 2017; Bajdek et al., 2016; Hansen et al., 2016; Qvarnström et al., 2016). Recently, coprolite studies have become increasingly multi-disciplinary (e.g. palaeobotany, palaeozoology, chemical analyses, biomarker analyses; see Zatoń et al., 2015), allowing us to obtain a greater amount of novel data.

Coprolite content is often described on the basis of thin sections (Chin, 2002, 2007a), but these are usually non-serial and made on a small number of specimens, rarely more than dozen thin sections in total (Chin and Kirkland, 1998; Chin, 2007b; Smith and Botha-Brink, 2011; Fiorelli et al., 2013; Bajdek et al., 2016). Such methods allow us to visualize details of even very delicate inclusions (Dentzien-Dias et al., 2013; Bajdek et al., 2016), yet any conclusions regarding the feeding habits of the coprolite producers are tenuous because of the small amount of material sampled. Coprolite studies based on an alternative method, chemical maceration (acid dissolution), are still rare and usually return a paucity of quantitative data (e.g. Kar et al., 2004; Vijaya and Singh, 2009; Khosla et al., 2015, 2016; Robin et al., 2016; Vajda et al., 2016). These two methods are destructive (Chin, 2002; Wood and Wilmshurst, 2016), and therefore the analyses should be well-planned and consider the most suitable methods, and the material should be properly documented, in order to maximize the amount of information that can be obtained.

Two non-destructive alternatives, namely computed tomography (Milàn et al., 2012a; Anagnostakis, 2013; Fiorelli et al., 2013; Bravo-Cuevas et al., 2017; Segesdi et al., 2017) and synchrotron microtomography (Qvarnström et al., 2017; Zatoń et al., 2017), can give detailed identification of inclusion material. Qvarnström et al. (2017) demonstrate that propagation phase-contrast synchrotron

* Corresponding author.
E-mail address: grzegorz.niedzwiedzki@ebc.uu.se (G. Niedźwiedzki).

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