Coprofile of a durophagous carnivore from the Upper Cretaceous Godula Beds, Outer Western Carpathians, Poland

Piotr BAJDEK1,*

1 Aleja Najświętszej Maryi Panny 20/20A, 42-200 Częstochowa, Poland

INTRODUCTION

Fossil feces are a precious source of information about ecology of extinct animals and ancient ecosystems (Thulborn, 1991; Hunt et al., 1994). Coprofiles have been described from various types of sedimentary rocks formed in both marine and non-marine environments during the Phanerozoic (Hunt et al., 1994; Hunt and Lucas, 2005). Cretaceous marine siliciclastic sediments have already yielded some vertebrate coprofiles (Chin et al., 2008; Eriksson et al., 2011; Mahaney et al., 2012). For example, Souto and Schwanken (2010) described two vertebrate coprofiles from turbidite sandstones of the Lower Cretaceous Maceió Formation, Brazil, formed during a marine transgression. Here, I describe a putative vertebrate coprofile from a marine deep-water turbidite sandstone.

GEOLOGICAL SETTING

The specimen described here comes from the Międzybrodzie Bialskie village, located 10 km to the south-east of Bielsko-Biała and 12 km to the north of Żywiec in the Outer Western Carpathian Mountains, southern Poland (Fig. 1). It was found by Dawid Mazurek (Polish Academy of Sciences) in an exposure on the shore of the Międzybrodzie Lake (Fig. 1C). The rocks exposed at the site are interbedded gray sandstones and gray shales representing the Godula Beds of the Carpathian flysch.

The Godula Beds were deposited in the Silesian Basin (northern Tethys) at the foot of the northern slope of the Silesian Ridge in a marine deep-water shifting system of fans and aprons dominated by turbidity currents (Słomka and Słomka, 2001, 2005; Bębenek, 2011). The deposition of the flysch series in the Silesian Basin lasted from the Cenomanian to the Oligocene – Early Miocene (Cieszkowski et al., 2006; Doktor et al., 2010; Bębenek, 2011). The Godula Beds are dated biostratigraphically based on foraminiferan microfossils, however, the precise age range of the beds is problematic and diachronic (see, Lemańska, 2005). They are generally thought to be Turonian–Lower Senonian (Słomka and Słomka, 2001; Bębenek, 2011) and their formation took about 10 million years (Słomka and Słomka, 2001), perhaps until the Campanian (Lemańska, 2005). The foraminiferan assemblages from the Godula Beds suggest that the beds were formed below the CCD in low oxygen and high energy conditions with a relatively high flux of organic matter (Lemańska, 2005).

The bottom surfaces of the sandstone beds at the site in Międzybrodzie Bialskie are covered by hieroglyphs and abundant, but mostly simple morphologically ichnofossils. Ichnofossils of the Godula Beds vary with lithofacies (Skupień et al., 2005). The shale beds contain the ichogenera Planolites, Thalassinoides and Chondrites, whereas within the sandstone beds there are such ichnogenera as Arthropycus, Helminthopsis, Ophiomorpha and Planolites (Skupień et al., 2009).

SPECIMEN DESCRIPTION

The specimen is stored in the Institute of Paleobiology, Polish Academy of Sciences, Warszawa and cataloged as ZPAL Tf.6. It is approx. 15 cm long, max. 2.6 cm wide, longitudinally

* E-mail: piotr.bajdek@gmail.com
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slightly wriggled in shape and progressively narrowed toward one end (Fig. 2). In cross-section the specimen is oval, approx. 2/3 as high as wide (Fig. 2C). It is exposed on the bottom surface of a sandstone block. The specimen contains a significant amount of shell fragments of inoceramids ranging from 0.5 mm up to 2.3 cm in length (Fig. 2B arrows; Figs. 3C and 4). At least 17 separate shell fragments were observed both on the surface and inside the specimen. The shells are oriented chaotically, often perpendicularly to the bedding and the largest ones are arranged lengthwise in the specimen. The coprolite is almost entirely composed of the same rock type as the host rock, which is a very finely grained sandstone; a siltstone fragment is also present in the specimen (Fig. 3). Reddish oxides are best visible on the surfaces of the specimen and in the host rock’s cracks.

INTERPRETATION AND DISCUSSION

TAPHONOMIC ANALYSIS

The specimen is interpreted as a coprolite due to its (a) elongated shape and three-dimensional morphology, (b) parallel orientation to the bedding, (d) content composed of fragmented bivalve shells, (e) chaotic orientation of the shells, i.e. amorphous matrix texture. It is difficult to explain the origin of this nodule by other biological, sedimentary or diagenetic processes. The groundmass texture of a coprolite is often amorphous and droppings tend to lie in the substrate in a stable position (Thulborn, 1991). These features can be useful in distinguishing coprolites from most of inorganic concretions and nodules as well as from other trace fossils, as sediment-filled burrows. It is supported by the high content and fragmentation of organic remains, that are characteristic for feces (Hunt et al., 1994).

Body fossils are extremely rare in the host sandstones (D. Mazurek pers. comm., 2013). Although foraminiferan microfossils are well-known (Lemarska, 2005; Szydło et al., 2007), most of the studied literature lacks information about body macrofossils from the Godula Beds (e.g., Cieszkowski, 2004; Słomka and Słomka, 2005; Cieszkowski et al., 2006; Bebenek, 2011). The general rarity of body macrofossils in the host rocks can be explained by (a) their deposition close to the CCD, (b) low oxygen conditions, (c) the harsh high energy environment and (d) the sedimentologic mechanism. Inoceramids have been, however, mentioned from the Godula Beds, e.g., by Bieda et al. (1963).

Fossil feces are sometimes a unique source of body fossils which otherwise would be missing or difficult to collect from the host sediments. This may be explained by:

- specific microenvironment and fossilization conditions within feces; for example, Chin et al. (2003) described fossilized muscle tissue within a Cretaceous coprolite;
- transport in the gastrointestinal tract of the producer far away from the place where the food components were consumed and/or selective accumulation and aggregation as food ingredients.
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Fig. 3. The interior of ZPAL Tf.6 photographed under the stereo microscope Olympus SZX10 equipped with the camera Olympus E-510

The specimen is broken in several separate fragments; weathered external as well as freshly exposed internal surfaces were examined; a – very fine grained sandstone, b – siltstone, c – shell fragments

These two mechanisms may co-occur. Yates et al. (2012) described the earliest post-Paleozoic freshwater bivalves as a content of coprolites suggesting that the thin shells have been preserved due to the specific microenvironment within the feces, whereas the surrounding siliciclastic sediments contained no shells. However, calcitic shells usually have a good fossilization potential (unless below the CCD) and no exceptional diagenetic conditions can be deduced from the coprolite from the Godula Beds. Moreover, although body macrofossils are rare in the Godula Beds, bivalve shells had already reported. This all suggests that the coprolite at hand should be interpreted basically as a simple aggregation of food ingredients rather than a case of an exceptional preservation in a specific microenvironment.

Feces as humpback whale droppings may be able to float on the ocean surface (Kieckhefer, 1992). However, a remote transport of the specimen at hand seems not probable, because:

- it is graceful in morphology and potentially delicate;
- rapid burial is often crucial for preservation of feces (e.g., Chin et al., 2003; Eriksson et al., 2011);
- it was made by an animal which fed on benthic fauna in a deep-water environment – floating feces on the sea surface would be more expected if produced by nektic animals feeding mostly near the water surface.

The specimen is exposed on the bottom surface of a sandstone bed. The feces were hypothetically produced close to the place of its discovery, and then buried by sediments of a turbidity current, rather than transported by the current. The fecal mass was substituted by siliciclastic material only preserving the original morphology of the feces and the content of calcite shell fragments.

REMARKS ON PALAEOBIOLOGY

Coprolite content reflects the diet of its producer (Hunt et al., 1994). However, digested diet components may vary significantly in both resistance for dissolution by stomach acids and their fossilization potential after leaving the gastrointestinal tract. For example, Sato and Tanabe (1998) described a supposed stomach content of a Cretaceous short-necked plesiosaur that included a large number of isolated calcite ammonoid jaws, but low-resistant aragonite ammonoid shells were missing. Because only the robust expected shells preserved in the coprolite studied here are relatively resistant, conclusions about the diet and habit of its producer may be misleading. It is difficult to rule out the simple possibility that remains of other species included in the diet have been completely dissolved. Nevertheless, the content of inoceramid shells is quite significant in this coprolite, suggesting that its producer at least partially fed on such benthic molluscs and had a good capacity of crushing sturdy shells. It moreover suggests that the source animal was a durophagous carnivore.

This coprolite seems too large to have been produced by an invertebrate, perhaps except by a large cephalopod. Among aquatic vertebrates both fishes and reptiles were potentially capable to produce feces of this diameter and volume. Because sharks and other groups of fishes including basal actinopterygians produce feces of spiral morphologies (Jain, 1983; Gilmore, 1992), the producer might be a teleost fish which lack the spiral intestinal valve, or a reptile. Non-spiral fossil feces of fishes and tetrapods may be difficult to distinguish between each other (Hunt et al., 1994).

A single probable actinopterygian scale was found in the host rocks at the site (D. Mazurek pers. comm., 2013). Moreover, inoceramid shells were described from stomach contents and coprolites of sea turtles from the Upper Albian Toolebuc Formation, Australia (Kear, 2006). Modern sea turtles may feed on nektic and benthic fauna in

Fig. 4. Inoceramid shells in the coprolite specimen ZPAL Tf.6 under a stereo microscope
A – weathered shell exposed on the specimen surface; B – small shell fragment inside the specimen
depths of several hundred of metres below the water surface in full marine ecosystems, even reaching 1200 meters of depth (Spotila, 2004). However, the protostegid turtle stomach contents described by Kear (2006) come from a shallow sea environment (<100 m depth). Although both fishes and reptiles could potentially produce this coprolite based on the morphology of the specimen and its content, a fish seems a more probable producer.

CONCLUSIONS

The examined specimen from the Upper Cretaceous sandstones of the Godula Beds is interpreted as a coprolite produced by a durophagous carnivore, which was probably a teleost fish, or possibly a reptile. It was most likely produced close to the place of its discovery and buried beneath sediments from a turbidity current. Although body macrofossils are rare in the Godula Beds, coprolites have a potential utility as a source of such fossils in these and supposedly in some other fossil-poor sedimentary rocks.

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