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Reduction of vertebrate coprolite diversity associated with the end-Permian extinction event in Vyazniki region, European Russia

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ABSTRACT

This study investigates the paleoecological significance of vertebrate coprolites collected from seven sections and three lithofacies of the uppermost Permian and lowermost Triassic succession from the Vyazniki site in the European part of Russia. The analyzed specimens (coprolites and possibly some cololites) were grouped into nine morphotypes (A–I). The coprolite morphotypes were characterized geochemically and compared to the record of other Permian and Triassic coprolites worldwide. Based on the stratigraphic position, shape, structure and composition, all morphotypes were linked to supposed producers. The phosphatic composition of most of the morphotypes and inclusions of arthropod remains, fish scales and bone fragments, suggest that they were produced by carnivores, but non-phosphatic, carbonate-rich, large and oval-shaped coprolites with impressions after plant remains have also been found. The extinction of terrestrial vertebrates around the Permian–Triassic boundary in Russia is interpreted to have occurred within a few thousands of years. Here, we show a pattern of coprolite morphotypes disappearing across this boundary that is consistent with a relatively sudden change in the vertebrate faunal composition across this interval.

1. Introduction

Coprolites (fossil feces) are important sources of paleoecological information and can reveal aspects of diets and ecology of extinct fauna (Chin and Kirkland, 1998; Chin et al., 2009; Wood et al., 2012; Dentzien-Dias et al., 2013; Bajdek et al., 2014). Difficult, but especially interesting is to ascribe the coprolite morphotypes to their producers (Chin et al., 1998; Chin, 2007; Owocki et al., 2012; Bajdek et al., 2014). This is important as coprolites may provide information on predator–prey relationships and allow reconstructions of trophic structures in ancient ecosystems (Chin et al., 2008; Zatoń et al., 2015).

Coprolite material can be a useful source of data on changes in ecosystems during mass extinctions. In recent years, Suazo et al. (2012) described Upper Cretaceous through lower Cenozoic vertebrate coprolites from the San Juan Basin, New Mexico, but concluded that morphologies and contents of those coprolites do not change significantly across the Cretaceous/Paleogene boundary. Nakajima and Izumi (2014) described Lower Triassic (Olenekian) coprolites of most likely nektonic animals from the marine deposits of the Osawa Formation, Japan, providing some information on the diversity and trophic structure of marine ecosystems following the end-Permian mass extinction. Brachaniec et al. (2015) described a rich coprolite collection from the latest Olenekian of Poland that implies that durophagous predation was intense during the Early Triassic. In addition, Brachaniec et al. (2015) suggested that the so-called predation-driven Mesozoic Marine Revolution had already started soon after the end-Permian extinction.

Since the published data on the distribution and diversity of the Upper Permian-Lower Triassic coprolites are scarce, the new data presented here may be of a particular interest. Our study of coprolite assemblages collected from the Permian–Triassic deposits of Vyazniki, presents new data about the changing trophic structures of the terrestrial vertebrate communities from the latest Permian to earliest Triassic in northern Pangea. We document the stratigraphic ranges of the various vertebrate coprolite morphotypes spanning the Permian–Triassic interval at Vyazniki (Fig. 1A), European part of Russia (Russian Platform), within seven sections exposed in five localities (Fig. 1B). This detailed record of coprolite diversity was then used as an indicator of changes in diversity of vertebrate populations in the ancient ecosystems. Coprolites in the uppermost Permian of Vyazniki was firstly

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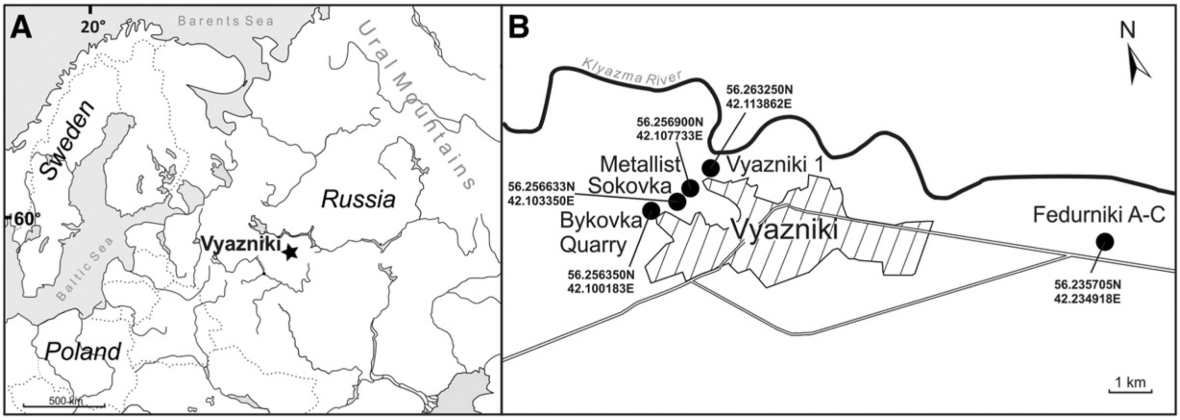

Fig. 1. Maps of the Eastern Europe (A) and the area around the town Vyazniki (B) showing the latitude and longitude of locations of coprolite-bearing fossil sites (positions are in decimal degrees; datum: WGS 1984). Modified from Newell et al. (2010) and Owocki et al. (2012).

mentioned by Sennikov (2004); Sennikov and Golubev (2006) and Newell et al. (2010) and then a more detailed description and geochemical analysis was presented by Owocki et al. (2011, 2012) and Bajdek et al. (in press). During our fieldworks near the town of Vyazniki in 2010 and 2013 we discovered new coprolite-rich intervals associated with different lithofacies, as well as vertebrate faunas from uppermost Permian and lowermost Triassic strata.

2. Geological setting

The section of the Permian and Triassic continental deposits is well-exposed in many parts of the Russian Platform. This Permo-Triassic sequences range in age from the late early Permian (Kungurian) to the Middle Triassic (Ladinian), a span of some 35 Myr (Newell et al., 2010). The upper Permian deposits cover a large part of the Russian Platform and are exposed in numerous sites in a north–south belt that extends from the Ural Mountains westward toward Moscow. The overlying Lower and Middle Triassic strata are less extensive and are exposed much less. The Upper Permian and Lower Triassic sequences from Vyazniki and Fedurniki are located around 800 km to the west of the Ural Mountains in the southeastern part of the Moscow Syncline. The profiles of the Permian and Triassic continental deposits are reduced in thickness in this part of the Russian Platform in comparison to broader basins in the eastern part of platform. The Vyazniki area received fine-grained sedimentation until the latest Permian and earliest Triassic, at which time there was an abrupt basinward shift of sandy facies into the former playa-lacustrine basin (Newell et al., 2010). The outcrops at Vyazniki and Fedurniki represent the distal part of an extremely large fluvial distributary system developed to the west of the Ural Mountains (Sennikov and Golubev, 2006, 2012; Newell et al., 2010). It is an approximately 100–150 m thick sequence which is most suitable for field research at the Bykovka Quarry (56.256350N; 42.100183E), Sokovka (56.256633N; 42.103350E), Metallist (56.256900N; 42.107733E), Vyazniki 1 (56.263250N; 42.113862E) and Fedurniki (56.235705N; 42.234918E) sites (Fig. 1B; see Sennikov and Golubev, 2006, 2012; Newell et al., 2010; Owocki et al., 2012; Lebedev et al., 2015). The exact position of the Permian–Triassic boundary (PTB) has not yet been clearly defined for this area and all suggestions have been based mainly on lithological criteria supported by some data on palynomorph, plant macrofossil, bivalve, insect, ostracod and vertebrate occurrences (Sennikov, 1996; Newell et al., 2010; Sennikov and Golubev, 2012; Golubev et al., 2012a,b; Lebedev et al., 2015). Recently, studies on well-preserved conchostracan fossils (Scholze et al., 2015) and the magnetostratigraphic record (Balabanov et al., 2015) have complemented the stratigraphic scheme of this part of the section.

The Permian–Triassic transitional section around the Vyazniki contains mainly a sedimentary succession of muddy playa-like deposits, which were abruptly overlain by sand-grade major channel deposits (Newell et al., 2010). This rapid change in the sediment flux was interpreted as a basin-wide erosional event of increasing sediment input from the Ural Mountains caused by the sudden extinction of plants in upland catchments areas (Newell et al., 2010).

In the study area, latest Permian (Zhukovian Regional Stage) deposits consist predominantly of lacustrine claystones and limestones as well as floodplain claystones, siltstones, sandstones and fluvial sandstones belonging to the Obnora Formation. The deposits of the Zhukovian Regional Stage are characterized by a diverse flora and fauna (e.g., Sennikov and Golubev, 2006, 2012; Golubev et al., 2012a,b). In contrast, the Lower Triassic parts of the studied sections were built up mainly of channel sandstone facies with rare intercalations of fossil-bearing layers. In the Vokhma Formation (Vokhmian Regional Stage) exposed at Fedurniki fluvial sandstones and mudstones contain mainly small vertebrate remains, including *Tupilakosaurus* sp. (e.g., Sennikov and Golubev, 2006, 2012; Scholze et al., 2015) and this section can be correlated with the lowermost Triassic *Tupilakosaurus wetlugensis* Zone of the Russian Regional Scale (e.g., Golubev et al., 2012a,b).

3. Faunal composition

Several sites at the Vyazniki locality have yielded abundant vertebrate bones, including fishes, amphibians and reptiles. The fauna demonstrates a transitional nature between the Late Permian and Early Triassic communities of Russia (Sennikov, 1996; Sennikov and Golubev, 2006, 2012). The uppermost Permian strata of Vyazniki area (Vyazniki 1, Sokovka, Bykovka Quarry, Metallist, Yartsevo, Petrino) have produced numerous teeth, isolated bones and scales of fish. In the fish-bearing, mainly sandy-mudstone intercalation layers, remains have been found of: sharks Hybodontiformes fam. indet.; actinopterygians *Mutovinia sennikovi* A. Minich, *Mutovinia* sp., *Strelnia* sp., *Toyemia blumentalis* A. Minich (see also Esin, 1995), *Toyemia* sp., *Isadia aristoviensis* A. Minikh, *Isadia* sp., skeletal elements of a new species of the genus *Geryonichthys*, and *Evenkia* (?) sp.; the chondrostean *Saurichthys* (?) sp., and also the large dipnoan *Permoceratodus gentilis* Krupina (Newell et al., 2010; Minikh et al., 2014; Pindakiewicz et al., 2015; Lebedev et al., 2015). The Vyazniki tetrapod fauna includes (Sennikov, 1996; Sennikov and Golubev, 2005, 2006, 2012): the temnospondyl *Dvinosaurus egregius* Shishkin, 1968, known from a complete skull and postcranial elements; Microsauria (?) fam. indet. (remains of supposed representatives of Lepospondyli), identified from vertebrae, limb bones and jaws (see Newell et al., 2010); the seymouriamorph *Karpinskiosaurus* sp., represented by vertebrae; the bystrowianid anthracosaur *Bystrowiana permira* Vjuschkov, 1957, based on vertebrae, large skull fragments and body scutes; the chroniosuchid anthracosaur *Uralerpeton tverdochlebovae* Golubev,