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UPPER PERMIAN VERTEBRATE COPROLITES FROM VYAZNIKI AND GOROKHOVETS, VYATKIAN REGIONAL STAGE, RUSSIAN PLATFORM

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ABSTRACT

Numerous coprolites have been found in the Vyazniki and Gorokhovets localities of European Russia. Five identified coprolite-bearing horizons occur in the upper Permian deposits of the Vyatkian Regional Stage. Coprolites were collected from mudstone with a coprolite breccia-like layer and also from intraformational conglomerates that were deposited in a floodplain and overbank environment. Two coprolite morphotypes (A and B) are recognized from size and shape analysis of 32 specimens. Morphotype A has long, nonsegmented feces. Smaller, cylindrical or tubular-shaped coprolites of morphotype B are commonly segmented. SEM images of the coprolite matrix show spheres and thin-walled vesicles with diameters 0.5–4 μm. Electron Micro Probe (EMP) analyses of polished thin sections show microcrystalline carbonate-fluoride-bearing calcium phosphate with small amounts of calcium replaced in the crystal lattice. Optical microscopy and EMP investigations show that iron and manganese oxides are responsible for elevated iron and manganese concentrations in the bulk mass of coprolites. Other metals (V, Ni) can be associated with oxides forming spheroids with diameters 3–10 μm. REEs (rare earth elements, U, and other trace element concentrations suggest significant eolian sediment input to the burial environment of the coprolites. The scats contain fish scales and bones of tetrapods (amphibians or reptiles). In one large-sized coprolite, a small fragment of therapsid bone was also found. Both morphotypes are matched to carnivorous taxa within the *Archosaurus rossicus* zone of the Eastern Europe. The size and shape of the best-preserved specimens suggest that they were possibly produced by a large therapsid, anthracosaur, or early archosauromorph predator.

INTRODUCTION

Numerous localities from the middle–upper Permian and Lower–Middle Triassic continental deposits of the European part of Russia have yielded isolated bone remains of small- to large-sized terrestrial tetrapods (Ivakhnenko et al., 1997; Tverdokhlebov et al., 2003, 2005; Sennikov and Golubev, 2006). Permo-Triassic continental redbeds from Russia provide an important record of changes to terrestrial environments and ecosystems before, during, and after the Permian-Triassic boundary (Newell et al., 1999, 2010; Zharkov and Chumakov, 2001; Benton et al., 2004; Shishkin et al., 2006; Shcherbakov, 2008; Krassilov and Karasev, 2009).

Variegated deposits of upper Permian claystones and sandstone beds were discovered in the town of Vyazniki in 1841 by R.J. Murchison during his expedition to European Russia (Murchison et al., 1845). The abundantly fossiliferous Vyazniki vertebrate locality was explored for the first time in 1951 and excavated in 1952, 1955, and 1956 by expeditions of the Paleontological Institute of the Academy of Sciences of the USSR headed by B.P. Vjuschkov (Efremov and Vjuschkov, 1955). This locality yielded abundant vertebrates, including fishes, amphibians, and reptiles. The Vyazniki fauna demonstrates a transitional nature between the late Permian and Early Triassic communities (Sennikov and Golubev, 2006). The Vyazniki tetrapod fauna includes the temnospondyl *Dvinosaurus egregius*, Microsauria family indet., the kotlassiomorph *Karpinskiosaurus secundus*, the parareptile *Obirkovia* sp., the anthracosaurs *Bystrowiana permira* and *Uralerpeton tverdochlebovae*, the archosauromorph *Archosaurus rossicus*, an anomodont Dicynodontidae genus indet., and the therocephalians *Moschowhaitsia vjuschkovi, Megawhaitsia patrichae*, and Moschorhinidae genus indet. (Sennikov and Golubev, 2006).

Interestingly, such trace fossils as trackways or footprints are rare in those deposits and only a few discoveries of tetrapod tracks have been reported from the Permian of Russia: amphibian tracks assigned to *Anthichnium* isp. from the southern Cis-Uralian Trough (Tverdokhlebov et al., 1997), reptile tracks described as cf. *Dromopus* isp. and cf. *Dimetropus* isp. from the lower Permian redbeds in northern Caucasus (Lucas et al., 1999), pareiasaurian tracks assigned to *Sukhonopus primus* Gubin and Bulanov 2003 from the bank of the Sukhona River in the northern part of Russia (Gubin et al., 2003), and a set of tracks made by a very large quadrupedal tetrapod (therapsid) assigned to *Brontopus giganteus* Heyler and Lessertisseur 1963 in Vyatkian Regional Stage, Orenburg Region (Surkov et al., 2007). In contrast, vertebrate coprolites are numerous and well preserved in the middle and upper Permian deposits of Russia. However, although they were mentioned in several geological papers (Ochev, 1974; Orlov, 1992; Silantiev, 1999; Silantiev et al., 2000a, 2000b; Sennikov and Golubev, 2012) they have not yet been described in detail.

Here we report on new vertebrate coprolite accumulations in the upper Permian strata (Vyatkian Regional Stage) of the Russian Platform from four localities (Bykovka, Sokovka, Metallist, Zhukov Ravine) exposed near Vyazniki and Gorokhovets (Fig. 1). We provide the first description of large coprolites with food remains discovered in the upper Permian strata of Europe.

GEOLOGICAL SETTING

Continental Permo-Triassic sequences in Russia range in age from the late early Permian (Kungurian) to 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 places in a north–south belt that extends from the Ural Mountains westward toward Moscow. The overlying Lower and Middle Triassic strata are less extensive. The upper Permian and Lower Triassic sequences from Vyazniki and Gorokhovets are located ~800 km 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 basins in the eastern part of platform and are about 100–150 m thick at Vyazniki and Gorokhovets sites. These sites received fine-grained sedimentation until the latest Permian and earliest Triassic

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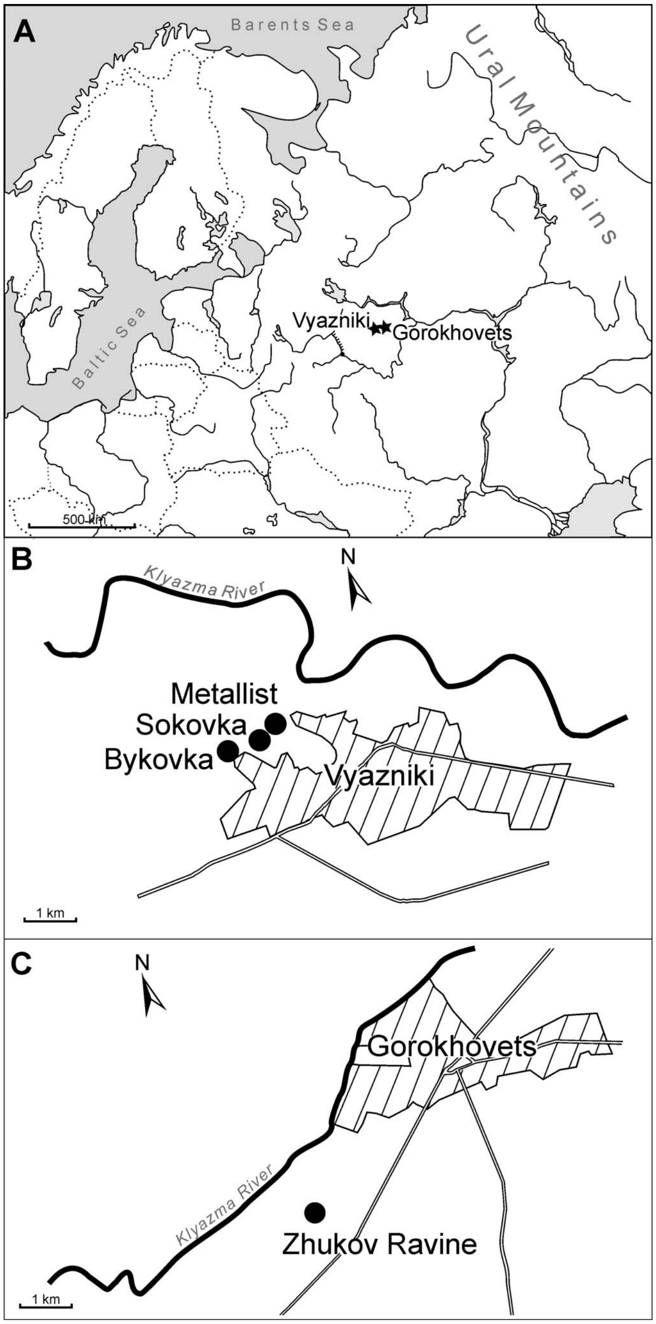

FIGURE 1—Location of the upper Permian Vyazniki (Bykovka) and Gorokhovets (Zhukov Ravine) sites. A) Investigated area relative to the outline of central and eastern Europe. B) Investigated area within the town of Vyazniki. C) Investigated area within the town of Gorokhovets.

(Fig. 2), at which time there was an abrupt basinward shift of sandy facies into the former playa-lacustrine basin (Newell et al., 1999, 2010). The outcrops at Vyazniki and Gorokhovets represent the distal part of an extremely large Permian fluvial distributary system developed to the west of the Ural Mountains (Sennikov and Golubev, 2006, 2012; Newell et al., 2010).

MATERIAL AND METHODS

Materials

Seventy coprolites (32 complete specimens) were collected from four exposures in two sites, including one abandoned quarry (Bykovka, Vyazniki), and artificial (Sokovka and Metallist, Vyazniki) and natural (Zhukov Ravine, Gorokhovets) exposures on the valley slope. The specimens described in this paper were found during field trips in the late summer of 2008 and 2010, jointly organized by the Institute of Paleobiology, Polish Academy of Sciences and University of Warsaw (Warsaw, Poland) and Borissiak Paleontological Institute, Russian Academy of Sciences (Moscow, Russia) to the Vyazniki and Gorokhovets localities.

Bykovka.—At this site a 5-m-thick section contains thin intervals of interlaminated greenish and red mudstone, siltstone, and fine-grained sandstone (in the upper part of the section), and also locally conglomeratic intraclasts in the sandstone (Fig. 2). Coprolites were found in mudstone, siltstone and sandstone beds in the uppermost part of the exposed profile (Figs. 3A–D).

Sokovka.—At this site a 20-m-thick succession of orange-brown and reddish-brown, weakly consolidated, fine- to coarse-grained sandstone is overlain by a gray mudstone interval ~3–5 m thick and a gray and yellow sandstone interval 4 m thick (Fig. 2). Coprolites were found in conglomerate intervals locally developed in the upper sandy succession.

Metallist.—At this site a 9-m-thick section of sandy deposits was excavated and analyzed in detail (Fig. 2). The orange-brown sandstone contains thin intervals with intraclasts and very hard, well-cemented intraclast conglomerate that can contain numerous bivalves. Coprolites were collected from intraclast intervals and also from two layers of well-cemented conglomerates (Fig. 3F).

Zhukov Ravine.—The Zhukov Ravine section is located ~2 km southwest of Gorokhovets, and comprises a ~60-m-thick section of upper Permian–Lower Triassic deposits. The basal part of the section comprises predominantly massive, rooted, red mudstone with subordinate beds of laminated brown-red mudstone, massive or ripple cross-laminated sandstone and pale gray, well-cemented micritic limestone with root voids. In the upper part of the Zhukov Ravine a well-cemented intraclast conglomerate (Fig. 2) marks an abrupt change from the mudstone and occasional limestone to a succession dominated by orange-brown, fine- to medium-grained, cross-bedded, weakly cemented sandstone. Coprolite material was collected from the well-cemented intraclast conglomerate layers (Fig. 3E).

Methods

Macroscopic Observations.—Surface morphological features that provide information about the coprolites' taphonomic history, such as breakage, adhesions, or desiccation cracks, were observed and noted in the database. Coprolite material subjected to destructive analytical techniques was first photographed and measured.

Optical Microstructure Observations.—Observations of coprolites were made with an optical microscope (NIKON Eclipse LV 100 POL; Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland), and opaque authigenic minerals were identified with a reflected-light microscope. Thin sections were made from five of the specimens for the study of internal structures and possible inclusions. The slabs were mounted on glass slides using epoxy, and then ground to an appropriate thickness. The thin sections were studied under a binocular microscope and photographed with a digital camera.

Statistical Test.—The 32 best-preserved specimens (complete specimens) were taken from the coprolite collection for statistical analysis. The length and width of the coprolites were measured with a vernier caliper. The Pearson's product moment correlation coefficient was calculated to test the statistical support for the existence of the two groups of coprolites.

SEM Microstructure Observations.—Material from five coprolites (both types) was analyzed with a Phillips XL-20 scanning electron microscope (SEM) (Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland) equipped with EDS detector ECON 6, system EDX-DX4i and a backscatter electron (BSE) detector for Compo or Topo detection (FEI product). This instrument was operated

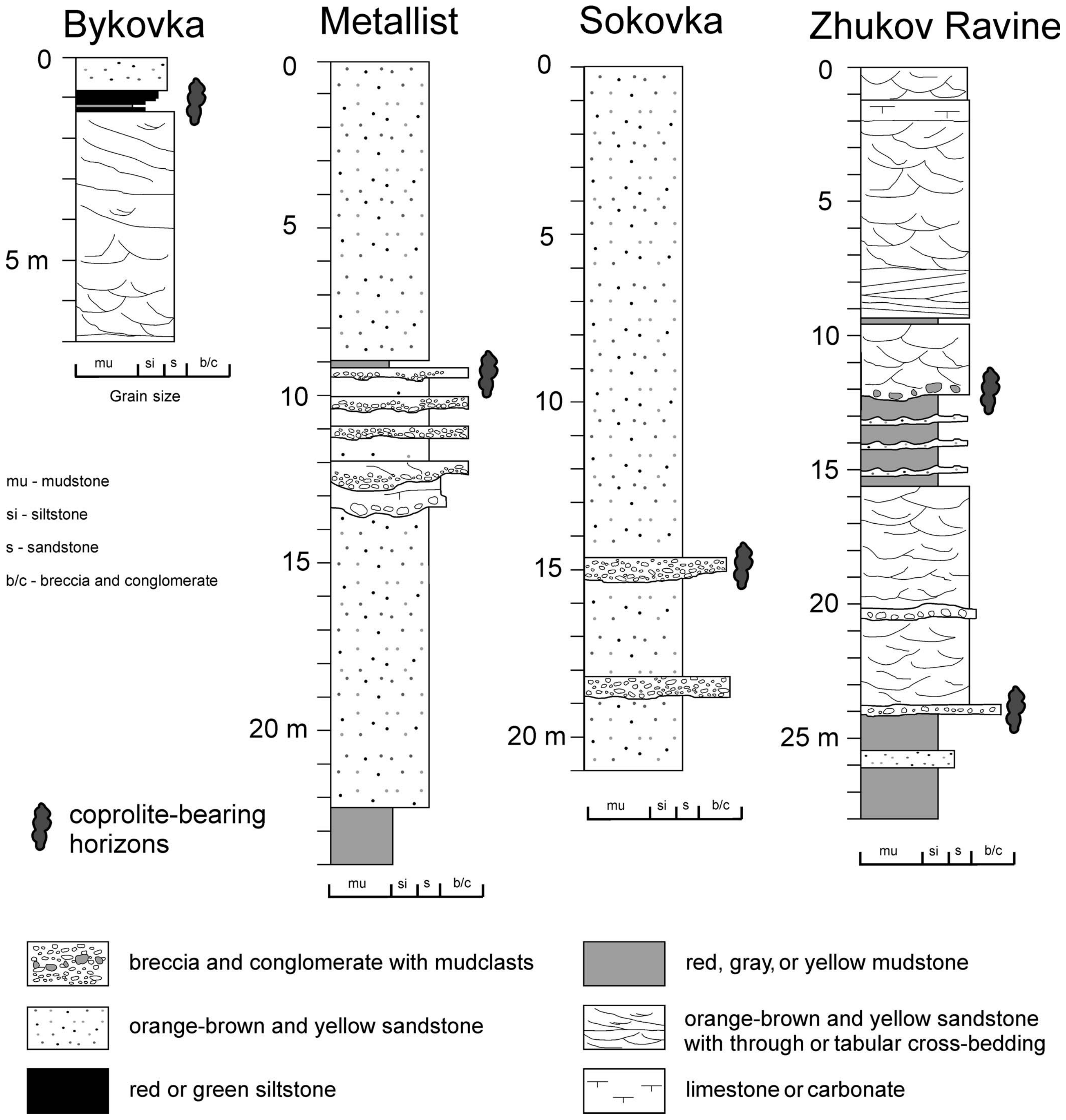

FIGURE 2—Upper Permian profiles with positions of coprolite-bearing deposits from Vyazniki and Gorokhovets (from Sennikov and Golubev, 2006; Newell et al., 2010, with additions and corrections).

at an accelerated voltage of 25 kV, a beam current of 98–103 nA, and a spot diameter of 4 µm.

Chemical Analyses.—Further chemical analyses of selected coprolites (from both types of coprolites) were made using a Cameca SX-100 electron microprobe at the Joint-Institute Analytical Complex for Minerals and Synthetic Substances (Faculty of Geology, University of Warsaw, Poland). The mineral compositions were determined in wavelength-dispersive spectral (WDS) mode on the EMPA using an accelerating potential of 15 KeV, a 20 nA beam current, 1 µm beam size, peak and background counting times of 20–30 s, and standard ZAF (PAP) correction procedures. A combination of natural and synthetic standards was used for calibration. Detection limits (3σ above background) are typically 0.01 wt%–0.03 wt% for Mg, Al, Na, Si, S, Cl, K, Ti; 0.05 wt%–0.06 wt% for Mn, Fe; 0.08 wt%–0.09 wt% for F; and 0.13 wt%–0.16 wt% for Ni, Ca, P.

Inductively Coupled Plasma–Mass Spectrometer.—The REEs (rare earth elements), U, and other trace elements were analyzed using a Inductively Coupled Plasma–Mass Spectrometer (Acme Analytical Laboratories Ltd., Vancouver, Canada). The 10 samples (from 10 coprolites) were pulverized by ceramic mill. The 4-acid digestion on 0.25 g split was made on obtained mesh. The splits were heated in HNO_3-$HClO_4$-HF to fuming and taken to dryness. The residues were dissolved in HCl. Solutions were analyzed by ICP-MS. The detection limits were between 0.02 and 0.1 ppm varying for different trace elements. The REE data were

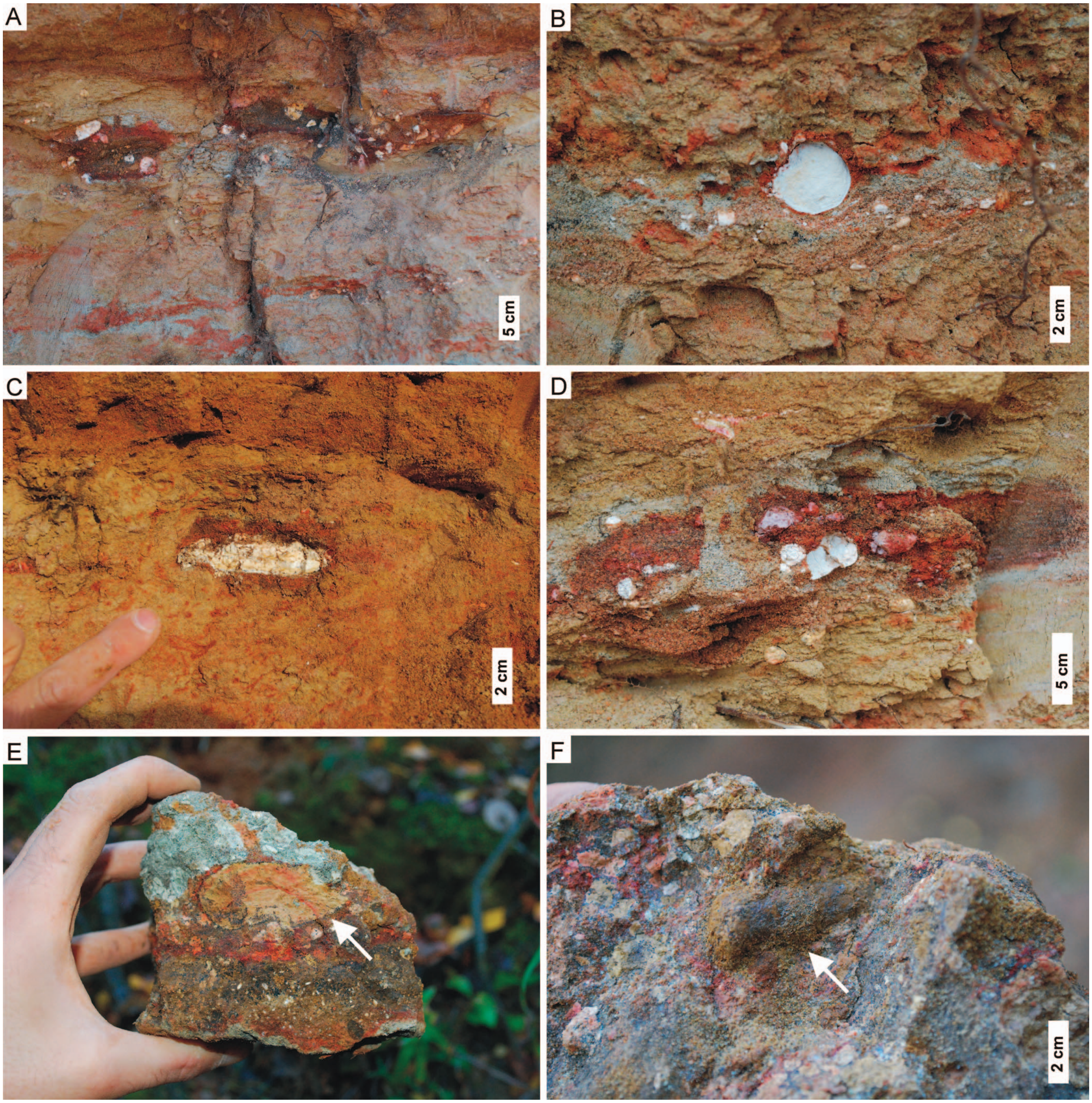

FIGURE 3—Details of coprolite occurrences analyzed during fieldwork profiles. A–D) Coprolite-bearing layers and coprolites exposed mainly as cross sections, Bykovka, Vyazniki (sections of quarry wall). E–F) Coprolites preserved in solid sandstone-conglomerate layer, Zhukov Ravine, Gorokhovets.

normalized (indicated by subscript N) to the Post-Archean Australian Shale (PAAS) (Taylor and MacLennan, 1985) to remove abundance effect. The REE patterns and elemental ratios (e.g., $(La/Sm)_N$, $(Sm/Pr)_N$) were compared with the patterns and ratios from natural waters presented in the literature (e.g., Elderfield et al., 1990; Trueman, 1999; Dia et al., 2002) to infer possible burial or early diagenetic environments.

RESULTS

Macroscopic Description and Statistical Test Results

The coprolites are reddish (purple or orange) or white in color and have a sharp outer contact with a clear separation from the host rock (Fig. 3B). A few coprolites observed in the field are not separated from their enclosing muddy or sandy deposits, but still have a sharp color boundary (Fig. 3E). A pitted pattern of bowl-shaped depressions occurs on a few specimens and probably is a record of erosion. The surface of the coprolites also exhibits small and undulating striations and grooves, which in some cases are branching. The bulk of the coprolites consist of fine-grained microcrystalline calcium phosphate that has replaced, in part, the original material that was present between the bone fragments. Some unidentified elements may represent fish scales or other hard parts (e.g., hairs, osteoderms) of the digested organism.

The coprolite collection was subdivided into two different groups of morphotypes (A and B) based on overall shape (Figs. 4A–F) and simple statistical methods (Figs. 4G–H).

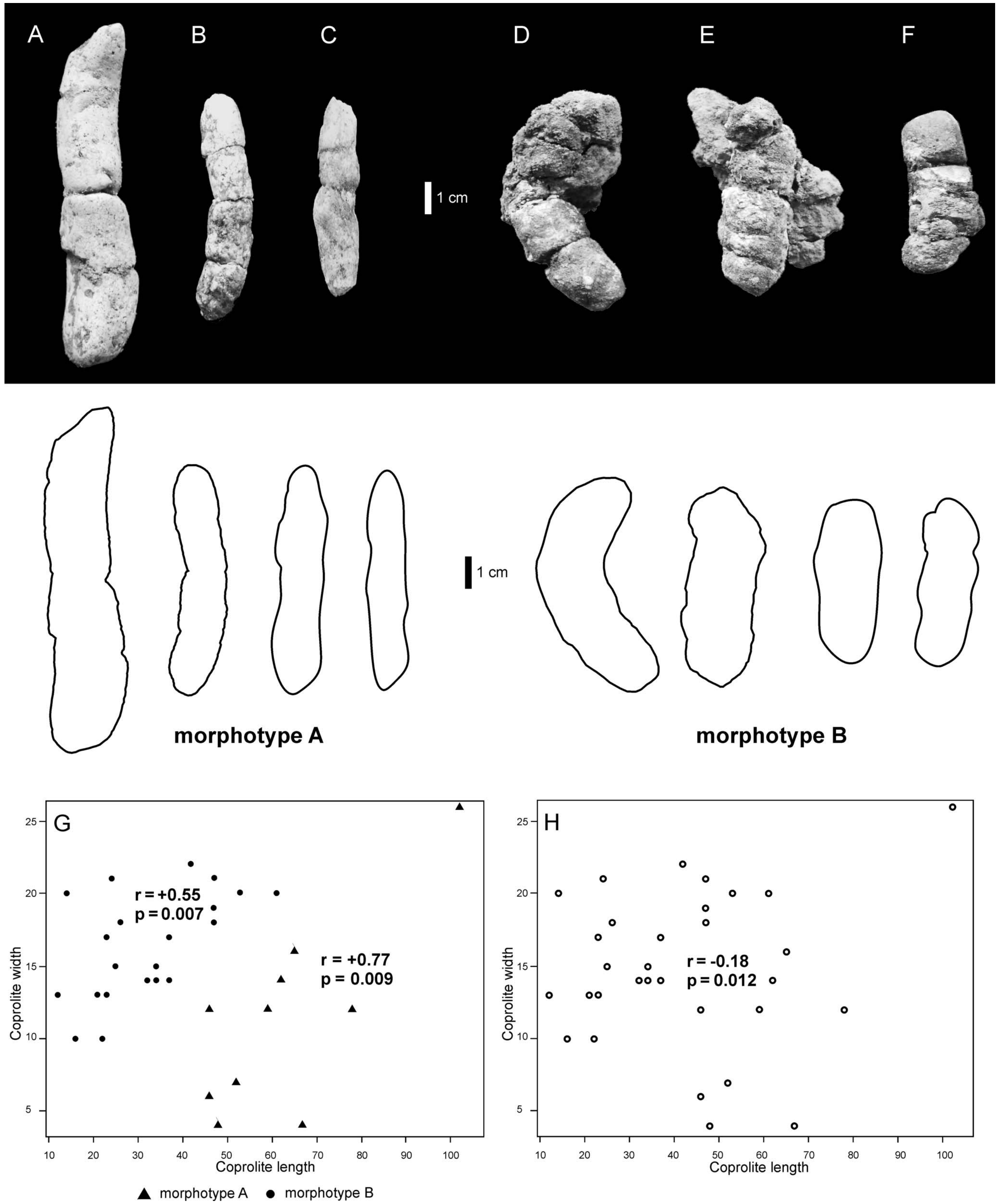

FIGURE 4—Photographs of lateral views of the best-preserved coprolites belonging to two morphotypes. A–B, E–F) Specimens from Bykovka, Vyazniki; C–D) specimens from Zhukov Ravine, Gorokhovets and G–H) scatter plots of the measured coprolites from Bykovka at Vyazniki. The Pearson product moment correlation coefficient r and p are calculated for G) each group and for H) the whole data set.

Two morphologies were observed among the coprolite specimens: the longer and thinner morphotype A (Figs. 4A–C) and the shorter and thicker morphotype B (Figs. 4D–F). To test the statistical support for these two morphotypes, correlation between coprolite width and length was calculated separately for each of the morphotypes and compared the correlation for whole pooled dataset. The groups are visualized in the scatter plot of measured parameters (Figs. 4G–H). The Pearson product moment correlation coefficients between coprolite length and

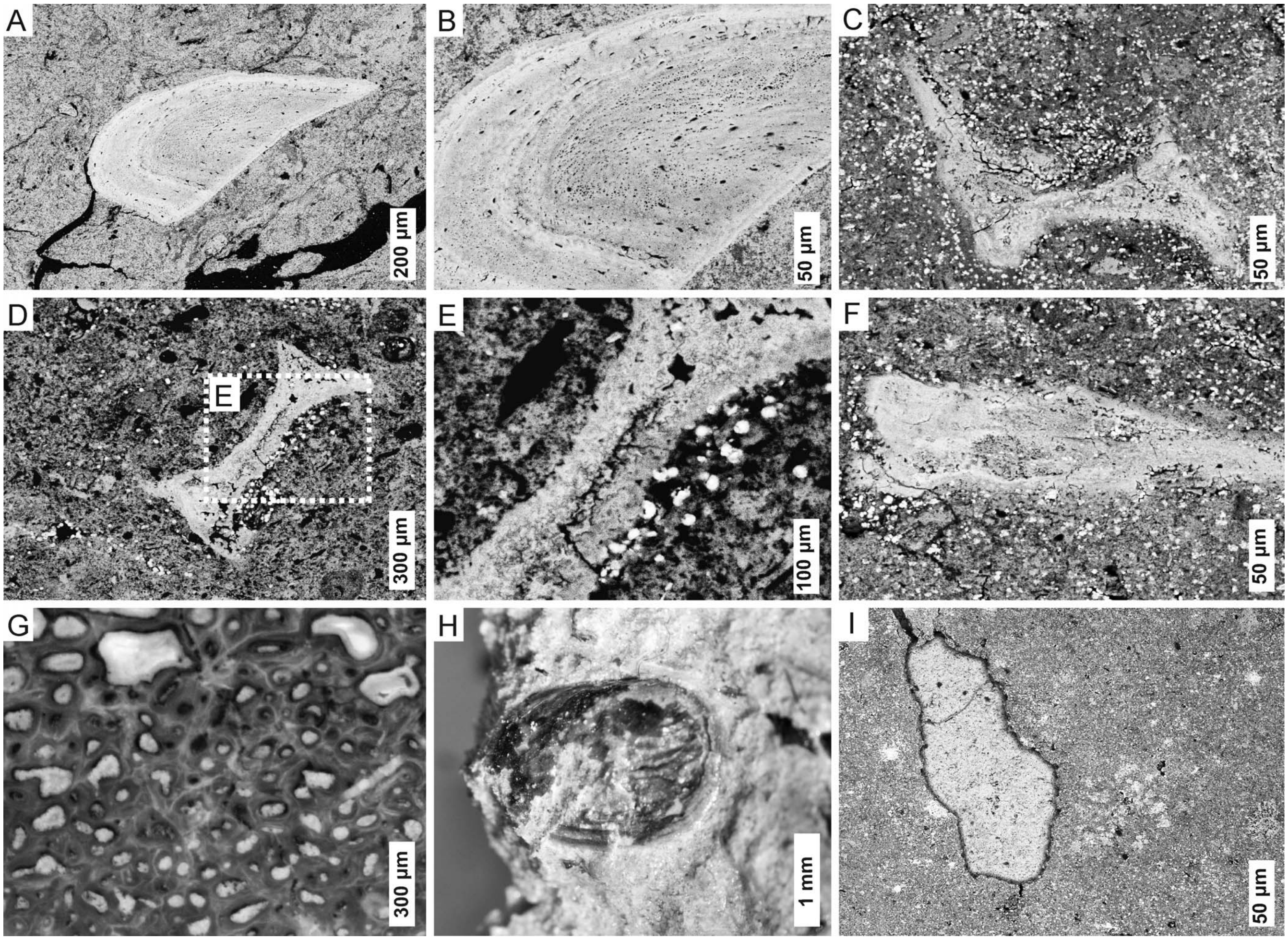

FIGURE 5—SEM images of thin sections (A–F, I), light microscope photograph of thin section (G), and photograph of coprolite surface (H) with organic remains recovered from five analyzed coprolite specimens from Bykovka, Vyazniki. A–F, I) Fish, small amphibian, or small reptile bones. G) Small part of therapsid bone from coprolite. H) Arthropod remain (probably conchostracean carapace) preserved in the coprolite surface.

width was r = 0.55 (p = 0.007) for morphotype B, and r = 0.77 (p = 0.009) for morphotype A. In contrast, for the pooled data the correlation coefficient was small and negative, r = −0.18. This simple test supports the existence of two distinct types of coprolites, and suggests that two different kinds of animals produced them. That the width of the coprolite increases with its length was supported by our analysis, and is probably a general rule for vertebrate coprolites. Farlow et al. (2010) argued that coprolite diameter might correlate better with scat-producer size (at least in carnivorous mammals) than does coprolite length, because incomplete scats may be pinched off during egestion, and later during the transportation and burial process.

The average sizes and overall shapes of two morphs are characterized as: morphotype A—large- to medium-sized, elongated, cylinder-shaped, nonsegmented feces with rounded or tapering ends (Figs. 4A–C), ranging from 46 to 104 mm long and 4 to 26 mm wide, and commonly containing fragments of bones; morphotype B—short cylindrical or tubular-shaped scats with flat, tapering, or convex ends, commonly segmented (Figs. 4D–F), ranging from 12 to 61 mm long and 10 to 22 mm wide, and very rarely containing bone fragments; bone fragments that do occur are very degraded. Both coprolite morphotypes contain bone fragments and in all cases the fragments are evenly distributed in a fine-grained microcrystalline calcium phosphate matrix (Fig. 5); bone fragments range from 0.1 to 25 mm in maximum dimension. Most bone fragments are from small prey. In two coprolites small vertebrae were found (Figs. 5C–E), one coprolite contains a large fragment of bone (25 mm) (Fig. 5G), and an arthropod remain (likely a conchostracan shell) was identified in one scat (Fig. 5H).

Identifying the prey species from the coprolite is more complicated than identifying the coprolite maker. Basic histological analysis of the bone inclusions resulted in the identification of two types of bone tissue: (1) well-vascularized, rapidly forming bone, probably therapsid, and most likely dicynodont or therocephalian (Fig. 5G); (2) poorly vascularized, slow-growing bone probably representing small fishes, amphibians, or reptiles (Figs. 5A–C).

SEM and EMP Observations

SEM images (both in scattered and backscattered electrons) show that the coprolite matrix has its bulk mass made of abundant spheres and thin-walled vesicles with 0.5–4 µm diameters. Electron Microprobe (EMP) analyses of polished thin sections show that the matrix is composed of microcrystalline carbonate-fluoride-bearing calcium phosphate with small amounts of calcium replaced in the crystal lattice by Na, Sr, and REEs. The micron-sized vesicles are interpreted as phosphatic pseudomorphs of organic structures in the original scat, and in size and shape resemble coccoid bacteria, which are common in the scat of recent and extinct animals (Fig. 6). The empty spaces inside vesicles suggest that bacterial cells were decomposed after mineralization was complete. The sulphur content in the phosphate is too elevated to be connected with barite (insufficient barium content and lack of barite in the coprolites)

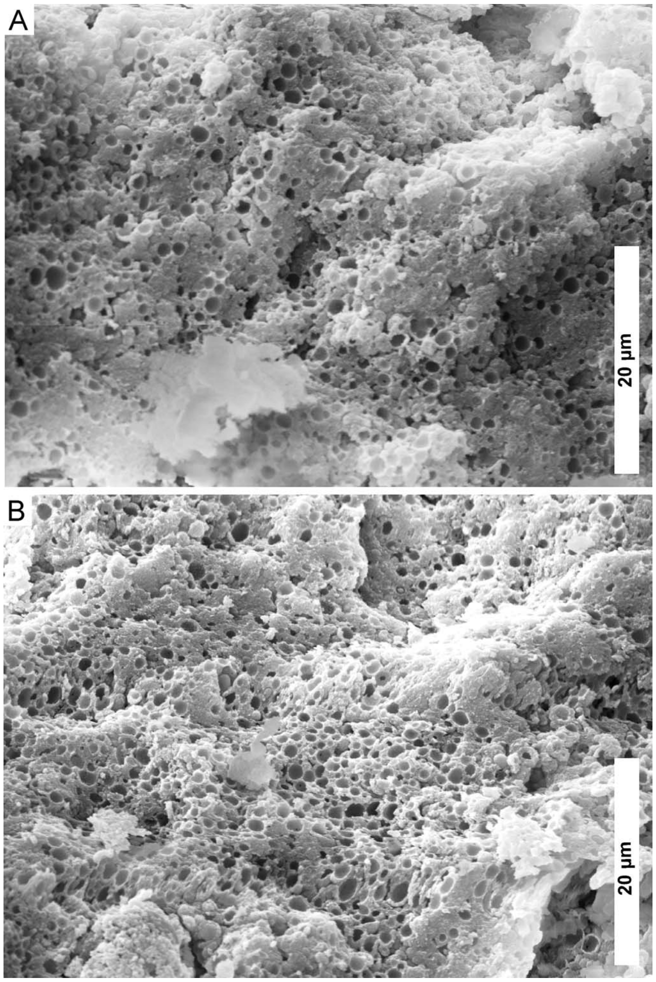

FIGURE 6—A–B) SEM images of the coprolite matrix showing numerous thin-walled mineral spheres; some of which have double layers with a thin void space between that may be the former location of bacterial cell walls (B).

and could be associated with sulphur from fecal content/organic remains (Table 1).

The optical microscopy and EMP investigations show that iron and manganese oxides are responsible for elevated iron (0.52 wt%–7.26 wt% Fe) and manganese (up to 1319 ppm) concentrations in the bulk mass of coprolites. Other metals (e.g., V, Ni) can be associated with oxides forming spheroids with diameters 3–10 µm. Rather rapid precipitation of dietary calcium phosphate is indicated by very small crystal size and preservation of delicate organic microstructures.

REE Geochemistry

The REE, U, Th, and other trace element concentrations measured in the phosphatic coprolites from Russia are given in Figures 7 and 8 and Table 2. All analyzed coprolite samples have very similar REE patterns at all sampled layers and localities, and their concentrations show no clear relationship to the amount of phosphate present in the scat. The shale-normalized REE concentration patterns are from all three sites and layers overlap (Fig. 8), and can be characterized by a relative enrichment of middle REE (MREE), peaking between Sm and Gd, (average $(La/Sm)_N = 0.40$, $n = 5$,), depletion of heavy rare earths (HREE, average $(La/Yb)_N = 1.06$, $n = 5$). White coprolite samples show a noticeable positive cerium anomaly that is absent in the reddish samples (Fig. 8).

TABLE 1—Major and minor element concentrations in the coprolites from Bykovka at Vyazniki (bulk mass ICP-MS analyses).

Wt%	Ca	Mg	Ti	Al	Na	K	S	Fe
Det. limit	0.02	0.02	0.001	0.02	0.002	0.02	0.04	0.02
BV-1	32.67	0.09	0.062	0.94	0.237	0.04	0.13	1.13
BV-2	29.36	0.07	0.050	0.94	0.224	0.03	0.11	5.44
BV-3	27.83	0.10	0.063	1.04	0.235	0.07	0.10	7.26
BV-I	28.88	0.20	0.113	1.53	0.351	0.22	0.16	1.44
BV-II	33.89	0.12	0.112	1.09	0.287	0.12	0.14	0.52

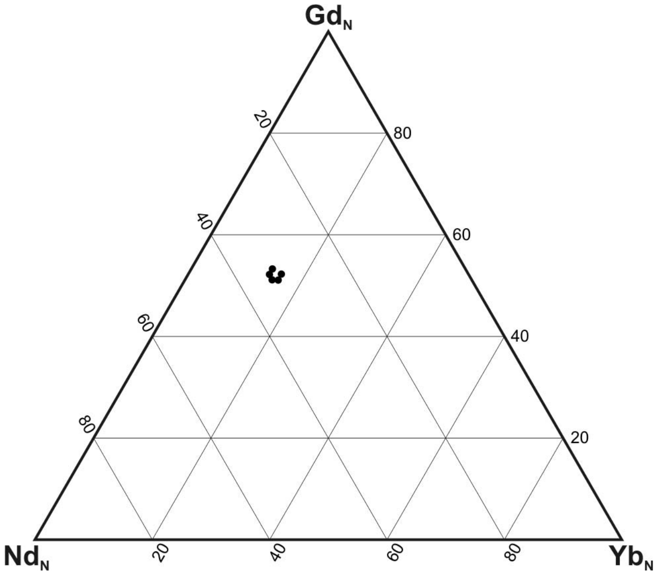

FIGURE 7—Ternary diagram of NASC-normalized REE in coprolites from Bykovka at Vyazniki. Coprolites from the different units have similar REE ratios, with overlap, suggesting that coprolites were fossilized at the same place or time and were not reworked from other deposits; Gd_N = Gadolinium, Yb_N = Ytterbium, Nd_N = Neodymium.

DISCUSSION

Coprolites are recognized by many different features that distinguish them from inorganic clasts, inorganic phosphate nodules, or other types of fossils or concretions of organic matter that potentially can be misinterpreted as coprolites (Thulborn, 1991). When studying coprolites, a primary objective is to try to identify the producer (Hunt et al.,

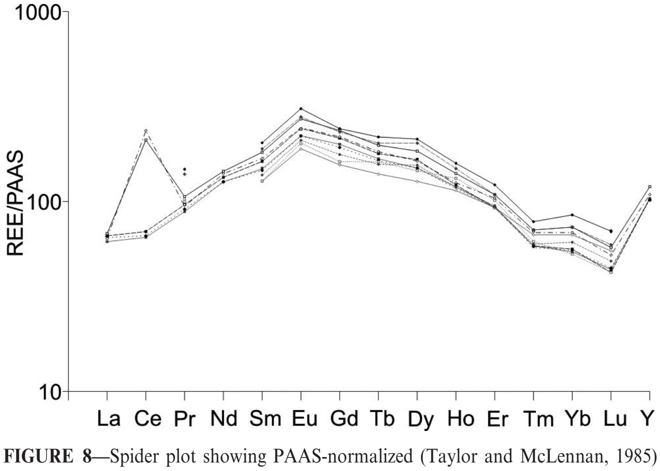

FIGURE 8—Spider plot showing PAAS-normalized (Taylor and McLennan, 1985) REE patterns in selected coprolites from Bykovka at Vyazniki; overlapping of plots suggests that coprolites represent a restricted sample (limited time averaging); note significant positive cerium anomalies for two reddish coprolite samples.

TABLE 2—REE and other trace element concentrations (ppm) in the coprolites from Bykovka at Vyazniki.

	La	Ce	Pr	Nd	Sm	Eu	Gd	Tb	Dy	Ho	Er	Tm	Yb	Lu	Y	U	Sr	V	Ba
Det. limit (ppm)	0.1	0.02	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	1	1	1
BV-1	>2000.0	>2000.0	1344.7	>2000.0	1163	338	1147.9	168.7	949.2	159.6	356.3	39	240	35.2	>2000.0	67	1042	84	679
BV-2	>2000.0	>2000.0	1273.1	>2000.0	1080.4	312.2	1111.2	157.3	888.7	150.7	317.7	35.5	208.2	29.9	>2000.0	85.5	976	139	647
VV-3	>2000.0	>2000.0	991	>2000.0	791.1	237	840.5	122.8	697.4	121.8	270	30.1	173.2	24.6	>2000.0	67.4	848	194	525
BV-I	>2000.0	>2000.0	948.1	>2000.0	729.6	208.9	745.5	108.9	564.4	114.1	274.5	33.7	187.3	27.7	>2000.0	50.1	1041	85	506
BV-II	>2000.0	>2000.0	937.5	>2000.0	734.9	229.3	770.7	126.9	646.1	134.2	296.3	30.7	149.9	21.2	>2000.0	106.9	1292	54	710
C-1	2590.1	17244.4	945.15	4646.2	1032.74	306.34	1117.25	155.13	815.8	141.34	319.89	35.71	209.8	29.03	3401.3	74.5	1061	257	681
C-2	2392.1	19233.9	860.1	4570.4	961.85	274.04	1047.08	143.09	734.46	126.77	305.16	34.48	194.65	26.54	3147.7	79.3	1040	264	576
C-3	2497.3	5307.3	822.77	4162.7	833.13	247.47	920.01	128.07	664.26	118.26	274.13	28.91	157.87	22.53	2968.9	71.1	1019	189	535
C-4	2541.5	5615.7	866.24	4384.2	927.8	273.67	1028.15	139.6	740.03	123.26	273.06	29.27	158.34	21.37	3063.1	60.5	1010	192	528
C-5	2382.1	5278.6	797.08	4156.8	844.78	249.55	953.08	131.41	669.3	121.21	278.19	29.51	154.74	22.21	3020.8	61.2	1012	236	522

1994; Chin, 2002; Smith and Botha-Brink, 2011). These are trace fossils that provide information about the feeding habits, digestive physiology, and trophic levels of ancient ecosystems (Thulborn, 1991; Chin et al., 1998; Chin, 2002), which cannot be gleaned from the body fossil record (but see Nesbitt et al., 2006). If the producer's affinity cannot be assigned, the utility of the coprolites for other paleobiological implications will be somewhat limited, but sometimes can be very useful for sedimentological and geochemical studies.

Some of the coprolites from Vyazniki and Gorokhovets resemble dung of modern felids and canids (in being elongate, cylindrical, and segmented; Walker, 1981; Farlow et al., 2010) and bone-bearing scats of tetrapods described from the upper Permian of the lower Beaufort Group, South Africa (Smith and Botha-Brink, 2011). The bulk of the studied coprolites consist of fine-grained microcrystalline calcium phosphate. The nature of this material is not clear, but it has a characteristic texture and in some instances contains abundant microscopic structures, probably microbial or fungal in origin. The original material inside the coprolite may represent some degree of the undigested remains of the prey species.

Animals that have been successfully matched to their coprolites include fish (Williams, 1972; Jain, 1983; Coy, 1995; Northwood, 2005; Milàn, 2010), crocodilians (Sawyer, 1981; Milàn, 2010), non-avian dinosaurs (see Thulborn, 1991; Chin et al., 1998; Chin, 2007), early synapsids (Smith and Botha-Brink, 2011), and mammals (Edwards and Yatkola, 1974; Mead et al., 1986; Farlow et al., 2010). The coprolites described herein were produced by a range of carnivorous tetrapods, based on their size and content, from the *Archosaurus rossicus* tetrapod zone of Eastern Europe (see Sennikov and Golubiev, 2006, 2012). As body size and scat diameter are positively correlated in modern carnivorous animals and dinosaurs (Edwards and Yatkola, 1974; see also Farlow et al., 2010), the same is likely true for other ancient predators. According to Farlow et al. (2010), body size and scat diameter are positively but loosely correlated in carnivorous and omnivorous mammals (see fig. 11 in Farlow et al., 2010), and assigning scats to different species of the same body size can be difficult (Davison et al., 2002; Chame, 2003; Farlow et al., 2010). The largest Vyazniki coprolites (morphotype A) are 15–26 mm in diameter and up to 104 mm long and were, therefore, most likely produced by large carnivores. The Vyazniki coprolite morphotypes contain different elements (morphotype A, coprolites with bones; and morphotype B, those with strongly digested, poorly preserved bone). Possible scat-maker candidates known from Vyazniki assemblage include the large therocephalian *Moschowhaitsia vjuschkovi* and the medium- to large-sized archosauromorph *Archosaurus rossicus*. We attribute the larger, cylindrical, elongated, nonsegmented coprolites with numerous bone remains inside them (morphotype A) to the large therocephalian. Smith and Botha-Brink (2011) came to similar conclusions about elongated coprolites with bone inclusions from the upper Permian of the Karoo Basin. The smaller, oval-shaped, sometimes tabular, and commonly segmented coprolites from Vyazniki, which generally do not contain bones inside (morphotype B), are possibly attributed to the archosauromorph reptile. In published accounts about basal archosaur (crocodilian) digestive processes, bones and teeth are said to be completely digested; no trace of mineralized tissues is left in the feces (Neill, 1971; Skoczylas, 1978). However, keratinous or chitinous tissues (hair, claws, insect cuticle) have been found in crocodile feces and, also very rarely, bone fragments or teeth have occurred (Fisher, 1981). Although complete digestion and various forms of incomplete digestion are common, only crocodilians are known to decalcify calcified tissues (Fisher, 1981). However, Farlow et al. (2010) report decalcified teeth as inclusions within coprolites from the late Neogene Pipe Creek Sinkhole site where no crocodilian remains have been found. In addition, Andrews and Evans (1983), Denys et al. (1992), and Munson and Garniewicz (2003) report on decalcified teeth in the scats of extant canids. So it may be that other kinds of carnivores than crocodilians can decalcify bones and teeth.

SEM images show that the coprolite matrix from Vyazniki has its bulk mass made of abundant spheres and thin-walled vesicles. Similar structures were described in a phosphatic coprolite from the Upper Cretaceous Hell Creek Formation, Montana (see fig. 3 in Hollocher et al., 2010). The micron-scale vesicles are interpreted as mineral pseudomorphs of organic structures in the original scat and resemble in size and shape such spherical bacteria.

There is general consensus that REE uptake is relatively fast (<100 kyr) and ceases once recrystallization is complete (Kohn, 2008; Trueman et al., 2008; Koenig et al., 2009; Suarez et al., 2010). Biogenic phosphate minerals have strong affinity for REE that are incorporated into vertebrate remains during fossilization. Because REE concentrations in the fossilizing remain (bone or scat) are affected by fluid chemistry and mineral reactions specific to the depositional environment where fossilization takes place, REEs in fossilized biogenic phosphates have been used by many researchers as tool for paleoenvironmental reconstructions, taphonomic, and paleoredox studies (e.g., Kolodny et al., 1996; Trueman, 1999; Metzger et al., 2004; Martin et al., 2005; Trueman et al., 2006; Cook and Trueman, 2009).

REE pore-water chemistry is influenced by such environmental factors as fluid pH, redox, and reactions with colloids (Erel and Stolper, 1993; Dia et al., 2002; Gruau et al., 2004). These geochemical conditions can generate three distinct REE patterns, which are light, middle, or heavy REE enriched (Trueman and Tuross, 2002). Such variations in REE signatures may be clearly visualized using ternary diagrams (Fig. 7). Samples plotting toward Yb will be enriched in HREE (heavy-group rare earth elements); toward Nd, enriched in LREE (light-group rare earth elements); and those plotting near Gd, in MREE (middle-group rare earth elements). A pattern concentrated in the middle of the diagram would not show signs of enrichment in any of the particular elements. All coprolite samples from Vyazniki and Gorokhovets group together closer to Gd, suggesting enrichment in MREE (Fig. 7).

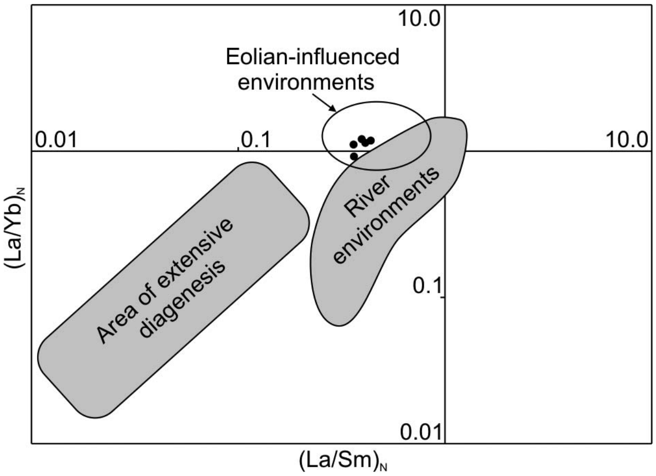

FIGURE 9—Shale-normalized ratios of REE concentrations in coprolites from Bykovka at Vyazniki. Note that fluvial settings are well separated in REE space, and that eolian-influenced localities are distinct from other other terrestrial settings. Coprolites from the upper Permian of Bykovka (filled circles) have similar REE compositions to organic remains from other eolian-influenced localities (data from Trueman, 1999; Cook and Trueman, 2009).

The HREE have enhanced solubility in the high-pH and alkaline seawater; thus, HREE enrichment is produced by preferential HREE-carbonate complexation and absorption of LREE by hydrous ferric oxides (Piepgras and Jacobsen, 1992). In contrast, river waters (e.g., Elderfield et al., 1990) are relatively enriched in MREE and LREE. Such patterns are suggested by many authors (e.g., Hanningan and Sholkovitz, 2001) to be developed due to decreased absorption of MREE on iron oxides or weathering of phosphate minerals.

Fossil biogenic phosphate REE concentrations and patterns, thus, reflect pore-water chemistries specific to different depositional and burial environments. Coprolites are more likely to record redox conditions in the bottom waters or ground waters as they must have become rapidly mineralized *in situ*. Phosphatization of coprolites probably occurs more rapidly than recrystallization of the bone apatite, as collagen significantly lowers the rate of bone recrystallization. Therefore trace element patterns in fossil bones may be more time averaged as bone recrystallization may take many millennia. The $(La/Yb)_N$ vs. $(La/Sm)_N$ pattern (Fig. 9) indicates that the samples inherited their REE content via early diagenetic quantitive uptake without fractionation rather than substitution mechanism during late diagenetic recrystallization (Reynard et al., 1999; Trueman et al., 2006), and together with SEM observations, indicate that examined coprolites are not affected by late/extensive diagenesis.

The $(Sm/Pr)_N$ (average 1.48, $n = 10$) vs. $(Sm/Yb)_N$ (average 2.48, $n = 10$) pattern is characteristic for terrestrial fluvial environments (Trueman, 1999) or dune and/or coastal sediments (data from Kasper-Zubillaga et al., 2008) with MREE enrichment and $(Gd/Yb)_N$ values (average 3.16, $n = 10$) typical for shallow groundwater, with circum-neutral pH values (Dia et al., 2002; Martin et al., 2005). The $(La/Yb)_N$ vs. $(La/Sm)_N$ pattern (Fig. 9) suggests significant eolian sediment input to the burial environment of the coprolites (e.g., Trueman et al., 2006; Cook and Trueman, 2009).

Cerium oxidation and fractionation in natural waters is widely used to study redox characteristics (e.g., Elderfield et al., 1990; Dia et al., 2002). Positive cerium anomalies indicate reducing environments while negative anomalies indicate oxidizing environments (Wright et al., 1987). Positive cerium anomalies present in the white coprolites (Fig. 8) suggest that early diagenesis occurred under more reducing conditions than in the reddish coprolite samples. Local anoxia would have been promoted by the organic matter–decay process in the scat. Reddish coprolites have significant content of the late diagenetic iron oxides whose presence may be responsible for the lack of cerium anomaly in the analyzed coprolite samples. The early diagenetic uranium uptake by the fossilizing scat could be enhanced by the presence of organic matter and/or high microcrystalline phosphate content in the bulk fecal mass.

CONCLUSIONS

Although coprolite morphology is variable due to variations in the scat maker (e.g., size, age, diet), it still provides useful information about diet and feeding behavior (Thulborn, 1991; Hunt et al., 1994; Chin et al., 1998; Chin, 2002, 2007). Tetrapods (medium-sized reptiles) likely produced these coprolites, based on comparisons of this material with coprolite finds from Permian, Triassic, Jurassic, and Cretaceous strata in Africa, Australia, Europe, and South and North America (Williams, 1972; Jain, 1983; Hunt et al., 1994; Smith and Botha-Brink, 2011). Coprolites provide valuable information about the digestive physiology of ancient animals and the trophic levels of ancient ecosystems (Chin, 2002).

We briefly discuss the paleobiological implications of these new observations. Coprolites from the upper Permian of Russia resemble bone-bearing scats of tetrapods described from the upper Permian of the lower Beaufort Group, South Africa (Smith and Botha-Brink, 2011) and scats of modern felids and canids (Walker, 1981; Farlow et al., 2010). Considering the relatively large size and presence or absence of large fragments of bones in coprolites collected from the *Archosaurus rossicus* tetrapod zone of Eastern Europe, we conclude that the coprolites described here were most likely produced by four kinds of carnivorous animals. Possible candidates include the temnospondyl *Dvinosaurus egregius*, the kotlassiomorph *Karpinskiosaurus secundus*, the anthracosaurs *Bystrowiana permira* and *Uralerpeton tverdochlebovae*, the archosauromorph *Archosaurus rossicus*, and the therocephalians *Moschowhaitsia vjuschkovi, Megawhaitsia patrichae*. The larger coprolites (morphotype A) were most likely produced by the large therapsid, e.g., therocephalian (probably *Moschowhaitsia vjuschkovi*). The smaller coprolites (morphotype B) were most likely produced by the early archosauromorph (probably *Archosaurus rossicus*), therapsid, or anthracosaur.

The common occurrence of undigested bone fragments in the elongated coprolites (morphotype A) indicates either relatively poor digestion (i.e., low acidic content) or a short gut-residence time of food, similar to extant predatory mammals and theropod dinosaurs (Johnson and Hansen, 1979; Emmons, 1987). In the smaller coprolites (morphotype B) bone fragments are very rare, which suggests good digestion or a long gut-residence time of food in the gastrointestinal tract. This type of etching is typical for extant archosaurs (crocodiles and alligators; see Fisher, 1981).

Two types of bone inclusions were found in the coprolites from the Vyazniki assemblage: (1) well-vascularized bone probably belonging to therapsids; (2) poorly vascularized bone probably representing small fish, amphibian, or reptile remains. Rapid precipitation of dietary calcium phosphate is indicated by preservation of delicate organic microstructures, including very small bones and possible bacterial forms. The geochemical data suggest burial of the coprolite association on a floodplain with significant eolian sediment input, and exclude any postproduction redeposition.

SEM images show that the coprolite matrix is composed of microcrystalline carbonate-fluoride-bearing calcium phosphate and its bulk mass made of abundant spheres and thin-walled vesicles 0.5–4 μm in diameter, which can be interpreted as phosphatic pseudomorphs of organic structures in the original scat, and resemble coccoid bacteria in size and shape.

The REE, U, Th and other trace element concentrations measured in the phosphatic coprolites from Russia show no clear relationship to the amount of phosphate present in the scat. All analyzed coprolite samples have very similar REE patterns at all sampled layers and localities. The

REE concentration patterns are characterized by a relative enrichment of middle REE (MREE) in all analyzed specimens. White coprolite samples show a noticeable positive cerium anomaly, which suggests reducing environments at the time of their burial. The REE patterns suggest significant eolian sediment input to the burial environment of the coprolites. The REE and SEM evidence indicate that analyzed coprolites appear to have undergone relatively little late diagenetic alteration.

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